Alien grass invasion of Renosterveld:
Influence of soil variable gradients

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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:

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Abstract

This thesis examines the role of agricultural activity in the process of invasion of west coast renosterveld fragments by annual alien grass species. This highly endangered vegetation type has less than 5% remaining, it is vital to understand the mechanisms allowing invasion of annual alien grasses in order to effectively prevent the loss of the many rare and endemic species found in west coast renosterveld. This study was divided into three major components.

Firstly the distribution of indigenous and alien plant species in relation to fence lines, separating active agricultural fields from untransformed vegetation, was described. Regression analysis was used to test for relationships between distances from agricultural fields and soil physical and chemical characteristics in natural vegetation. Cover by annual alien invasive grasses in untransformed vegetation decreased significantly with distance away from agricultural land.

Secondly alien and indigenous grass seed banks were sampled along the transects, at the same sites, in order to establish whether the seed banks correlated with above ground cover. Results varied among sites and seed banks were correlated with the vegetation cover at only one site. It appears that there are a multitude of factors determining the distribution of annual alien grass cover.

Thirdly a greenhouse experiment established the role that nitrogen plays in the success of the alien grass *Avena fatua*. This species was grown in competition with three indigenous species, an annual forb (*Dimorphotheca pluvialis*), a geophyte (*Oxalis purpurea*) and an indigenous perennial grass (*Tribolium uniolae*) at three levels of soil nitrogen. The geophyte was largely unaffected, while growth of the annual and indigenous perennial grasses was negatively affected by competition with *A. fatua*. Nitrogen did not seem to affect competitive interactions.

Management of these renosterveld patches, in order to conserve them effectively, will require a multi-faceted approach, including prevention of further invasion and removal of invasive grasses already present.

Opsomming

Hierdie tesis ondersoek die rol van landboubedrywighede in eenjarige uitheemse grassoorte se verdringing van stukke Weskusrenosterveld. Daar is tans minder as 5% van hierdie hoogs bedreigde soort plantegroei oor. Dit is noodsaaklik om te verstaan watter meganismes dit vir die eenjarige uitheemse indringergrassoorte moontlik maak om inheemse plantegroei te verdring ten einde die verlies van vele skaars en endemiese spesies in Weskusrenosterveld te voorkom. Hierdie studie is in drie hoofdele verdeel.

Eerstens is die verspreiding van inheemse en uitheemse plantegroei in verhouding tot heininggrense met aktiewe landbougrond beskryf. Met behulp van regressie-ontleding is fisiese en chemiese grondkenmerke in deursnitte in verhouding tot die afstand van die heininggrens beskou. Plantegroeidata is as persentasies in 'n bepaalde deursnit ingesamel. Daar is bevind dat eenjarige uitheemse indringergrassoorte beduidend afneem namate die afstand van die heininggrens toeneem.

Tweedens is monsters van die inheemse en uitheemse grassaadbanke in die deursnitte van dieselfde toetsterreine ontleed ten einde die verband tussen die saadbanke en bogrondse bedekking te bepaal. Die terreine het almal verskillende resultate opgelewer. Een van die terreine kon met die saadbankverspreiding gekorreleer word terwyl die oorblywende twee terreine geen verband met die saadbanke getoon het nie. Die verspreiding van eenjarige uitheemse indringergras blyk dus deur 'n menigte faktore bepaal te word.

Derdens is daar met behulp van 'n kweekhuisproef vasgestel watter rol stikstof in die sukses van die uitheemse grassoort *Avena fatua* speel. Vir hierdie proef moes *Avena fatua* met drie inheemse spesies meeding, naamlik 'n eenjarige forb (*Dimorphotheca pluvialis*), 'n geofiet (*Oxalis purpurea*) en 'n inheemse meerjarige grassoort (*Tribolium uniolae*) ten einde drie stikstofvlakke in die grond te verkry. Die geofiet het feitlik

onaangetas gebly terwyl die eenjarige en inheemse plante in ŉ groter mate geraak is. Stikstof blyk dus nie juis mededingende spesie-interaksie te beïnvloed nie.

Die bestuur van Weskusrenosterveld ten einde dit doeltreffend te bewaar verg dus ŉ meervlakkige benadering, wat die voorkoming van verdere verdringing en die verwydering van reeds teenwoordige indringergrassoorte insluit.

Dedication

This thesis is dedicated to my family and friends who supported me through all the stages of my thesis.

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Chapter 1

Renosterveld: the system and anthropogenic pressures

1.1 Introductory remarks

This thesis focuses on the issue of annual alien invasive grasses in west coast lowland Renosterveld, particularly on the role of agricultural edge effects in invasion processes. These edge effects include addition of fertilizers, seed bank sources and water, as well as a range of soil physical features resulting from the proximity of agriculture. The competitive advantage created by these effects is also investigated experimentally.

The Cape Floristic Region (CFR) is a hotspot of biodiversity and anthropogenic pressure. The dense human population in the CFR exerts significant pressure on the diverse natural community, often altering it from its perceived natural and sustainable condition. Renosterveld, part of the fynbos vegetation endemic to the Cape, is located in this biome. Renosterveld is fairly drab in appearance for most of the year, however, in spring, it reveals a colourful and diverse display of geophytes, 200 species, from 70 genera and 9 families (Cowling *et al.* 1986). Floristic endemism in the renosterveld is not as common as in fynbos. However, the former is home to a third of the species endemic to the CFR (Cowling *et al.* 1986, Low and Rebelo 1996).

Renosterveld has suffered heavily under the pressures of human urbanization and agricultural development due to its location in areas of fertile soil and good rainfall (Cowling *et al.* 1986). To date approximately 85 % of west coast and south coast renosterveld has been transformed to some form of agriculture and 0.7 % is formally conserved (Reyers *et al.* 2001). Fragmentation of renosterveld has left small patches located on the west and south-west coastal lowlands amidst cereal and pasture crops (Kemper 1997). Agriculture in the surrounding landscape has altered environmental gradients, influencing vegetation structure and facilitating invasion of alien grass species. These invasive grasses pose a direct threat to the endemic species that remain and consequently have become a subject of research (Rebelo 1995, Kemper 1997, von Hase *et al.* 2003, Krug 2004, Musil *et al.* 2005).

Agriculture is dependent on external sources of water and nutrients for higher yields, consequently fertilizers, pesticides and water are applied to crops, and the potential drift from wasteful additions could have implications for renosterveld fragments. Correct application of pesticides and herbicides is possible and would mitigate the damage this drift causes. Renosterveld ecosystems may be altered through these additions possibly making them less suitable for indigenous plant species. Renosterveld fragments provide an environment that supports these well-adapted plant and animal species, many of which are endemic and have a high species turnover. Consequently a decrease in diversity of these fragments results in an overall decrease of regional diversity. These fragments provide shelter and corridors for migration of plant and animal species. Recently there has been an effort to understand processes in renosterveld systems in order to develop management strategies for protection, restoration and sustainable utilization of the remaining fragments (Kemper *et al.* 1999, Krug 2004, Walton 2006). Alien invasive grasses are a major obstacle to achieving these objectives and this study aims to provide more knowledge of the processes of invasion and to assist in reaching these conservation goals.

1.2 Research Objectives

The general objective of this study was to give greater insight into the functioning of ecological boundaries under human induced change, thereby providing information necessary for land use policies and conservation planning. To support efforts to control/contain and manage invasive grass species, the focus of this study was on soil variable gradients such as chemical, physical, hydraulic, surface condition and small-scale disturbance. The effects of agricultural landuse on these soil properties could explain invasion patterns. Patterns of habitat invasibility may be explained by soil nutrient and disturbance gradients and considered in chapter 2. Measuring both of these together is necessary to compare these two factors (Brooks 1999). The particular alien and indigenous grass species, their distribution and characteristics also influence invisibility and are dealt with in chapter 3. Competitive interactions between indigenous and alien species are influenced by alterations to the habitat. The possible competitive outcomes of these anthropogenic habitat changes are deliberated in chapter 4. The study builds on previous work regarding the environmental determinants facilitating invasion of renosterveld, such as Suretha van Rooyen's (2003) work on the influence of fire and grazing. It also should contribute to the information available about restoration of renosterveld. Initial restoration efforts will also be better supported by this information, as it may contribute to explanations of invasion processes. Using this information, measures can be put in place to prevent re-invasion of restored areas.

This thesis is divided into five chapters, each dealing with a different aspect of the facilitation of alien annual grass invasion in renosterveld patches through adjacent agriculture. The data collected were reviewed in the light of previous work and finally this information was combined in a final chapter. Chapters 2 to 4 contain the results of field or green house trials and are described in more detail below.

Chapter 2

The objective of Chapter 2 was to test the hypothesis that elevated levels of nutrient resources should favour faster growing annual invasive grasses. Gradients in nutrient concentration are expected to occur from crop land to natural vegetation and are expected to play a role in facilitation of alien grass invasions in renosterveld. Knowledge of these soil gradients is important to understand how invasion and spread of alien grasses is occurring. In this chapter vegetation changes and soil chemical and physical changes from agricultural fields down slope into renosterveld patches were measured. It was expected that in fenced, protected renosterveld reserves there would be a gradient of decreasing water infiltration and plant available nutrients from the agricultural fields inwards towards pristine renosterveld. Small-scale natural disturbance such as animal diggings especially in fragment edges were expected to create microsite conditions suited to grass invasion. Elevated water and nutrient levels in fragment edges would further support the establishment of alien grasses.

Changes in vegetation were grouped according to functional types including perennial shrubs, annual shrubs, annual herbs, geophytes, alien grass and indigenous grass. Least squares regressions tested whether measured plant functional group covers, soil physical and chemical properties and other habitat factors correlated with increasing distance from the centres of renosterveld fragments.

Chapter 3

The aim of this chapter was to establish patterns of distribution and abundance, of the alien and indigenous grass species, along gradients from agricultural lands into renosterveld patches. The relationship between the distribution of the annual invasive seed bank in relation to distance from the agricultural field was also assessed. Alien grass seed bank densities were expected to: (1) be distributed in relation to soil variables along a gradient and (2) decrease from agricultural fields through fragment edges and into pristine renosterveld. Developing an understanding of this allows more effective management of the alien invasive grasses.

Chapter 4

Competition between species plays a larger role under more favourable habitat conditions. When abiotic factors such as soil nutrients, light and water availability are no longer limiting, competition becomes a more important driver of community composition. This chapter aimed to measure the competitive interaction between indigenous plant functional types and annual invasive grasses, with different levels of nutrients. Alien invasive grasses were increasingly more successful than indigenous grasses, annual herbs and geophytes along an increasing nutrient gradient. This experiment was conducted in a controlled environment (greenhouse) in order to isolate the competitive effect. *Avena fatua* (annual alien invasive grass) was grown under a range of nutrient conditions in competition with three indigenous plant species (*Oxalis purpurea*, *Dimorphotheca pluvialis* and *Tribolium uniolae*).

1.3 Study ecosystem

Unlike fynbos, renosterveld is found on moderately fertile, shale derived soils where rainfall is between 350 and 650 mm/yr (Boucher 1983, Cowling and Holmes 1992). Renosterveld is ecotonal to fynbos and succulent karoo, fynbos occurring where soils are oligotrophic and karoo occurs where there is lower rainfall (Low and Rebelo 1996). Renosterveld has been broadly subdivided into west coast and south west/south coast renosterveld (Agulhas plain) (Low and Rebelo 1996). This study focuses on west coast renosterveld (Boland and Swartland areas). The area has a Mediterranean climate with hot, dry summers. West coast renosterveld vegetation is generally located on the Malmesbury Group shales, Cape Granite Suite and Klipheuwel Formation shales which these form heavy clays and loamy soils. The landscape is often characterized by heuweltjies (nutrient-enriched soil overlying buried termite mounds) that support more shrubby communities (Low and Rebelo 1996).

Small leaved asteraceous shrubs are the dominant growth form in renosterveld, with Poaceae and geophytes forming the understorey vegetation (Rebelo 1995, Low and Rebelo 1996). The families Proteaceae, Ericaceae and Restionaceae tend to be of low abundance or are absent. Different soils support slightly different vegetation mixes. Sand and clay tends to have more fynbos elements while on granites there is a mix of renosterveld and thicket species (Rebelo 1995). The structure of renosterveld vegetation is governed by an intermediate level of disturbance (Boucher 1983). Local heterogeneity is created by heuweltjies (termite mounds) and animals digging in the soil.

Renosterveld is considered to be a fire adapted vegetation type although it has no known fire frequency regime (von Hase *et al.* 2003). One idea is that a short fire interval maintains larger scale heterogeneity, creating patches of pioneer communities and climax species (Rebelo 1995). It is possible that the fire interval is longer as some plants indicate a dependence on longer cycles of three to ten years (Rebelo 1995). Grazing and browsing interact with this fire regime creating a dynamic system that shifts between a grass and shrub dominated state (Heydenrych 1995, Rebelo 1995).

This study focused on west coast renosterveld, which has more C_3 grass species and a greater diversity of geophyte and annual species than South Coast renosterveld (Moll *et al.* 1984). There is a large species overlap with fynbos, 54 % according to a broad-scale survey (Boucher 1983). A third of species endemic to fynbos are present in renosterveld systems (Low & Rebelo 1996).

1.4 Research approach

Possible relationships between the distance from the agricultural fields and soil variables, vegetation changes and seed bank changes were tested in the light of the proposed model (Figure 1.1).

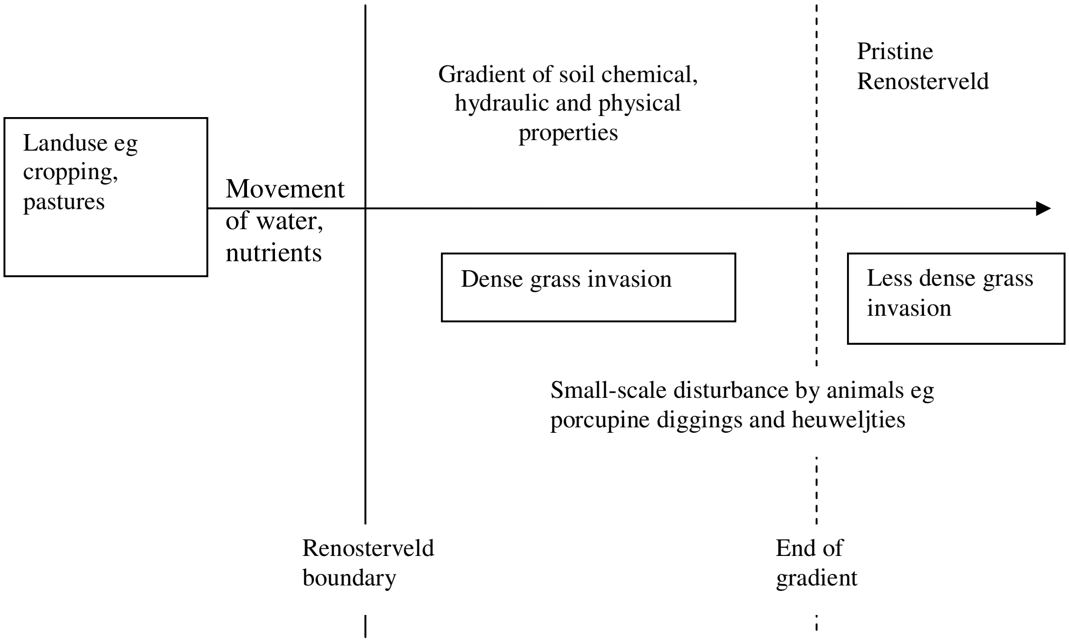

Figure 1.1: Hypothetical model of the soil gradient from an agricultural field into adjacent natural renosterveld vegetation.

Figure 1.1 shows how a soil variable gradient in renosterveld fragment edges caused by adjacent agricultural inputs of fertilizer might facilitate grass invasions. Agricultural lands act as sources for alien invasive grass seed. These fields also supply water and nutrients in the form of runoff due to irrigation and fertilizing practices. Natural disturbance creates suitable recruitment sites for seeds, the raised water and nutrient content of the soil gives annual alien invasive grasses a competitive edge. It is hypothesized that this competitive edge lessens further into the patch as the gradient of high nutrients and water decreases. Beyond this gradient the natural vegetation is able to dominate the landscape.

1.5 Study Sites

A number of renosterveld fragments or reserves were selected from the West coast region. Site selection was based on very specific criteria, namely: the sites needed to be renosterveld fragments down slope of active agricultural fields, have no unnatural grazing pressure or fire occurrence for at least 10 years, and have an invasion front of alien invasive grasses (observable edge effect). Also, the sites needed to exclude heavy grazing and burning as much as possible in order to isolate the effect of adjacent agricultural activity, since alien annual grasses are more abundant in landscapes that are heavily grazed (Steinschen *et al.* 1996, Walton 2006) or frequently burned (van Rooyen 2003). There were difficulties in matching sites; consequently slope and adjacent agriculture were prioritized in site selection. The current classification of the vegetation for one of the sites where I worked is FFH6, Elgin Shale Fynbos. The other two are FRS9, Swartland Shale Renosterveld (Mucina & Rutherford, 2006). This study commenced prior to these reclassifications, consequently, Low and Rebelo's (1996) term "renosterveld' was followed for these plant communities throughout the thesis.

1.5.1 Jan Briers Louw Geometric Tortoise Reserve

Figure 1.2: Jan Briers Louw Geometric Tortoise Reserve, view from the road (left), fence line of patch (right).

The Jan Briers Louw Geometric Tortoise Reserve is located at 33º 45' 45" S and 18º 50' 07" E. It is a privately owned farm on the R312 Southwest of Paarl. It comprises 28 ha of Lowland fynbos and renosterveld and is surrounded by old lands and ploughed fields with populations of *Acacia saligna*. Grasses occur beneath these acacias. There are areas that have not been burned or grazed in over 10 years along the fence line (Van Rooyen 2003). Heuweltjies are also found in the reserve. These nutrient rich mounds formed by termites are frequented by animals. There is a range of herbivores such as *Psammobates geometricus* (Geometric tortoise) (Baard 1993), *Sylvicapra grimmia* (Common duiker) and *Raphicerus campestris* (Steenbok) (Walker 1986) grazing the renosterveld but at low intensity. This site is currently classfied as FRS9.

1.5.2 Mulderbosch Farm

Figure 1.3: Mulderbosch Wine Estate, sample site on the horizon (left), alien grasses in old shrub stand (left).

This site is just outside Stellenbosch on the R304, 33º 52’ S and 17º 49’ E. The patch of renosterveld is located in the fold between two hills. It is surrounded on all sides by vineyards and large sections of it are invaded by pines. There is also a thick understorey of grass in all of the invaded areas and also in an old ploughed field. The section used in this study is an old uninvaded part that is downslope from a vineyard. There are no large mammalian browsers in this area. This site is currently classified as FRS9.

1.5.3 Paul Cluver Estate

Figure 1.4: Paul Cluver Wine Estate sample patch on the left of horizon and vineyard on the right.

The Paul Cluver Estate is located within the Kogelberg Biosphere Reserve, just off the N2 past Grabouw, 34º 9’ S and 19º 2’ E. The patch used in this study is in the reserve of the farm, downslope of a vineyard. The reserve is stocked with a number of large browsers such as-.*Damaliscus dorcas dorcas* (Bontebok), *Oryx gazelle* (Gemsbok) and *Taurotragus oryx* (Eland). The vegetation is not strictly renosterveld because it was reclassified by Mucina and Rutherford (2006) as Elgin Shale Fynbos. Nevertheless, it does have renosterveld elements. This site is currently classified as FFH6.

1.6 Literature review

There are several environmental and habitat factors that affect vegetation structure and invisibility. These include fragmentation, disturbance, chemical and physical soil environment, alien invasive grasses, fire, grazing and the seed bank. Some examples are presented below:

1.6.1 Fragmentation

The concept of habitat fragmentation is based on the theory of island biogeography which proposes a relationship between species richness and island size resulting from a dynamic equilibrium between species extinction and immigration (MacArthur & Wilson 1967). This theory proposes that there is a relationship between species number and isolation and size of marine islands they are on, as a result of a dynamic equilibrium between extinction and immigration. Fragmentation of ecosystems creates islands of vegetation that often function according to this theory. Fragmentation impacts two aspects of ecosystems, namely spatial arrangement and processes that affect the system (Hobbs 2001). Spatial considerations include isolation and biogeographic concerns such as fragment size, shape, position relative to others, connectivity and metapopulation theory and analysis.

The impacts of spatial arrangement of renosterveld fragments have been investigated by Kemper (1997), who focused on the landscape patterns, vegetation composition, diversity and guild structure. There is lower species richness, composition and diversity among larger renosterveld fragments than among smaller fragments, possibly due to greater stability in larger fragments and an increased susceptibility to extinction, colonization and invasion processes of smaller fragments (Kemper *et al.* 1999). Higher numbers of alien and annual species were found on smaller fragments. This was expected since the edge effect is greater and these species are better equipped to persist and colonize with these kinds of disturbances.

1.6.2 Disturbance

Disturbance in a functioning system occurs in different forms and regimes as well as at different scales. Variable disturbances have a multitude of effects on taxa at each biological level. Disturbance, be it natural or of anthropogenic origin, produces effects that are influenced by the state of the system prior to the disturbance. These effects are therefore dependent on a range of biotic and physical factors (White and Pickett 1985).

An example is the vegetation structure of renosterveld. Since there is so little left it is difficult to establish what to manage for. There is some evidence that renosterveld was once a grassland but, could also have been a shrubland dominated by *Elytroppapus rhinocerotis* (recently renamed *Dicerothamnus rhinocerotis*). Cowling (1984) posed the possibility that south coast renosterveld was once a grassland dominated by *Themeda triandra.* The disturbance regime would have been altered from an intensive pulse grazing by indigenous animals with a variable fire frequency to a regime of regular burning and overgrazing by livestock. Bush encroachment would have occurred, resulting in the vegetation structure observed in renosterveld at present. In this altered system state, disturbance that may have been occurring prior to this large-scale change may now be having different effects on the system. The following subsections focus on a few disturbance features affecting renosterveld environments, which are pertinent to this study.

1.6.2.1 Fire and alien invasive grasses

There is no known fire frequency for renosterveld although it is thought to be shorter than fynbos. Fire is an important ecological driver; it removes plant canopy cover creating space for recruitment and also returns nutrients to the soil, acting as a short-term fertilizer (Hobbs 1992).

Fire is part of many natural disturbance regimes and therefore in itself does not necessarily promote invasion. It could, however, do so if combined with another form of disturbance such as nutrient inputs. Invasion by fire adapted species could then increase the fuel load and consequently the fire frequency (Hobbs and Huenneke 1992). With a high surface to volume ratio and high dry biomass, grasses burn readily and recover from fires quickly (D’Antonio and Vitousek 1992). Heterogeneous environments are created and grasses are able to respond quickly and dominate nutrient rich conditions (Hobbs 1992). They quickly form a canopy and intercept light thus limiting the light available for slower growing species. Soil conditions are altered through changes to the boundary layer, the canopy and increased litter results in increased humidity and thus increased rates of remineralization (D'Antonio and Vitousek 1992). C_4 grasses are more efficient at nitrogen use than C_3 grasses and therefore only in nitrogen enriched conditions will the C_3 grasses be able to dominate (Richardson *et al.* 2000). When disturbance levels are high, grasses that allocate more energy to seed dispersal should be able to colonise faster than species that allocate more energy to root mass (Richardson *et al.* 2000).

Grasses are ecosystem engineers capable of changing the functioning of a system. They alter nutrient cycling, microclimate and chemistry. In the Hawaii Volcanoes National Park, plant species composition has been altered through alien grass invasion, altering structure and function of the system (Mack and D'Antonio 2003). In this study net and gross nitrogen mineralization and nitrification were measured across three vegetation treatments; 1) grass removed, 2) woodland invaded by grass, 3) woodland invaded and burned resulting in only grassland. The grass invasion changed the timing of nitrogen cycling but not the quantity. Conversion to grass from the natural vegetation resulted in nitrogen cycling that was 3.4 times greater. Chemical composition of soil organic matter (SOM) was altered through microclimate conditions of soil moisture and temperature.

Invasive annual grasses in grassland communities have been found to out-compete perennial grasses for soil moisture, ultimately reducing their reproductive output and seedling growth (Dyer & Rice 1999). The dense litter layer produced by annual grasses plays a role in restructuring the community. Litter tends to decrease plant richness in grasslands or herbaceous communities. It can cause changes in soil moisture and temperature regimes, possibly favouring seedling predator communities (Facelli 1994) and favouring pathogens (Facelli *et al.* 1999). The physical presence of litter could inhibit the successful establishment of seedlings (Carson & Peterson 1990, Facelli & Pickett 1991).

The importance of the competitive interactions between annual invasive grasses and native perennial grasses varied down slopes in a study of the direct and indirect competitive effects of annual invasive grasses in Australian grassland (Lenz *et al.* 2003). The physical presence of litter, leachates and changes to soil temperature and moisture may change soil microclimate conditions. Litter has a positive effect on annual grass growth in the greenhouse and in the field and possible negative feedback on other species (Facelli *et al.* 1999, Evans 1972).

Through changing environmental conditions they are able to create a more favourable habitat for themselves.

Alien grasses that are widespread and common in the CFR, include *Avena fatua*, *Briza maxima*, *Briza minor*, *Bromus pectinatus* and *Lolium perenne* (Duvenhage 1993). These species are originally from fire-adapted and grazed systems around the Mediterranean. They are often introduced as contaminants of crop seed and thereafter transported on the hair of animals or via their dung. Other alien grass species found in wetter areas and near areas of nutrient enrichment include *Pennisetum clandestinum*, *P. setaceum* and *P. macruorum.* Europe and the Mediterranean are largely the source of naturalized alien grasses for southern Africa (60%). The remaining species are from central and southern America, Africa, Asia, North America and Australasia (Milton 2004). The majority of southern Africa's grass species are $C_{4,}$ all the annual alien invasive grasses and many of the invasive perennial grasses are C_3 grasses. C_3 type grasses have a carbon-fixing pathway that is more efficient in areas where the growing season is cool. C_4 grasses have a more efficient nitrogen fixing pathway where the growing season is warm. Alien invasive grasses are currently a serious problem in riparian areas of the Western Cape but are not obviously threatening renosterveld. This however, may change in the face of increasing anthropogenic influence in the landscape and global warming (Milton 2004). Higher levels of CO_2 and increased inputs of nitrogen through fertilizers allow the nitrogen use efficiency of C_3 type grasses to be more effective. Increased nitrogen availability and increased atmospheric CO_2 will increase the advantage that C_3 type grasses have over the C_4 grasses.

1.6.2.2 Grazing

Livestock grazing over long periods (decades) can affect significant ecosystem changes including changes in vegetation structure and composition as well as alterations to soil variables such as chemistry and physical characteristics (Hobbs 2001). Certain species can decrease in abundance while others increase. Often the pattern is a decrease in native species and increase in alien species (Yates *et al.* 2000). There is evidence of these ecosystem changes globally.

In Australian rangelands grazing of perennial cover has resulted in loss of litter cover, nutrients, microtopography changes, soil compaction, decrease in soil water infiltration rates and increased erosion (Yates *et al.* 2000) and severe alteration to the structure and function of this system. In the Chilean Matorral the abundance of native species decreased while alien herb species increased along a gradient of increasing grazing intensity, a decrease in soil nutrient (nitrogen, phosphorous and potassium) content was found along this gradient (Holmgren *et al.* 2000).

In Renosterveld, high densities of sheep graze in the Overberg, while in the Darling and Philadelphia areas there is a high intensity of cattle grazing. This has a detrimental impact on the natural veld (von Hase *et al.* 2003). This intensity of grazing is expected to alter soil variables through trampling, nutrient enrichment and removal of palatable species. By removing indigenous plants the competition for resources decreases. Exclusion of grazing from renosterveld reserves can be predicted to result in a loss of species due to competition with few canopy shrubs dominating (Rebelo 1995). van Rooyen (2003) found that grazing facilitated a higher degree of invasion than burning or the control (no fire or grazing). Nutrient addition, livestock grazing and fire could be combining synergistically and facilitating grass invasions. Cowling *et al.* (1986) proposed that intense grazing could be a successful management strategy. In combination with spring burning it would promote a larger grassy component suitable for higher carrying capacity.

1.6.2.3 The soil environment; physical disturbance and chemical disturbance

Species are distributed along environmental gradients such as soil fertility, moisture and salinity and are thus distributed according to biotic and abiotic limiting factors (Jurjavcic *et al.* 2002). Microclimates influence plant and animal communities and these communities in turn influence microclimates. Microclimates are influenced by the nature of soils, and the microclimate in turn influences soil mineralization and decomposition processes determining chemical composition (Scougall *et al.* 1993). Soil structure and composition provides the habitat for germination and growth, forming part of a feedback system with plants and animals. Plants and indirectly animals complete nutrient cycling and influence soil structure and moisture content.

In a study by Yelenik *et al.* (2004), *Acacia saligna* enriched the soils in fynbos vegetation by altering the nitrogen cycling regime. The nitrogen enriched soils led to an increase in weedy grass species thus preventing revegetation of the natural fynbos. Examples of the role animals play include badger (*Taxidea taxus*) excavated mounds in tall grass prairies (USA) that support a different suite of plant (Hobbs and Huenneke 1992), while in Californian annual grasslands, gopher (*Geomys bursarius*) activity provides substrate for seedling establishment (Hobbs and Huenneke 1992).

In renosterveld there is a suite of animals that burrow or forage by digging in the soil e.g. *Orycteropus afer* (Aardvark), *Sus scrofa* (Feral pig), *Georychus capensis* (Mole rat) (Shiponeni 2002). Another suite of animals graze the plants e.g. *Damaliscus taurinus* (Blue wildebeest), *Taurotragus oryx* (Eland), *Oryx gazelle* (Gemsbok). Suretha van Rooyen (2003) has already found an association between animal activity and alien grass density in renosterveld. She found that there was a more pronounced association in sites that had been recently burned or grazed. By influencing soil nutrient and water variables, conditions for plant germination and growth are altered allowing different, better suited, or alien species to invade. Once these species have arrived they are often able to alter soils to further perpetuate themselves and to spread. Larger scale forms of disturbance such as fire and grazing then add further complexity to this situation.

Nutrient additions in ecosystems around the world have affected growth rates, productivity, plant phenology, species composition and rates of succession. Ecosystem processes, for example quantity and quality of litter-fall, also have an influence on nutrient cycling rates and alter vegetation structure and function. Nutrient addition in large quantities could retard succession and favour nutrient-demanding early successional species. The primary macronutrients for plant growth are nitrogen (N), phosphorous (P) and potassium (K), and these are the most commonly added as fertilizer (Bandel *et al.* 2002). Secondary macronutrients are magnesium (Mg), Sulphur (S) and Calcium (Ca) (Bandel *et al.* 2002). These are less frequently added in fertilizing practises. Micronutrients that are required at much lower concentrations but are also important for plant functioning include boron (B), copper (Cu), iron (Fe), chloride (Cl), manganese (Mn), molybdenum (Mo) and zinc (Zn).

The soil texture and pH play important roles in the availability of these nutrients. Sandy soils tend to lose nutrients quickly through leaching, while soils with a higher organic or clay content, retain nutrients and water more efficiently (Bandel *et al.* 2002). Soils in the renosterveld habitats tend to have a higher clay component. Nutrient availability is influenced strongly by soil pH and can in fact regulate the availability of nutrients. This is especially true for phosphorus, which is most available between pH 6.0 and 7.5. In general, the availability of nitrogen, potassium, calcium, and magnesium decreases rapidly below pH 6.0 and above pH 8.0 (Bandel *et al.* 2002).

Pot experiments indicated that high nutrient levels could in fact kill sclerophyllous fynbos species or reduce growth rates and weedy species are favoured (Brown and Mitchell, 1986). Nutrient pollution in the CFR includes industrial emissions, drift from aerial application of herbicides, insecticides and fungicides, application of fire retardants, fertilizing and runoff in agricultural and forestry areas (Stock and Allsopp 1992).

In the Hawkesbury Sandstone area (Australia) a study established that post fire regrowth of vegetation was much more rapid in nutrient enriched soils and low in native diversity (Thomson and Leishman 2005). This nutrient enrichment has a well-supported relationship with suburban development and the subsequent invasion by alien plants.

Another study in the Hawkesbury Sandstone area focused on the role that disturbance, plant attributes and herbivory play in alien plant success (Lake and Leishman 2004). All plant types except for the native non-invasive species were found to increase in biomass with higher nutrient soils. Alien species had higher survival rates at high nutrient sites. Sites without any disturbance had lowest alien invasive plant numbers. Physically disturbed sites on low fertility soils supported only one alien species. This suggests that nutrient enrichment is important for alien invasion. Alien species cover was highest and native species richness lowest where nutrient enrichment was high. Non-invasive and alien invasive species had lower levels of herbivory than native species. This lack of herbivory could easily explain invasion success. In physically disturbed sites of higher soil fertility alien species were small herbs or grasses well adapted for disturbance. The most consistent difference was found between invasive and non-alien invasive species was specific leaf area (SLA) - a larger SLA facilitated invasion. Species with a higher SLA have a shorter investment return rate and can grow faster. Alien species did not occur at sites that were not subject to nutrient enriched storm water runoff. Sites that were physically disturbed but had no nutrient runoff supported only one alien species. So, for these nutrient poor environments, nutrient enrichment is required for successful invasion to occur.

Distribution of species could be limited by abiotic factors at the stressful end of a physical gradient and by competition/predation at the less stressful end (Conell 1961). Hobbs and Atkins (1988) found that in the Australian wheat belt, introduced species established where soils were disturbed and nutrient enrichment appeared to increase growth. Seeds of alien annuals were found in all of the five vegetation types in the Australian wheat belt, but were more common in the heath and shrub vegetation rather than the woodlands. When the woodlands were disturbed and had nutrients added, establishment of alien annuals increased, but there were no consistent results of this in the shrub areas.

Altering the natural role that these small and larger disturbances play, alters conditions of the microclimates and these conditions favour alien plants. In the western Australian wheat belt many alien plants were found in pastures around the reserve. These edges were where the concentration of soil nitrogen was greatest (Hester and Hobbs 1992). This was attributed to fertilizer and stubble drift from adjacent pastures and /or an increase in plant litter. Hester and Hobbs (1992) looked at burnt and unburnt shrubland and woodland communities in the western Australian wheat belt, in terms of nutrients and native versus alien species. There was no discernable gradient of nutrients in the woodland and a greater abundance of aliens throughout the woodland. Possibly the more open structure was less of a barrier to soil nutrient movement. Fire had no apparent impact on colonization of alien plants while it increased native colonization in the shrublands. In the woodland there was a reduction in colonization of both native and alien species.

The Netherlands has also been an area where a concentration of work on boundary/edge effects has taken place. The effect of nutrient rich arable fields on the biomass production of boundary vegetation was tested in research by Kleijn (1996). Biomass of boundary vegetation was found to be significantly greater. A study by Kleijn and Snoeijing (1997) tested the effects of N, P, K fertilization (three concentration levels) and pesticide addition (four concentration levels), in a low productive meadow and high productive fallow field. Fertilizing resulted in a gradual loss of species particularly those of low stature. Fertilizers decreased species richness, biomass and individual species abundance with greater affect than pesticides. In another study from the Netherlands (Schippers *et al.* 2002) the impacts of three treatments, high, low and no levels of N, P, K were investigated; these effects were tested with and without mowing. A spatial plant competition model was also created to evaluate competition for nitrogen and light. Experimental results and modelling results were fairly congruent, both indicating that when fertilizing and disturbance was intensive, perennial plant diversity was low.

1.6.3 Seed bank

To gain some insight into the most effective restoration methods for these renosterveld patches, life history characteristics, such as the seed bank, provide valuable background for strategies. A seed bank is a collection of ungerminated seeds capable of replacing adult plants (annuals or perennials) that die through disturbance, disease or removal by animals or humans. All seeds in the soil or litter are called the seed bank. Seed banks can be transient, that is, seeds germinate within the year subsequent to dispersal or persistent, that is, seeds remain in the soil for over a year after dispersal. The persistent seed bank is a reserve of genetic potential accumulated through time and represents genetic diversity for the population to respond to natural selection.

In a study in northern Sydney, Australia, King and Buckney (2001) assessed the distribution of alien and native seed banks in relation to distance from an urban edge. This was also compared to the above ground vegetation. The density and cover of alien species was found to be highest near the edge. The above ground cover did not reflect the soil seed bank as regards the native and alien species. Above ground vegetation was a poor indicator of the seed bank contents for alien and indigenous flora. The results from this study indicate that invasive plants are restricted by suitable conditions. A conclusion from this study was the number of alien plants present in urban bush may change with a change in conditions such as physical disturbance or nutrient enrichment. These changes would favour germination of these species. This would imply that even though alien species may be present in the seed bank, by preventing unnatural alterations to the environment the germination of these species can be prevented.

1.6.4 Conclusions

This review of the literature has highlighted issues of direct relevance to the hypotheses that I will be testing in this thesis. On the basis of the literature there is evidence that disturbance by grazing, digging, and fire, together with or independently of nutrient addition to oligotrophic ecosystems, is likely to promote invasions of alien annual grasses.

1.7 References

Bandel, A.V., James, B.R., John J. and Meisinger, J.J. 2002. Basic Principles of Soil Fertility II: Soil Properties Department of Agronomy, University of Maryland at College Park http://www.agnr.umd.edu/MCE/Publications/Publication.cfm?ID=151 (accessed 12/07/06)

Baard, E.H.W. 1993. Distribution and status of the geometric tortoise *Psammobates geometricus* in South Africa. *Biological Conservation*. 63. 235-239.

Brooks, M.L. 1999. Habitat invasibility and dominance by alien annual plants in the western Mojave desert. *Biological Invasions.* 1. 325-337.

Boucher, C. 1983. Floristic and structural features of the coastal foreland vegetation south of the Berg River, Western Cape Province, South Africa. *Bothalia.* 14. 669-674.

Carson, W.P. and Peterson, C.J. 1990. The role of litter in an old field community. Impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia.* 85. 8-13.

Conell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus. Ecology.* 42. 710-23.

Cowling, R.M. and Holmes, P.M. 1992. Flora and Vegetation. *In*: Cowling, R.M. (Ed.) The Ecology of Fynbos. Nutrients, fire and diversity. Oxford University Press, Cape Town. Pp. 62-112.

Cowling, R.M. 1984. A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. *Bothalia.* 15. 115-228.

Cowling, R.M., Pierce, S.M. and Moll, E.J. 1986. Conservation and utilization of South Coast Renosterveld, an endangered South African vegetation type. *Biological Conservation.* 37. 363-377.

D'Antonio, C.M. and Vitousek, P.M. 1992. Biological invasions by Alien grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics.* 23. 63-87.

Duvenhage, A.J. 1993. *Die voorkoms van uitheemse kruidgewasse in die natuurlike plantegroei van die Stellenbosch omgewing*. Unpublished M.Sc.Thesis, University of Stellenbosch.

Dyer, A.R and Rice, K.J. 1997. Intraspecific and diffuse competition: The response of Nasella pulchra in a California grassland. *Ecological Applications*. 7(2). 484-492.

Evans, R.A. 1972. Germination and establishment of *Salsola* in relation to seedbed environment 2. Seed distribution, germination and seedling growth of *Salsola* and microenvironment monitoring of the seedbed. *Agicutural Journal*. 64. 219-224.

Facelli, J.M. 1994. Multiple indirect affects of plant litter affect the establishment of woody seedlings in old fields. *Ecology*. 75. 1727-1735.

Facelli, J.M. and Pickett, S.T.A. 1991. Plant litter its dynamics and effects on plant community structure. *Botanical Reviews*. 57. 1-52.

Facelli, J.M., Williams, R., Frickers, S. and Ladd, B. 1999. Establishment and growth of seedlings of *Eucalyptus oblique*. Interactive effects of litter, water and pathogens. *Australian Journal of Ecology*. 24. 484-494.

Hester AJ and Hobbs RJ. 1992. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science*. 3. 101-108.

Heydenrych, B. 1995. Wildflowers of the Darling Renosterveld, can they be maintained for future generations? *Veld and Flora*. June. 72-73.

Hobbs, R.J. 2001. Synergisms among habitat fragmentation, livestock grazing and biotic invasions in Southwestern Australia. *Conservation Biology*. 15. 1522-1528.

Hobbs, R.J. 1992. Disturbance, Diversity and Invasions; Implications for conservation. *Conservation Ecology*. 6. 324.

Hobbs R.J. and Atkins, L. 1988. Effect of disturbance and nutrient additions on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology.* 13. 171-179.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology. 6. 324-337.

Holmgren, M., Avilés, R., Sierralta, L., Segura, A.M. and Fuentes, E.R. 2000. Why have European herbs so successfully invaded the Chilean matorral: Effects of herbivory, soil nutrients and fire. *Journal of Arid Environments.* 44. 197-211.

Jujarvcic, N.L., Harrison, S. and Wolf, A.T. 2002. Abiotic stress, competition and the distribution of the grass *Vulpia microstachys* in a mosaic environment. *Oecologia.* 130. 555-62.

Kent, M. and Coker, P. 1992. Vegetation description and analysis: a practical approach. CRC Press, Boca Raton. Pp. 363.

Kemper, J. 1997. *The Effects of fragmentation of South Coast Renosterveld on vegetation patterns and processes*. M.Sc. thesis, University of Cape Town, South Africa.

Kemper, J., Cowling, R.M. and Richardson, D.M. 1999. Fragmentation of Southern African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*. 90. 103-111.

Kleijn, D. 1996. The use of nutrient resources from arable fields by plants in field boundaries. *Journal of Applied Ecology.* 33. 1433-1440.

Kleijn, D. and Snoeijing, G. Ineke. J. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical changes caused by low levels of herbicides and fertilizers. *Journal of Applied Ecology.* 34. 1413-1425.

King, S. A. and Buckney, R.T. 2001. Alien plants in the soil-stored seed bank of urban bushland. *Australian Journal of Botany.* 49. 717-720.

Krug, C.B. 2004. The Renosterveld restoration project, understanding and restoring West Coast renosterveld. *Veld and Flora.* June. 68-70.

Lake, J, C and Leishman, M. R. 2004 Invasion success of Exotic Alien plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation.* 117. 215-226.

Lenz, T.I., Moyle-Croft, J.L. and Facelli, J.M. 2003. Direct and indirect effects of Exotic annual grasses on species composition of a south Australian grassland. *Austral Ecology.* 28. 23-32.

Low, A.B. & Rebelo, A.G. (Eds.). 1996. *Vegetation of South Africa, Lesotho and Swaziland.* A companion to the Vegetation Map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Mack, M.C. and D'Antonio, C.M. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecological Applications.* 13. 154–166.

MacArthur, R.H., and Wilson, E.O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton, New Jersey.

Milton, S. 2004. Grasses as invasive alien plants in South Africa. *South African Journal of Science.* 100. 69-75.

Moll, E.J., Campbell, B.M., Cowling, R.M., Bossi, L., Jarman, M.L. and Boucher, C. 1984. A description of major vegetation categories in and adjacent to Fynbos biome. South African National Scientific Programmes Report No. 83.

Mucina, L. and Rutherford, M.C. (eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia 19*, South African National Biodiversity Institute, Pretoria.

Musil, C.F., Milton, S.J. and Davis, G.W. 2005. An empirical examination of different management strategies for managing alien invasive grass infestations in a South African West-Coast reserve. *South African Journal of Science.* 101. 337-344.

Rebelo, A.G. 1995. Renosterveld: conservation and research. *In:* Low, A.B. and Jones, F.E. (eds). The sustainable use and management of renosterveld remnants in the Cape Floristic Region. Proceedings of a symposium. Flora Conservation Committee report 1995/4. Botanical Society of South Africa, Kirstenbosch, 32-42.

Reyers, B., Fairbank, H.H.K., van Jaarsveld, A.S. and Thompson, M.W. 2001. South African vegetation priority conservation areas- a coarse filter approach. *Diversity & Distributions.* 7. 79-89.

Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.I., Midgley, G.F., Milton, S.J., Powrie, L., Rutherford, M.C., Samways, M.J. and Schulze, R.E. 2000. Invasive alien organisms and global change: A South African perspective. *In:* Mooney, H.A and Hobbs, H.A. (eds). The impact of global change on alien species. Island Press, Washington D.C. Pp. 303-349.

Schippers, P. and Joenje, W. 2002. Modelling the effect of fertilizer, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agriculture, Ecosystems and Environment.* 93. 351-365.

Scougall, S.A., Majer, J.D. and Hobbs, R.J. 1993. Edge effects in grazed and ungrazed Western Australian wheatbelt remnants in relation to ecosystem reconstruction. *In*: Saunders, D.A., Hobbs, R.J. and Erlich, P.R. (eds), Nature Conservation 3: Reconstruction of fragmented systems. Surrey Beatty and Sons; North Chipping. Pp. 163-178.

Shiponeni, N.N. 2003. *Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa*. M.Sc. thesis, University of Stellenbosch.

Simpson, R.L., Allessio Leck, M. and Thomas Parker, V. 1989. Seed banks: General Concepts and Methodological Issues. *In*: Leck, M.A., Parker, T.V. and Simpson RL (eds) Ecology of Soil Seed Banks. Academic Press Inc. San Diego. 1-7.

Steinschen, A. K., Gorne, A. and Milton, S.J. 1996. Threats to Namaqualand flowers outcompeted by grass or exterminated by grazing? *South African Journal of Science.* 92. 237-242.

Stock, W.D. and Allsopp, N. 1992. Functional perspective of ecosystems. In: Cowling, R.M. (ed) Fynbos: Nutrients, fire and diversity. Oxford University Press, UK. Pp. 62-112.

Thomas, G.W. Exchangeable cations. 1982. *In*: Page, A.L., Miller, R.H. and Kenney, D.R. (eds) *Methods of soil analysis. Part 2. Chemical and microbiological properties.* Soil science society of America, Madison, Wisconsin. Pp. 167-180.

Thomson, V.P. and Leishman, M.R. 2005. Post fire vegetation dynamics in nutrient enriched and non-enriched sclerophyll woodland. *Austral Ecology.* 230. 50-60.

Van Rooyen, S. 2003. *Factors affecting alien grass invasion into West Coast Renosterveld fragments.* M.Sc. thesis, University of Stellenbosch.

Von Hase, A., Rouget, M., Maze, K. and Helme, N. 2003. A fine scale conservation plan for the Cape Lowlands Renosterveld: Technical report Sept 2003. Report No. CCU 2/03 Cape Conservation Unit. Botanical Society of South Africa Pvt Bag X167735 Claremont.

Walker, C. 1986. Wildspore. C. Struik (Pty) Ltd, Cape Town.

Walton, B.A. 2006. *Vegetation patterns and dynamics of renosterveld at Agter-Groenberg Conservancy, Western Cape, South Africa*. MSc. thesis University of Stellenbosch.

White, P.S. & Pickett, S.T.A. (1985) Natural disturbance and patch dynamics – An introduction. *In:* White, P.S. & Pickett, S.T.A.(eds). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press Inc., New York. Pp. 3 – 13.

Yates, C.J., Norton, D.A. and Hobbs, R.J.2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south western Australia: implications for restoration. *Australian Journal of Ecology.* 25. 36-37.

Yelenik, S.G., Stock, W.D. and Richardson, D.M. 2004. Ecosystem impacts of invasive *Acacia saligna* in South African fynbos. *Restoration Ecology*. 12. 44-51.

Chapter 2

Vegetation changes and soil chemical and physical gradients from agricultural fields down slope into renosterveld patches

2.1 Abstract

Vegetation changes and soil chemical and physical changes from agricultural fields down slope into renosterveld patches have been assessed. Changes in vegetation with distance from the agricultural field were quantified in terms of cover by functional types (perennial shrubs, annual shrubs, annual herbs, geophytes, alien grass and indigenous grass). Chemical and physical characteristics such as nutrients, pH, soil water, soil density, litter, stone cover and animal disturbance were regressed against distance along each transect. Perennial plant cover increased into patches of natural renosterveld vegetation, while alien invasive annual grasses decreased significantly. Geophyte abundance increased significantly with increased alien annual grass cover, however the diversity was lower in the homogenized grass landscape. Nutrient gradients varied across the study sites. Data suggested that fertilizing played a role in facilitating alien annual grass invasion when grazing and animal disturbance was low. Soil crusts, often a feature of renosterveld landscapes, were often found destroyed where there was heavy grazing and increased animal activity, thus creating more recruitment sites for alien invasive annual grasses.

Keywords: agricultural impacts; alien invasive grasses; fertilization.

2.2 Introduction

Environmental determinants of invasibility include disturbance regime, environmental stress, competition, mutualisms, propagule pressure and resource availability as well as community structure and type of ecosystem (Milbau *et al.* 2005). Agriculture is dependent on external inputs of resources for higher yields, consequently fertilizers, pesticides and water are added.

The effect of nutrient enrichment on adjacent vegetation has been investigated by several authors including Scougall *et al.* (1993), Kleijn (1996), Kleijn *et al.* (1997), King and

Buckney (2001), Schippers and Joenje (2002), Van Rooyen (2003) and Milbau *et al.* (2005). Biomass of natural vegetation adjacent to nutrient-enriched areas was found to be significantly greater and was restricted to conditions that favoured their success. Drift from wasteful additions of water or nutrients to croplands adjacent to renosterveld fragments could have implications for their conservation, including invasion of such fragments by alien weeds.

Previous studies have found environmental conditions to play a significant role in vegetation dynamics. King and Buckney (2001) worked in northern Sydney, Australia and assessed alien and native seed bank distribution in relation to distance from urban edges; density and cover of alien species proved to be highest near the edge. Seed bank distribution was also compared to above ground cover however neither the native or alien species above ground were representative of the seed bank composition. Invasive plants were determined to be restricted by suitable conditions. A conclusion from this study was that with a change in environment, such as physical disturbance or nutrient enrichment, the distribution and density of alien plants present in natural vegetation fragments in urban areas may change. This would imply that the germination of alien invasive species can be prevented, in spite of their presence in the seed bank, by preventing unnatural alterations to the environment. In another example, decrease in germination success of the grass, *Lolium perenne,* was found to be related to water and nutrient availability and temperature in gaps (Milbau *et al.* 2005). Germination of invasive species *Lolium perenne* was inversely related to biomass of surrounding vegetation. A strong positive relationship between light availability and growth of *Lolium perenne* was found. A higher above ground biomass could result in higher resource use below ground and therefore less available resources for invaders (Milbau *et al.* 2005). In addition higher above ground biomass would increase competition for space and light.

In this chapter, we test the hypotheses that (1) alien grass cover decreases with distance from agricultural fields, (2) that soil fertility decreases with distance from agricultural land, (3) that soil fertility (rather than other variables such as disturbance, soil texture or perennial vegetation) is the best predictor of alien grass cover.

2.3 Study ecosystem

Ecotonal to fynbos and succulent karoo, renosterveld occurs on moderately fertile, shale derived soils where rainfall is between 350 and 650 mm/yr (Cowling and Holmes 1992, Boucher 1983). Renosterveld has been broadly subdivided into west coast and south west/south coast renosterveld (Agulhas plain). This study was conducted within west coast renosterveld (Boland and Swartland areas). Renosterveld falls within an area of Mediterranean climate with hot, dry summers and cold wet winters. West coast renosterveld has heavy clays and loamy soils derived from the Malmesbury Group shales, Cape Granite Suite and Klipheuwel Formation shales. Nutrient rich termite mounds or heuweltjies, support more shrubby communities and are prominent in the landscape (Low and Rebelo 1996).

2.4 Study Sites

Three sites were used, Jan Briers Louw Geometric Tortoise Reserve (JBL), Mulderbosch Wine Estate (MWE) and the Paul Cluver Estate (PCWE). Detailed descriptions of these sites are to be found in Chapter 1, pages 6-8.

2.5 Methods

Refer to Chapter 1 (section 1.6.) for general research approach description and model. This chapter presents data showing patterns in vegetation structure and soil chemical and physical attributes over a spatial and vegetation gradient from agricultural fields down slope into renosterveld patches.

2.5.1 Sampling design

At each site, three transects with similar orientation were set up running perpendicular to the renosterveld: agricultural boundary. Each transect was situated such that 1/4 of the length was in the agricultural area, 2/4 in the fragment edge and 1/4 in the pristine area. 3 x 3 m^2 quadrates were distributed along each transect (Figure 2.1).

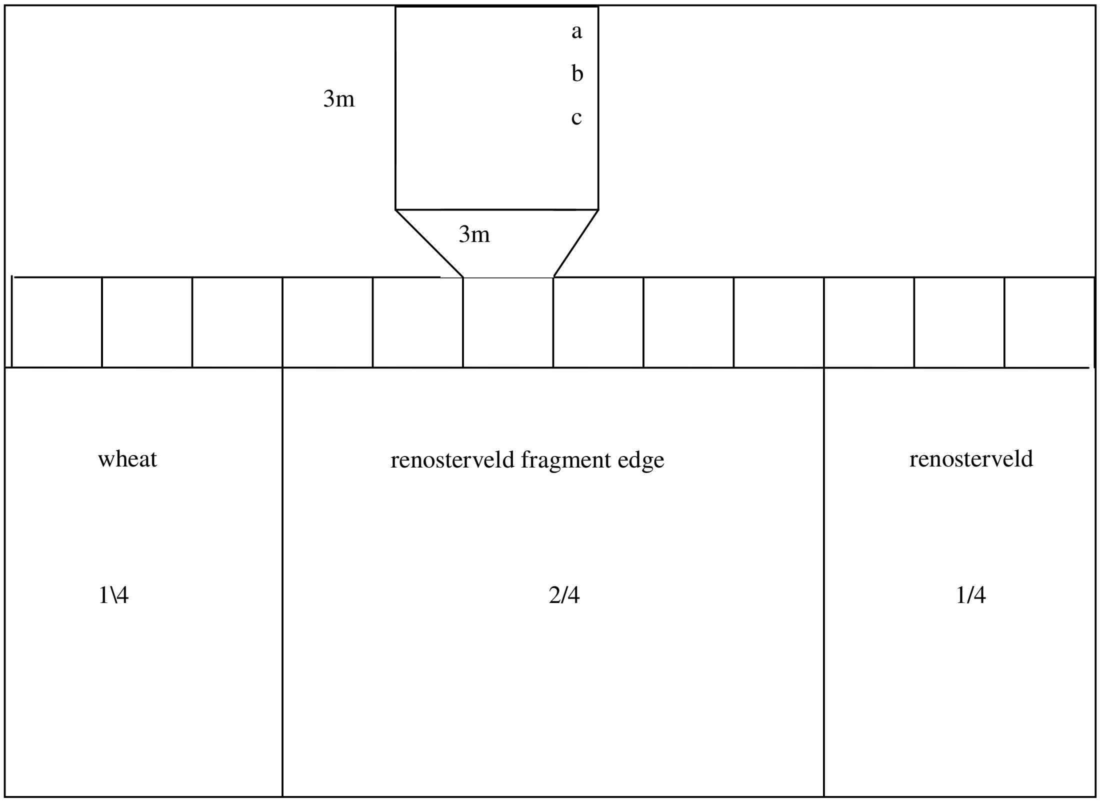

Figure 2.1: Transect design for sampling soil variables, vegetation changes and alien grass seed bank across a gradient from wheat farming through fragment edges into pristine renosterveld. Each quadrate was 3 m x 3 m. Point (a) was a sample point for soil chemistry, point (b) was a sample point for infiltration and point (c) was a soil density sample point.

To assess the relationship between species or functional groups and habitat conditions and to investigate possible associations between indigenous shrubs and alien grasses (van Rooyen 2003), plant species diversity, density and functional type were measured along a gradient from fragment edges into pristine renosterveld. Within each quadrate each species was identified to genus level at least and percentage cover recorded. Species were also divided into functional types (herbaceous annuals and perennials, annual and perennial grasses, geophytes and alien versus indigenous species).

2.5.2 Soil surface condition

Soil surface conditions were assessed since they play a role in germination and growth. Within each quadrate the following was estimated: cryptogram cover, litter, bare ground, stones and signs of animal disturbance as percentage cover in each quadrate.

2.5.3 Soil chemistry, density and water infiltration

The soil chemistry and physical conditions were assessed for their role in germination and growth. Within each quadrate there was a sample for nutrient content and pH, the first 2 cm of soil (as this is the region where most seeds germinate) was taken. In addition each sample point was briefly described. Field infiltration was conducted using a can with a diameter of 7.5 cm; both ends were opened and it was inserted into the ground to a depth of 1.5/2 cm, and a known quantity of water (200 ml) was poured in. The can was inserted into the ground with as little disturbance to the crust as possible, water was poured in and the time taken for it to be absorbed was measured. Soil moisture was measured by taking a standard core sample of soil and weighing it before and after drying. Soil density was determined by taking the dry mass of this core and dividing by the volume of the core.

Soils were analyzed for carbon (total), nitrogen (NO_3^- and NH_4^+), phosphorus, soluble calcium, magnesium, sodium and potassium as well as pH, electrical conductivity and exchangeable cations. Soils were sampled to a depth of 5 cm and were air dried and sieved to < 2 mm. The following analyses on samples were performed by Bemlab[1]: Electrical conductivity (EC) and pH 1:5 and 1:2.5 soil water extracts (Rhoades 1982): pH in 1 M KCl: water-soluble (1:5) cations (Rhoades 1982): and ammonium acetate –extractable cations using the centrifuge procedure in Thomas (1982), analysed by atomic absorption spectrometry: water soluble (1:5) anions by ion chromatography: extractable P using Bray-2 extract as described by Bray and Kurtz (1945): total C and N by complete combustion using a Eurovector Euro EA Elemental Analyzer: and labile C (or readily oxidisable C) with a modified Walkley-Black method using (i) 5 ml instead of 20 ml, as described by Chan *et al.* (2001).

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[1] Bemlab Pty (Ltd), ECI building W21, De Beers Rd, Somerset West

2.5.4 Data Analysis

Data were processed in Microsoft Excel. Data showed a normal distribution (Kent & Coker 1992, Wheater & Cook 2000), justifying use of parametric statistics. Each soil chemical and physical characteristic was regressed (y=mx+c), using a Spearman correlation, against the gradient of sample sites from the wheat fields through the fragment edge into pristine renosterveld using STATISTICA 7. This established correlative relationships between distance from the inputs of water and fertilizers and the nutrient and moisture conditions inwards to pristine renosterveld. Vegetation cover in percentage as well as the vegetation heights was regressed against this same distance gradient from wheat fields through the edge and into pristine renosterveld. Penetrometer readings were analysed using analysis of variance. The sites were further ordinated on the basis of the environmental, physical and chemical variables with distance from the fence by principal component analysis (PCA) with Biodiversity Pro Ver. 2 software (McAleece 1997). The correlations were performed using SPSS software (SPSS Inc., Chicago, USA) statistical package (SPSS 1997).

2.6 Results

Alien annual grass cover decreases significantly with distance into renosterveld patches for all study sites (Figure 2.2), moreover annual grass cover decreases exponentially as the shrub cover increases (Figure 2.3).

2.6.1 Vegetation survey

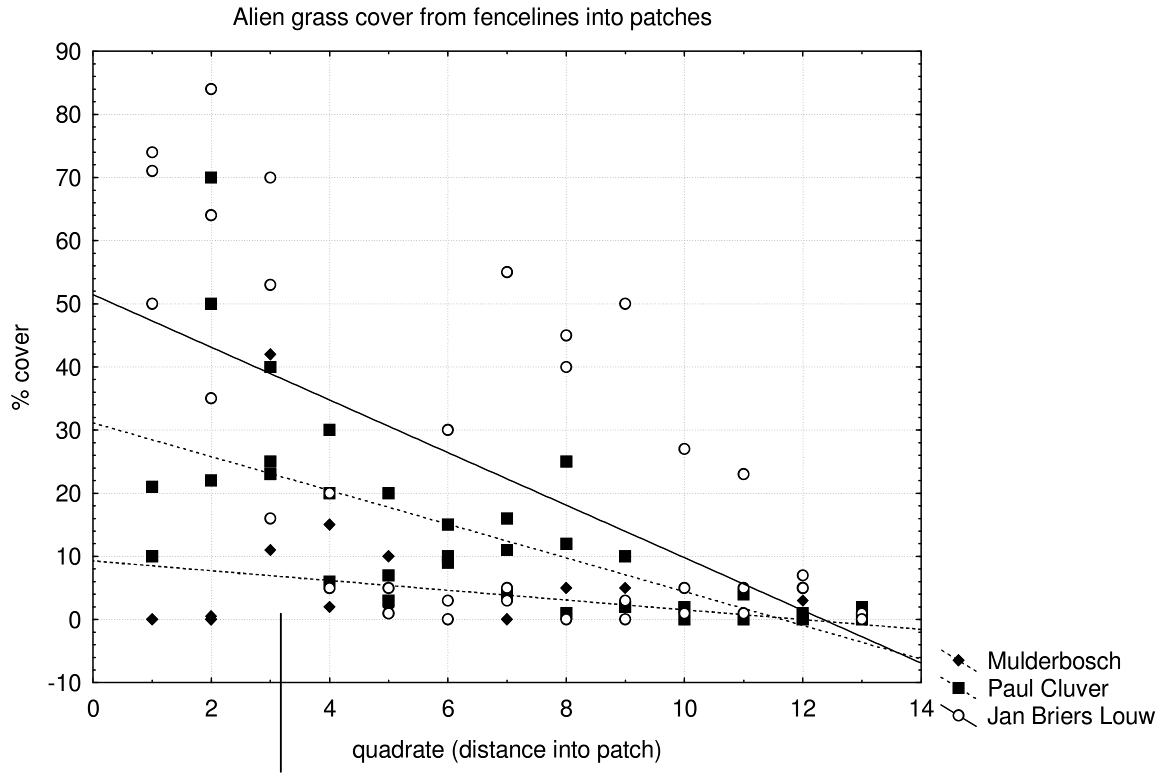

Figure 2.2: The relationship between alien grass cover and distance into the patch for all sites. Each quad represents 3 m. At point three the fence line occurs. Mulderbosch: $y = 9.3013 - 0.7738*x$; $r = -0.3120$, $p = 0.0532$; $r^2 = 0.0973$, Paul Cluver: $y = 31.141 - 2.6722*x$; $r = -0.6676$, $p = 0.00000$; $r^2 = 0.4457$,Jan Briers Louw: $y = 51.4487 - 4.1667*x$; $r = -0.6040$, $p = 0.00005$; $r^2 = 0.3648$.

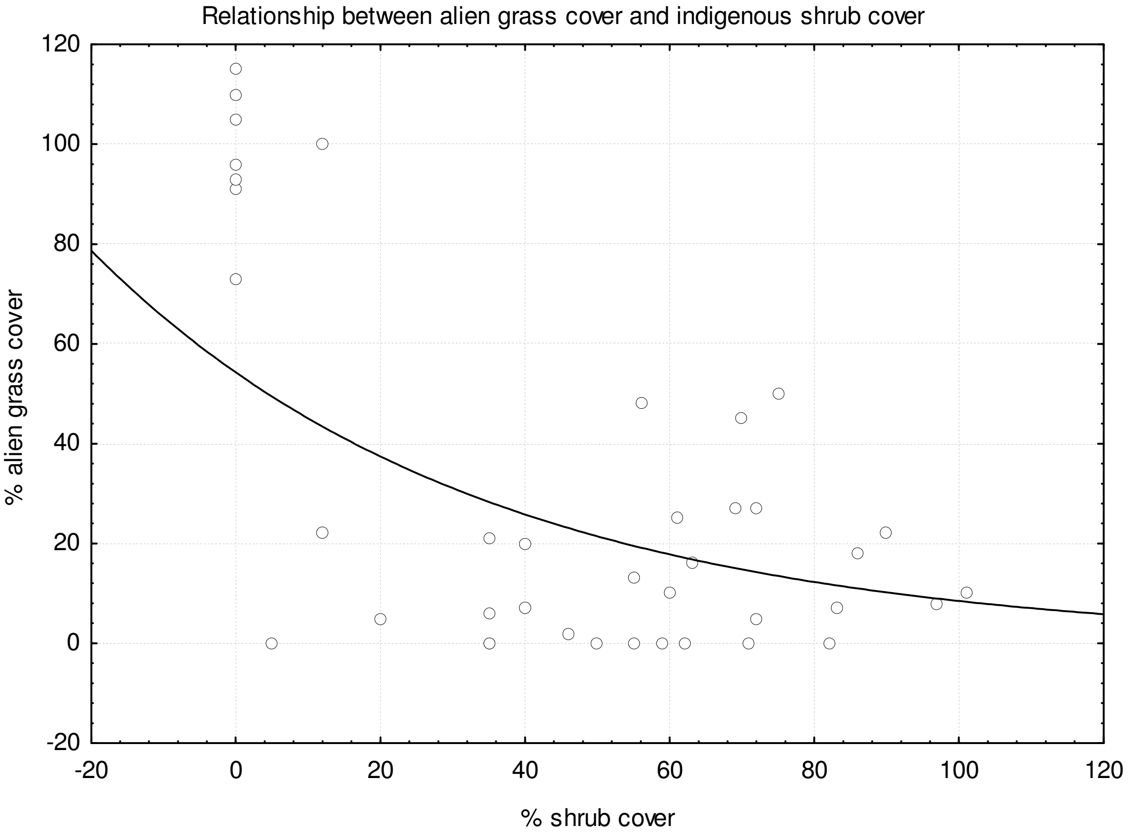

Figure 2.3: The relationship between alien grass cover and indigenous shrub cover, r=-0.6348, p<0.001. The relationship is a significant decreasing one.

At Jan Briers Louw Geometric Tortoise Reserve (JBR) (Table 2.1), weedy annuals and alien grasses decreased significantly into the indigenous patch and correlated positively with each other. Perennial shrubs increased significantly into the patch, while indigenous grasses showed no significant trend with distance into the patch ($p>0.05$). Alien grass cover decreased as perennial shrub cover increased ($r = -0.503$, $p < 0.001$). The abundance of geophytes significantly increased with alien cover, however there was a significant increase in diversity of geophytes into the patch ($r = 0.421$, $p < 0.01$). The plant community near the fence line was virtually homogenous and dominated by alien perennial and annual grasses. Thus there was less microscale variability within the soils and above ground. Geophyte species that favour specific conditions were absent and a greater abundance of fewer species was observed. Where the soil surface appeared to have been undisturbed for a longer period (no digging, lack of cryptogram/moss cover, no trampling) there were more species present. It was observed that further into the patches species clumped together and varied in a short space, alpha diversity was higher deeper into patches than on the edges where the grasses homogenized the area.

Table 2.1: Trends in plant cover with distance from an agricultural field at Jan Briers Tortoise Reserve. Data used in regressions were percentage projected canopy cover in 3 x 3 m quadrates for of various plant guilds and distance (in quadrates) away from the edge of the transformed landscape.

Regression pair	**N**	**r**	**r^2**	**p**
Alien grass versus distance	39	-0.604	0.364	***
Annuals versus distance	39	-0.062	0.004	***
Indigenous grass versus distance	39	0.313	0.098	NS
Perennial shrub versus distance	39	0.570	0.325	***
Geophytes versus distance	39	0.0977	0.010	NS
Annuals versus aliens	39	0.537	0.288	***
Indigenous grass versus aliens	39	0.216	0.047	NS
Perennial shrub versus aliens	39	-0.503	0.253	***
Geophytes versus aliens	39	-0.312	0.097	NS
Geophyte diversity versus distance (species in 3 x 3 m quadrate)	39	0.421	0.177	**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

At Paul Cluver Wine Estate (PCWE) (Table 2.2), alien grasses decreased significantly with distance into the patch ($r=-0.668$, $p<0.001$), this was again an indication that conditions were more favourable closer to the agriculture patches. Weedy annuals and indigenous grass had a slightly decreasing trend into the PCWE patch. Perennial shrubs increased significantly downslope ($r=0.643$, $p<0.001$) and decreased significantly with alien grasses ($r=-0.551$, $p<0.001$). This again correlates with a decrease in competition from alien invasive grasses. Geophyte abundance increased significantly into the patch and had a significant decreasing relationship to alien grass cover. These results reflect the increased availability of space and light. Annual cover increased significantly with alien grasses as they did at JBR. There was a significant increasing trend for diversity of geophyte species into the patch.

Table 2.2: Trends in plant cover with distance from an agricultural field at Paul Cluver Wine Estate. Data used in regressions were percentage projected canopy cover in 3 x 3 m quadrates for of various plant guilds and distance (quadrates) away from the edge of the transformed landscape.

Regression pair	**N**	**r**	**r^2**	**P**
Alien grass versus distance	39	-0.668	0.446	***
Annuals versus distance	39	-0.295	0.087	NS
Indigenous grass versus distance	39	-0.314	0.098	NS
Perennial shrub versus distance	39	0.643	0.414	***
Geophytes versus distance	39	0.372	0.138	*
Annuals versus aliens	39	0.57	0.324	***
Indigenous grass versus aliens	39	0.0524	0.0027	NS
Perennial shrub versus aliens	39	-0.551	0.303	***
Geophytes versus aliens	39	-0.339	0.115	*
Geophyte diversity versus distance	39	0.372	0.138	*

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

At Mulderbosch Wine Estate (MWE) the decrease in alien grass cover into the MWE indigenous patch was not significant at the 95% confidence level (Table 2.3). Indigenous grasses and perennials had a significant, increasing trend into the patch as they did in the previous sites. Geophyte abundance did not increase down the slope as in JBR and PCWE. There were also no significant relationships between the plants functional types and alien invasive grasses. Geophyte diversity did increase into the patch.

Table 2.3: Trends in plant cover with distance from an agricultural field at Mulderbosch Wine Estate. Data used in regressions were percentage projected canopy cover in 3 x 3 m quadrates for of various plant guilds and distance (quadrates) away from the edge of the transformed landscape.

Regression pair	**N**	**r**	**r^2**	**P**
Alien grass versus distance	39	-0.312	0.0973	NS
Annuals versus distance	39	-0.171	0.029	NS
Indigenous grass versus distance	39	0.376	0.141	*
Perennial shrub versus distance	39	0.342	0.117	*
Geophytes versus distance	39	-0.033	0.001	NS
Annuals versus aliens	39	0.155	0.024	NS
Indigenous grass versus aliens	39	-0.083	0.007	NS
Perennial shrub versus aliens	39	-0.06	0.004	NS
Geophytes versus aliens	39	-0.091	0.008	NS
Geophyte diversity versus distance	39	0.438	0.192	**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

2.6.2 Soil chemical characteristics

The pH was higher in the fields than in the reserve of JBR (Appendix 2.1). At JBR pH was generally high and above six on the edge of the patch or in the vineyard (Appendix 2.1). It then decreased significantly into the patch (Table 2.4). Where pH was higher in JBR transect three, it was on a heuweltjie with a pH range between 5.8 and 6.1 (Appendix 2.1).

There were few significant relationships between the nutrient variables and distance into the JBR reserve. Carbon had a significant decreasing trend with alien grass cover. There was also a near significant relationship between alien grass cover and potassium. Sodium, magnesium, potassium and nitrogen had no relationship either with distance from the edge or in relation to alien cover.

The PCWE site had stronger evidence of nutrient gradients. pH was generally high and above six on the edge of the patch or in the vineyard (Appendix 2.2). It then decreased significantly into the patch (Table 2.5). Sodium had a significantly decreasing gradient down the slope and increased significantly with alien grass cover. Potassium increased significantly into the patch and had a significant decreasing relationship with alien grass cover. Calcium had a significant decreasing trend with distance into the patch but no significant relationship with the alien grass distribution. Magnesium increased significantly into the patch and had a significant negative relationship with alien grass cover. Carbon and nitrogen increased significantly into the patch and were significantly negatively related to alien grass cover. This site has stronger evidence of the influence that soil chemistry has on the distribution with alien grasses and also has stronger patterns in relation to distance from actively fertilized fields.

At MWE pH decreased significantly down the slope from values above six outside of the patch to values well below six inside the patch (Appendix 2.3, Table 2.6). There were no significant changes in nutrient distribution down the slope. There were no significant relationships between soil chemical characteristics and alien grass distribution.

Table 2.4: Regression results for soil chemical characteristics at the JBR site. Soil chemical characteristics are regressed against distance from the fence into the patch and against alien grass cover.

Regression pair	**N**	**r**	**r^2**	**p**
pH versus distance	39	-0.198	0.039	NS
pH versus aliens	39	0.26	0.068	NS
Na cmol/kg versus distance	39	-0.159	0.025	NS
Na cmol/kg versus aliens	39	-0.059	0.003	NS
K cmol/kg versus distance	39	-0.354	0.125	NS
K cmol/kg versus aliens	39	0.073	0.005	NS
Ca cmol/kg versus distance	39	-0.064	0.004	NS
Ca cmol/kg versus aliens	39	0.17	0.029	NS
Mg cmol/kg versus distance	39	0.011	0.000	NS
Mg cmol/kg versus aliens	39	0.2	0.040	NS
C % versus distance	39	0.117	0.014	NS
C % versus aliens	39	-0.33	0.109	*
N % versus distance	39	0.165	0.027	NS
N % versus aliens	39	-0.368	0.135	NS

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

Table 2.5: Regression results for soil chemical characteristics, PCWE. Soil chemical characteristics are regressed against distance from the fence into the patch and against alien grass cover.

Regression pair	**N**	**r**	**r^2**	**p**
pH versus distance	39	-0.445	0.198	**
pH versus aliens	39	0.245	0.060	NS
Na cmol/kg versus distance	39	-0.52	0.270	***
Na cmol/kg versus aliens	39	0.2	0.040	NS
K cmol/kg versus distance	39	0.666	0.444	***
K cmol/kg versus aliens	39	-0.58	0.336	***
Ca cmol/kg versus distance	39	-0.357	0.127	*
Ca cmol/kg versus aliens	39	0.16	0.026	NS
Mg cmol/kg versus distance	39	0.626	0.392	***
Mg cmol/kg versus aliens	39	-0.655	0.429	***
C % versus distance	39	0.687	0.472	***
C % versus aliens	39	-0.536	0.287	***
N % versus distance	39	0.542	0.294	NS
N % versus aliens	39	-0.76	0.5776	**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

Table 2.6: Regression results for soil chemical characteristics, MWE. Soil chemical characteristics are regressed against distance from the fence into the patch and against alien grass cover.

Regression pair	**N**	**r**	**r^2**	**P**
pH versus distance	39	-0.449	0.202	**
pH versus aliens	39	0.126	0.016	NS
Na cmol/kg versus distance	39	-0.022	0.000	NS
Na cmol/kg versus aliens	39	0.003	0.000	NS
K cmol/kg versus distance	39	-0.186	0.035	NS
K cmol/kg versus aliens	39	-0.017	0.000	NS
Ca cmol/kg versus distance	39	-0.405	0.164	NS
Ca cmol/kg versus aliens	39	0.157	0.025	NS
Mg cmol/kg versus distance	39	-0.220	0.048	NS
Mg cmol/kg versus aliens	39	0.044	0.002	NS
C % versus distance	39	0.031	0.001	NS
C %versus aliens	39	0.071	0.005	NS
N % versus distance	39	0.093	0.009	NS
N % versus aliens	39	0.170	0.029	NS

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

2.6.3 Soil Physical characteristics

At JBR (Table 2.7), litter, stone cover, animal disturbance and bare ground had significant increasing relationships into the patch. These corresponded to increases in alien grass cover for this site however regression against alien grass distribution indicated there were no relationships between alien grasses and cover variables. The only exception is litter which had a near significant relationship.

At PCWE litter, animal disturbance and soil water increased significantly into the patch (Table 2.8). Stone cover, bare ground and soil density decreased significantly into the patch. Litter decreased significantly with alien grass cover. Soil density increased significantly with alien grasses.

At MWE there was a significant positive relationship between alien grass cover and litter. Animal disturbance increased significantly down the slope for the regression (Table 2.9). Stone cover decreased significantly into the patch, animal activity increased significantly into the patch however neither was related to the distribution of alien grass cover. Soil density decreased significantly down the slope this was most likely related to an increase in perennial shrub cover.

Table 2.7: Regression results for soil physical characteristics**,** JBR. Soil physical characteristics were regressed against distance and distribution of alien grass cover.

Regression pair	**N**	**r**	**r^2**	**p**
Litter versus distance	39	0.340	0.116	*
Litter versus aliens	39	-0.300	0.090	NS
stones versus distance	39	0.490	0.240	**
stones versus aliens	39	-0.232	0.054	NS
animal disturbance versus distance	39	0.290	0.084	NS
animal disturbance versus aliens	39	-0.211	0.045	NS
bare ground versus distance	39	0.330	0.109	*
bare ground versus aliens	39	-0.450	0.203	**
cryptogram cover versus distance	39	0.037	0.001	NS
cryptogram cover versus aliens	39	-0.270	0.073	NS
soil water versus distance	39	0.063	0.004	NS
soil water versus aliens	39	0.124	0.015	NS
soil density versus distance	39	-0.090	0.008	NS
soil density versus aliens	39	0.136	0.018	NS

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

Table 2.8: Regression results for soil physical characteristics, PCWE.

Regression pair	**N**	**r**	$\mathbf{r^2}$	**p**
Litter versus distance	39	0.611	0.373	***
Litter versus aliens	39	-0.488	0.238	***
stones versus distance	39	-0.740	0.548	***
stones versus aliens	39	0.042	0.002	**
animal disturbance versus distance	39	0.410	0.168	*
animal disturbance versus aliens	39	-0.270	0.073	NS
bare ground versus distance	39	-0.530	0.281	***
bare ground versus aliens	39	-0.216	0.047	NS
cryptogram cover versus distance	39	-0.150	0.023	NS
cryptogram cover versus aliens	39	0.103	0.011	NS
soil water versus distance	39	0.340	0.116	*
soil water versus aliens	39	-0.061	0.004	NS
soil density versus distance	39	-0.463	0.214	**
soil density versus aliens	39	0.470	0.221	**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

Table 2.9: Regression results for soil physical characteristics**,** MWE.

Regression pair	**N**	**r**	$\mathbf{r^2}$	**p**
Litter versus distance	39	0.041	0.002	NS
Litter versus aliens	39	0.344	0.118	*
stones versus distance	39	-0.375	0.141	*
stones versus aliens	39	-0.088	0.008	NS
animal disturbance versus distance	39	0.404	0.163	*
animal disturbance versus aliens	39	-0.166	0.028	NS
bare ground versus distance	39	-0.285	0.081	NS
bare ground versus aliens	39	-0.206	0.043	NS
cryptogram cover versus distance	39	0.008	0.000	NS
cryptogram cover versus aliens	39	-0.070	0.005	NS
soil water versus distance	39	0.000	0.000	NS
soil water versus aliens	39	0.060	0.004	NS
soil density versus distance	39	-0.400	0.160	*
soil density versus aliens	39	0.167	0.028	NS

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. NS=$p \geq 0.05$.

2.6.4 Soil penetrability

Open ground was significantly less penetrable than animal disturbed, grass and vegetation areas, $p< 0.001$ (Figure 2.4). The cover variables animal disturbed, alien grass and natural vegetation had means that were not significantly different (a) whereas open ground had a significantly different mean to all three of the other cover variables.

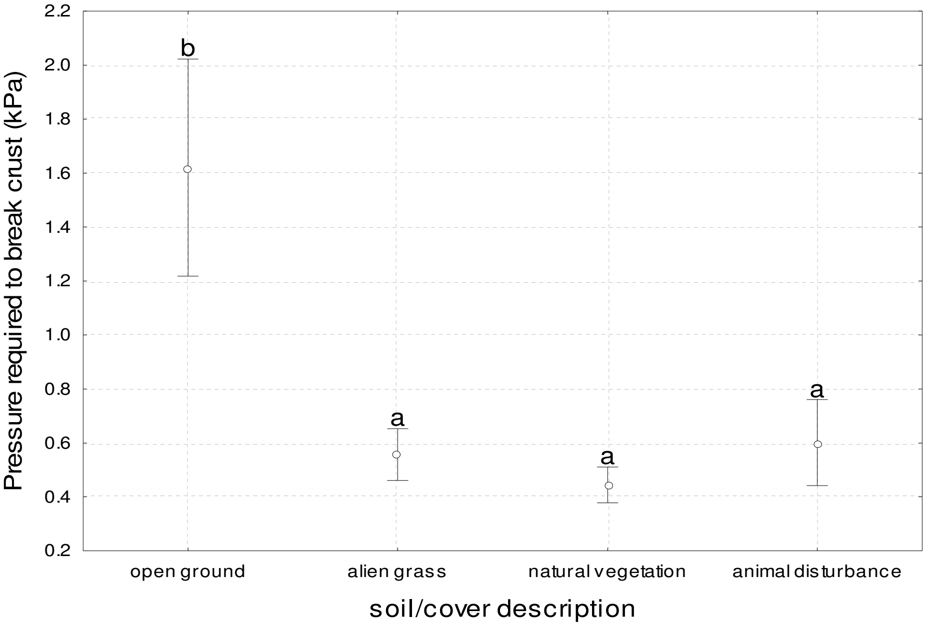

Figure 2.4: Soil penetrability under four cover variables in renosterveld landscapes.

2.6.5 PCA analysis of all variables

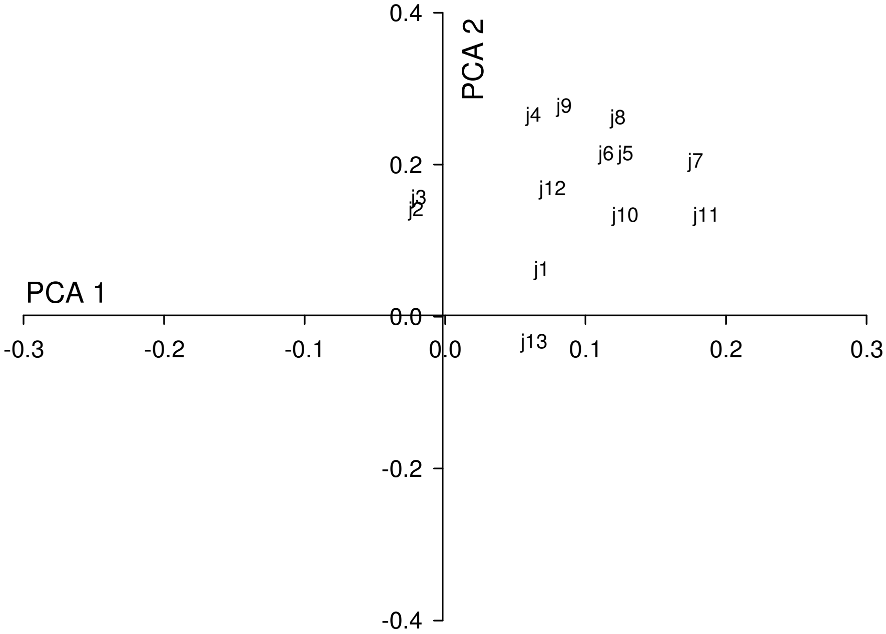

Figure 2.5: PCA ordination of JBR site on the basis of the environmental, physical and chemical variables with distance from the fence. The PCA axis 1 and 2 accounted for 52 and 13 % variation respectively.

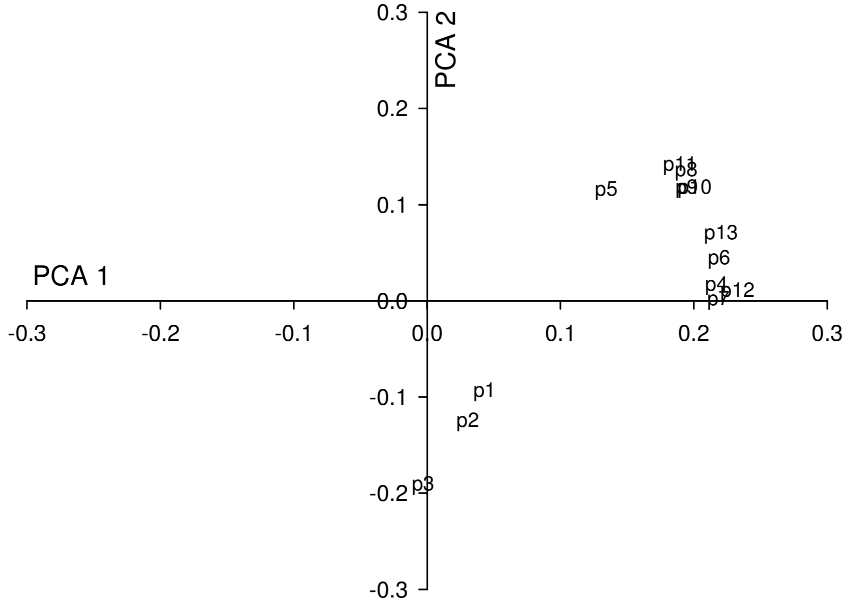

Figure 2.6: PCA ordination of PCWE site on the basis of the environmental, physical and chemical variables with distance from the fence. The PCA axis 1 and 2 accounted for 33 and 20 variation respectively.

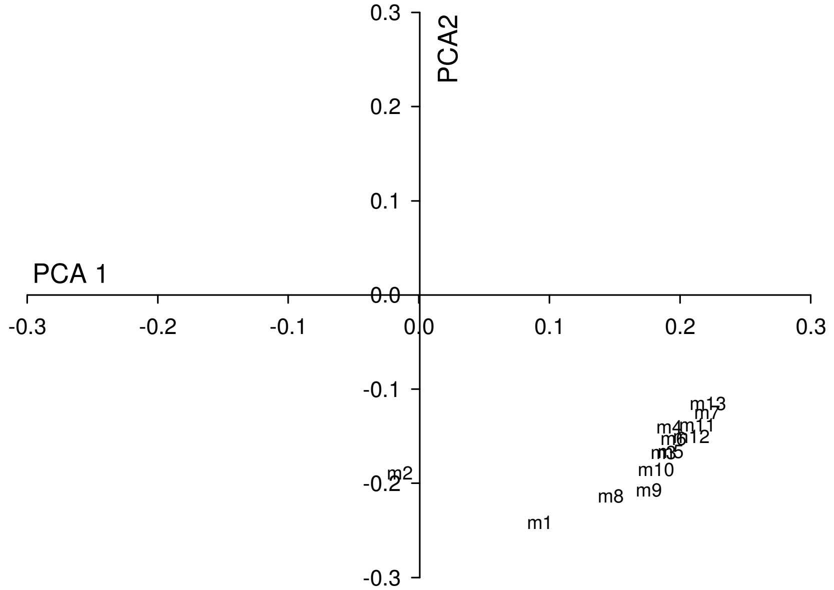

Figure 2.7: PCA ordination of MWE site on the basis of the environmental, physical and chemical variables with distance from the fence. The PCA axis 1 and 2 accounted for 69 and 5 variation respectively.

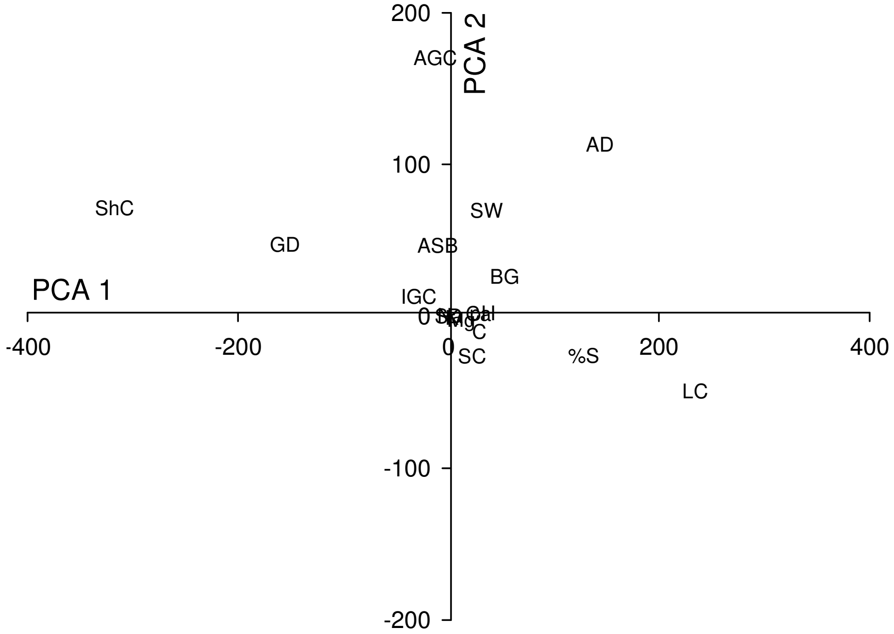

Figure 2.8: PCA ordination of environmental, physical and chemical variables with distance from the fence. The PCA axis 1 and 2 accounted for 42 and 11 variation respectively.

PCA analysis revealed that for JBR the first quadrate was distinctly different from the next two quadrates (fence line quads). All three quadrates were very different from the rest (figure 2.5). Animal disturbance lies in the same part of the PCA quadrant and is an important factor in defining this split. Figure 2.6 reveals that again the first two quadrates are quite separate from the remaining quadrates. Stone cover is an important factor for this area of the quadrant and these quadrates were in the vineyard and at the fence line where stones were a major feature (figure 2.8). The first two quadrates of MWE are quite different from each other and the remainder of the quadrates (figure 2.7). Stone cover played a larger role in these quadrates than with the PCWE quadrates (figure 2.8). Refer to appendix 2.4 for correlation matrix.

2.7 Discussion

2.7.1 Vegetation

Annuals and alien grasses co-occurred significantly in Jan Briers Louw (JBR) and Paul Cluver (PCWE). Both groups are opportunistic pioneer species. They co-occurred close to the fence line where a synergy of factors created a favourable environment for growth and establishment. Perennial shrub cover increased into patches for all sites and had a negative relationship with alien grass cover, this could be linked to clearing on the boundary and shrub re-growth being limited by competition from alien invasive grasses. Grasses have proven to be significant competitors for perennial shrubs (D'Antonio and Vitousek 1992), significantly reducing regeneration of shrubs (Hobbs and Atkins 1991). The clearing of the first four meters between the fence and the natural vegetation in the PCWE and JBR reserves created a space where there was an abundance of light and moisture. These conditions are good for opportunistic species such as alien annual grasses. In a study to evaluate the effect of nitrogen, mowing and boundary width on patch diversity, perennial diversity was found to be greater where nutrient input and degree of disturbance was low, cuttings removed and the boundaries were wide (Schippers and Joenje 2002). This strategy could easily be applied to renosterveld patches as it is clear that there is an edge effect.

Further into the patch the shrubs are older and provide a significant cover of shade. It was also observed that they prevent rain from reaching the soil surface during light showers, thus reducing the frequency with which moisture reaches the soil surface. This creates a more stressful environment for germination and seedling development. Milbau *et al.* (2005) found a decrease in germination success of alien invasive grasses in relation to water, nutrient availability and temperature in gaps. Water proved to be more available where there was a lower above ground biomass. A strong positive relationship between light availability and growth of *Lolium perenne* was found (Milbau *et al.* 2005). This again concurs with the renosterveld study sites, as there was more light and space available closer to the fence due to clearing of the taller shrubs.

Perennial shrubs and indigenous grasses increased significantly into the JBR and Mulderbosch (MWE) patches, as the alien annual grasses and annual species had less of a competitive advantage further from the fence line (refer to chapter 4). This suggests a more favourable growing environment for these plants further away from the fence line. These plants would be in direct competition with the alien invasive grasses and are adapted to natural conditions of this environment. The direct competitive interactions are investigated in a controlled environment in chapter 4, where indigenous grasses seemed to be more successful than alien grasses in unfertilized soils. The added anthropogenic disturbance features give the alien invasive species a competitive advantage. There was a significant increase in species diversity with distance into the patch at the PCWE and MWE sites. This relationship was more pronounced in the case of JBR because the alien grasses were homogenous at the fence line. Geophyte abundance increased significantly with alien grass cover, however this relationship was driven by one species of geophyte. This site was the most heavily grazed and only the most resilient geophyte species persisted such as *Spiloxene aquatica, Romulea tabularis* and several *Oxalis* species.

2.7.2 Soil nutrients

Nitrogen runoff from agricultural practices and the movement of livestock from fields to natural vegetation in fragmented landscapes has facilitated alien grass invasion (Hobbs 2001). It was expected that at the fence line there would be higher concentrations of nutrients and these would promote the growth of alien invasive grasses. Increased nutrient levels have been found to increase growth rates of alien plants (Hester and Hobbs 1992, Kleijn 1996, Kleijn and Snoeijing 1997, Lake and Leishman 2004, Thomson and Leishman 2005). Increased nitrogen levels either through nitrogen fixing plants or fertilizers have proven to increase growth and abundance of annual grasses, thus allowing them to out-compete perennial species (Paschke *et al.* 2000, Yelenik *et al.* 2004).

Nutrients varied in the landscapes of the study sites. This was anticipated considering that every crop has very specific requirements for maximum productivity. Also, each site has its own suite of environmental characteristics. There are many soil characteristics that influence the availability of micronutrients in the soil. These include soil type, texture, organic matter content, oxides and moisture (Shuman 1998). Soil chemistry was highly variable between the sites. This variability can be attributed to the crops specific to the adjacent farmlands and furthermore the specific nutrient requirements of the soils. Farmers regularly test soils and fertilize according to recommendations for the highest productivity of the crop. Irrigation regimes are also dependent on the crop requirements. Watering often commences prior to natural winter rainfall regimes. Unnaturally timed water additions in conjunction with temperatures are warmer, favour opportunistic species such as annual alien invasive grasses.

Across all the sites there was a significant decrease in pH. At JBR, pH was quite consistently <6, a pH where nutrients are less available to plants (Bandel *et al.* 2002). The pH was higher in the pasture or fields than in the reserve, probably because of addition of agricultural lime. Walton (2006) found this to be the case for old fields at Elandsberg near Wellington. Soil pH was also higher on a heuweltjies where it ranged from 5.8 to 6.1. Heuweltjies closer to the edges of fragments had a higher density of alien invasive grasses as a result of dispersal of the alien invasive seed bank. In the western Australian wheat belt many alien plants were found in pastures around the reserve, in a pattern similar to the edge effect observed in renosterveld. These edges were where the concentration of soil nitrogen was greatest (Hester and Hobbs 1992). This was attributed to fertilizer and stubble drift from adjacent pastures and /or an increase in plant litter. The seed bank only penetrates the fragment to a particular distance in some cases and is present on the heuweltjies where they have a competitive edge over indigenous species. It was on these heuweltjies that there was a high density of annual alien invasive grasses. At MWE and PCWE, pH decreased significantly down the slope from six outside the fence to four inside the fence in renosterveld patch. Microclimate effects were also evident, in PCWE the pH suddenly increased where a wash (small drainage line) intersected the transect. These washes concentrate nutrients and increase pH. Another example of raised pH was in JBR where pH was higher under thick litter areas. Nutrient availability is influenced strongly by soil pH and can in fact regulate the availability of nutrients. This is especially true for phosphorus, which is most available between pH 6.0 and 7.5. In general, the availability of nitrogen, potassium, calcium, and magnesium decreases rapidly below pH 6.0 and above pH 8.0 (Bandel *et al.* 2002).

The heuweltjies also provide ideal recruitment sites and enhanced nutrient status due to termite activity, as soils are disturbed through an increased frequency of trampling and digging (van Rooyen 2003). Animals have proven to be drivers of plant communities in USA tall grass prairies; such as badger (*Taxidea taxus*) gopher (*Geomys bursarius*) activity provides good seedling recruitment sites (Hobbs and Huenneke 1992). There are several animals in renosterveld that could perform this function e.g. *Orycteropus afer* (Aardvark), *Sus scrofa* (Feral pig), *Georychus capensis* (Mole rat) (Shiponeni 2002). van Rooyen (2003) has already found an association between animal activity and alien grass density in renosterveld.

Another study in the Hawkesbury Sandstone area (Australia) focused on the role that disturbance, plant attributes and herbivory play in alien plant success (Lake and Leishman 2004). All plant types except for the native non-invasive species were found to increase in biomass with higher nutrient soils. Alien species had higher survival rates at high nutrient sites. Sites without any disturbance had lowest alien invasive plant numbers. Physically disturbed sites on low fertility soils supported one alien species. This suggests that nutrient enrichment is important for alien invasion. Alien species cover was highest and native species richness lowest where nutrient enrichment was high. Non invasive and alien invasive species had lower levels of herbivory than native species. This lack of herbivory could easily explain invasion success. In physically disturbed sites of higher soil fertility alien species were small herbs or grasses. These patterns found by Lake and Leishman (2004), were observed in the data collected from this study.

Differences in plant attributes make some plant species better adapted to certain disturbance regimes than others. The most consistent difference was found between alien invasive and non-invasive alien was specific leaf area (SLA) - a larger SLA facilitated invasion (Lake and Leishman 2004). Species with a higher SLA have a shorter investment return rate and can grow faster (Lake and Leishman 2004). Alien species did not occur at sites that were not subject to nutrient enriched storm water runoff. Sites that were physically disturbed but had no nutrient runoff supported only one alien species. So for these nutrient poor environments nutrient enrichment is required for successful invasion to occur. Alien species suffered less from herbivory. Specific leaf area of alien invasive species was consistently higher than that of non alien invasives and natives.

Potassium (K) and alien grass cover were positively related at the PCWE site, potassium decreased into the patch. Potassium is a primary nutrient requirement for plants and it is often added as a fertilizer. Carbon had a significant slightly decreasing trend with alien grass cover. Carbon (C) and nitrogen (N) increased significantly into the PCWE patch and were significantly negatively related to alien grass cover. Nitrogen and carbon could be distributed the way they are because of history and the way they are distributed in the soil catina. They tend to concentrate further down-slope. A higher above ground biomass could also increase the carbon content of the soil. The higher proportion of shrub cover and scarcity of grasses would also mean that nutrients in the first 0.1 m of soil are not being cycled as much the topsoil closer to the fence. Nutrients are therefore remaining in the top 0.1 m of soil.

2.7.3 Soil physical characteristics

Animal disturbance increased into all three patches. This was possibly because the fence line was too exposed for them, because there was less shrub cover, or because the resources that they forage for were less abundant in fields. For example, foxes feed on indigenous fruit, scorpions, grasshopper, beetle larvae and lizards, and porcupines feed on roots and bulbs. The animals present in these patches were all indigenous species and therefore are less likely to utilize the edge of patches. Litter increased significantly into the JBR and PCWEpatches and this corresponded with an increase in shrub cover and decrease in annual alien grasses.

Increased litter was a result of increased shrub cover and the shrub cover has a larger influence over the success of the alien.

Stone cover and bare ground had significant increasing trends into the JBR, patch this could be the result of a higher percentage of alien grass cover. Stone cover, bare ground and soil density decreased significantly into the PCWE, these variables could be linked.

2.7.4 Penetrability of soil

Biological soil crusts inhibit annual grass establishment, while disturbances such as animal trampling and fire break these crusts facilitating the successful germination of alien invasive grasses (Wickow-Howard 2003). Where the soil crust had been destroyed by animal activity, grass cover or by vegetation the annual alien grasses had a better recruitment site. Small scale disturbance (animal diggings, trampling, browsing and termite mounds) have been found to correlate with alien grass establishment (Van Rooyen 2003). In this study it was observed that alien grasses were often colonising diggings and were prevalent on termite mounds, there was a stronger association between animal activity and alien grass cover where there was a high grazing intensity or a recent fire. Animals act as vectors for grass seeds and deposit these when they dig in the soil (Richardson *et al.* 2000). Many alien invasive grasses are adapted to disperse in this way with greater efficiency than indigenous grasses (Rouget *et al.* 2001). Browsers reduce canopy cover, increasing light availability and allowing more rain to reach the soils, nutrients are released from the soil through trampling and digging and hollows collect seed (Kotanen 1995). Increased grazing frequency or disturbance to the soil crust creates more colonization sites for alien invasive annual grasses.

2.8 Conclusions

There are a wide variety of natural and anthropogenic factors that play a role in facilitating the successful spread of alien invasive grasses. Alterations to vegetation and soil structure through animal activity of anthropogenic or natural origins provide recruitment sites for alien invasive grasses. The chemical alteration of the soils also favours alien invasive grass species that are capable of utilizing these resources more efficiently. Other factors that have proven to be important to invasion processes include past land use and current development, both of which have proven to be strongly correlated with alien invasion (Lundgren *et al.* 2004). Soil chemistry was unlikely to be a major facilitator in the invasion processes at the JBR. Litter, stone cover, animal disturbance and bare ground had significant increasing relationships into JBR; however these didn't correlate with grass cover. This was possibly because grasses were already covering the areas where the increased cover of these variables provided a more favourable growing environment. It was more likely that the invasion of these grasses was more strongly related to animal activity and seed bank distribution. PCWE had stronger evidence of the influence that soil chemistry has on the distribution with alien grasses and also had stronger patterns in relation to distance from actively fertilized fields. Fertilizers could be playing a more prominent role in invasion patterns of this area. The lack of significant results for the MWE site could be due to other features of the soils. The soils in this site were particularly rocky and there were large boulders creating an irregular surface. There were no significant relationships between soil chemical characteristics and alien grass distribution. This was explained by the short invasion front of this site. The alien grasses were only dense within the first two quads in these transects. They had not extended beyond this point yet because they have not been present for long enough or there was some other environmental feature preventing further invasion.

The majority of renosterveld patches that remain are there due to circumstances that make them non viable for agricultural use. These reasons could be anything from a substrate that is too rocky, such as the fragment at MWE, to a slope that is too steep for ploughing (for example on PCWE). The implications are that each site will often have a suite of influences and conditions that are specific to it. Although similar pressures may be exerted on these remnants the response of the alien invasive grasses and indigenous species varies, depending on the existing conditions and history of the patch. A buffer zone would be of benefit to all of these sites as an edge effect occurs at all of them be it physical, chemical, environmental r a combination.

2.9 References

Bandel, A.V., James, B.R., John J. and Meisinger, J.J. 2002. Basic Principles of Soil Fertility II: Soil Properties Department of Agronomy, University of Maryland at College Park http://www.agnr.umd.edu/MCE/Publications/Publication.cfm?ID=151 (accessed 12/07/06)

Bray, R.H. and Kurtz, L.T. 1945. Determination of total, organic and available forms of phosphorus in soils. *Soil Science.* 59. 39-45.

Chan, K.Y., Bowman, A. and Oates, A. 2001. Oxidizable organic carbon fractions and soil quality changes in an oxic Paleustalf under different pasture leys. *Soil Science.* 166. 61-67.

Crawley, M.J. 1987. What makes a community invisible? Colonization, succession and stability. (eds) A.J. Gray, M.J. Crawley and P.J. Edwards. Blackwell scientific publications, Oxford, UK. Pp. 429-453.

D'Antonio, C.M. and Vitousek, P..M. 1992. Biological invasion by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics*. 23. 63-87.

Hester, A.J. and Hobbs R.J. 1992. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science*. 3 (1). 101-108.

Hobbs, R.J. 2001. Synergisms among habitat fragmentation, livestock grazing and biotic invasions in Southwestern Australia. *Conservation Biology*. 15 (6). 1522-1528.

Hobbs, R.J. and Atkins, L. 1991. Interactions between annuals and woody perennials in a Western Australian wheatbelt reserve. *Journal of Vegetation Science*. 23. 2643-2654.

Kent, M. and Coker, P. 1992. *Vegetation description and analysis.* John Wiley & Sons, Ltd., New York.

King, S. A. and Buckney, R.T. 2001. Exotic plants in the soil-stored seed bank of urban bushland. *Australian Journal of Botany*. 49. 717-720.

Kleijn, D. 1996. The use of nutrient resources from arable fields by plants in field boundaries. *Journal of Applied Ecology.* 33. 1433-1440.

Kleijn, D. and Snoeijing, G. J. Ineke. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical changes caused by low levels of herbicides and fertilizers. *Journal of Applied Ecology*. 34. 1413-1425.

Koler, C.S. and Lodge, D.M. 2001. Progress in invasion biology predicting invaders. *Trends in Ecology and Evolution*. 16. 199-205.

Kotanen, P.M. 1995. Responses of vegetation to a changing regime of disturbance: Effects of feral pigs in a Californian coastal prairie. *Ecography*. 18 (2). 190-199.

Lake, J, C and Leishman, M. R. 2004 Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation.* 117. 215-226.

Low, A.B. & Rebelo, A.G. (Eds.). 1996. *Vegetation of South Africa, Lesotho and Swaziland.* A companion to the Vegetation Map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Lundgren, M.R., Small, C.J. and Dreyer, G.D. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of Southern New England, *NorthEastern Naturalist*. 11 (3).313-332.

Milbau, A., Nijs, I., de Raedemaecker, F., Reheul, F. and de Cauwer, B. 2005. Invasion in Grassland gaps: the role of neighbourhood richness, light availability and species complementarity during two successive years. *Functional Ecology*. 19. 27-37.

McAleece, N. 1997. *Biodiversity Pro.* Available from URL: http://www.sams.ac.uk/dml/projects/benthic/bdpro Assessed 25 December 2004.

SPSS (1997) SPSS Base7.5 Application Guide. SPSS, Chicago. 389.

Paschke, M.W., McLendon,T. and Redente, E.F. 2000. Nitrogen availability and old-field succession in a shortgrass steppe*. Ecosystems*. 3. 144-258.

Rhoades, J.D. 1982. Soluble salts. *In:* Page, A.L., Miller, R.H. and Kenney, D.R. (eds). *Methods of soil analysis. Part 2. Chemical and microbiological properties.* Soil science society of America, Madison, Wisconsin. Pp 167-180.

Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.I., Midgley, G.F., Milton, S.J., Powrie, L., Rutherford, M.C., Samways, M.J. and Schulze, R.E. 2000. Invasive alien organisms and global change: A South African perspective. Mooney, H.A and Hobbs, H.A.

(eds) *The impact of global change on alien species*. Island Press, Washington D.C. Pp. 303-349.

Rouget, M., Richardson, D.M., Milton. S.J. and Polakow, D. 2001. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. *Plant Ecology*. 152. 79-92.

Schippers, P. and Joenje, W. 2002. Modelling the effects of fertilizer, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agriculture, ecosystems and environment*. 93. 351-365.

Scougall, S.A., Majer, J.D. and Hobbs, R.J. 1993. Edge effects in grazed and ungrazed Western Australian wheatbelt remnants in relation to ecosystem reconstruction. *In*: Saunders, D.A., Hobbs, R.J. and Erlich, P.R. (eds). Nature Conservation 3: Reconstruction of fragmented systems. Surrey Beatty and Sons; North Chipping. Pp. 163-178.

Thomas, G.W. Exchangeable cations. 1982. *In*: Page, A.L., Miller, R.H. and Kenney, D.R. (eds) Methods of soil analysis. Part 2. Chemical and microbiological properties. Soil science society of America, Madison, Wisconsin. Pp.167-180.

Thomson, V.P. and Leishman, M.R. 2005. Post fire vegetation dynamics in nutrient enriched and non-enriched sclerophyll woodland. *Austral Ecology*. 230. 50-60.

Van Rooyen, S. 2003. *Factors affecting alien grass invasion into West Coast Renosterveld fragments*. M.Sc. thesis, University of Stellenbosch.

Walton, B.A. 2006. *Vegetation patterns and dynamics of renosterveld at Agter-Groenberg Conservancy, Western Cape, South Africa*. MSc. thesis University of Stellenbosch.

Wheater, C.P & Cook, P.A. 2000. *Using statistics to understand the environment.* Routledge Taylor & Francis group, London.

Wicklow-Howard, M., Serpe, M., Orm, J., Stokes, J. and Rosentreter, R. 2003. Effects of biological soil crusts on seed germination of *Bromus tectorum*. In: Allsopp, A.R. Palmer, S.J.Milton, K.P. Kirkman, G.I.H. Kerley, C.R. Hurt and C.J. Brown. N. (eds). Rangelands in the New Millenium. Proceedings 7th International Rangeland Congress. Document Transformation Technologies, Pretoria. Pp. 1276-1278.

Yelenik, S.G., Stock, W.D. and Richardson, D.M. 2004. Ecosystem impacts of invasive *Acacia saligna* in South African fynbos. *Restoration Ecology*. 12 (1). 44-51.

Chapter 3

Annual invasive grasses in renosterveld: Distribution of alien and indigenous grass cover and seed banks from agricultural boundaries into natural vegetation fragments

3.1 Abstract

Alien and indigenous grass seed banks were sampled along a gradient from agricultural fields into indigenous renosterveld patches. Fifteen indigenous grasses were encountered and thirteen alien grasses. *Avena fatua, Briza maxima, Briza minor, Cynodon dactylon, Poa Annua, Bromus diandrus* and *Lolium perenne* were found across all sites. Alien grass cover declined rapidly into the patch for all three sites. Indigenous grasses accounted for far less cover and did not vary much on either side of the fence line although in two of the sites the indigenous grass cover increased from the fence line into the natural vegetation fragment. Seed banks of alien grass species did not correlate with above ground cover of these species, and alien seed banks penetrated further into natural vegetation than the grass cover. Physical disturbance of natural vegetation is therefore likely to result in an increase in alien grass cover.

Keywords: fragment edges; invasion; microclimate.

3.2 Introduction

Alien annual grasses are elements in cape fynbos landscapes that, to the untrained eye, are not obvious ecological threats. However the potential damage that these species can cause gives reason for concern. At present, 12 % of southern African grass species are alien (Milton 2004). Successful invasion by a species depends on its own traits, the characteristics of the habitat it invades, and the interaction of these two. Traits common to invasive species include broad native range, good dispersal and short generation times (Milbau *et al.* 2005). The annual alien grass seed bank, including its distribution and relationship to above ground indigenous and invasive grasses, is the focus of this chapter. Seed bank features of a potential invasive are large seed crops and long seed production periods along with prolonged seed viability and good dispersal mechanisms (Milbau *et al.* 2005).

Establishing life history characteristics such as those associated with the alien invasive seed bank, provides a valuable background for intervention strategies and restoration efforts. A seed bank is defined by Allessio *et al.* (1989), as a collection of ungerminated seeds capable of replacing adult plants (annuals or perennials) that die through disturbance, disease or removal by animals or humans. Transient seed banks germinate within a year of dispersal, whereas persistent seed banks are capable of remaining viable in the soil for more than a year (Allessio *et al.* 1989). The persistent seed bank is an accumulation through time of genetic diversity, it allows the population to respond to a wide variety of environmental conditions and changes (Allessio *et al.* 1989).

Temporal variability-interrelationships between environmental fluctuations, seed production, dispersal, habitat quality and germination are responsible for temporal patterns. Some species lack any form of dormancy and if they do not germinate at the first opportunity, have little chance of survival. Species may disperse during periods unsuitable for germination and germinate once conditions are ideal. Most species have some form of dormancy at the time of dispersal although delays in germination can be risky.

Seasonality has a large influence on availability of germination sites. Germination timing usually relies on predictable, seasonal variation such as winter rain in Mediterranean climates (Thomas and Kelly 1989). Germination cues can be extrinsic or intrinsic at the ideal time for germination. The ability of populations to respond to cues (effectively habitat filters) determines the composition of the vegetation (Thomas and Kelly 1989). Between-year variation selects for persistent seed banks (Thomas and Kelly 1989). In fynbos and renosterveld environments this type of variation can be generated by fire. On the smaller scale habitat quality can vary and can result from animal digging, trampling or gap formation. Persistent seed banks cued to disturbance allow a population to disperse temporally to sites where resources are. Within a vegetation type soil conditions such as texture, pH or other physical conditions influence the development and size of the seed banks, just as predation and competition can select for persistence (Thomas and Kelly 1989).

Alien invasive grasses are a major threat to renosterveld due to a broad spectrum of physiological features. Alien invasive grasses are well suited to environments that are frequently disturbed by heavy grazing, fire and other anthropogenic influences such as agriculture and urbanization. Alien invasive grasses have a high surface to volume ratio and high dry biomass, grasses burn readily and recover from fires quickly (D'Antonio and Vitousek 1992). Heterogeneous environments are created and grasses are able to respond quickly and dominate nutrient rich conditions (Hobbs 1992). They quickly form a canopy and intercept light thus limiting the light available for slower growing species. Soil conditions are altered through changes to the boundary layer, the canopy and increased litter results in increased humidity and thus increased rates of remineralization (D'Antonio and Vitousek 1992). C_4 grasses are more efficient at nitrogen use than C_3 grasses and therefore, only in nitrogen enriched conditions, will the C_3 grasses be able to dominate (Richardson *et al.* 2000). When disturbance levels are high, grasses that allocate more energy to seed dispersal should be able to colonise faster than species that allocate more energy to root mass (Richardson *et al.* 2000). Renosterveld has its own fire regime governing a successional community. Nutrient and water addition from adjacent agricultural areas could potentially alter soil variables and growing conditions after fires. These conditions could be better suited to alien grasses rather than the indigenous post fire colonizers.

This study assesses the seed banks and above ground composition of alien and indigenous grass of three renosterveld fragment sites. Alien invasive grass distribution, density and germination across a gradient from agricultural and grazing fields into natural veld were hypothesized to have patterns corresponding to microclimate conditions. These patterns are further hypothesized to have a relationship with distance from the fence line that separates agricultural landuse from natural vegetation.

3.3 Study Sites

Study sites included Jan Briers Louw Geometric Tortoise Reserve, Paul Cluver Wine Estate and the Mulderbosch farm. Refer to Chapter 1 for further details on study sites. These sites had visible invasion fronts of alien annual grasses. Sites are not strictly renosterveld but matched according to slope and presence of adjacent field.

3.4 Methods

3.4.1 Fieldwork

Possible relationships between the distance from the agricultural fields and distribution of alien and indigenous grasses and seed bank changes were tested in the light of the proposed model.

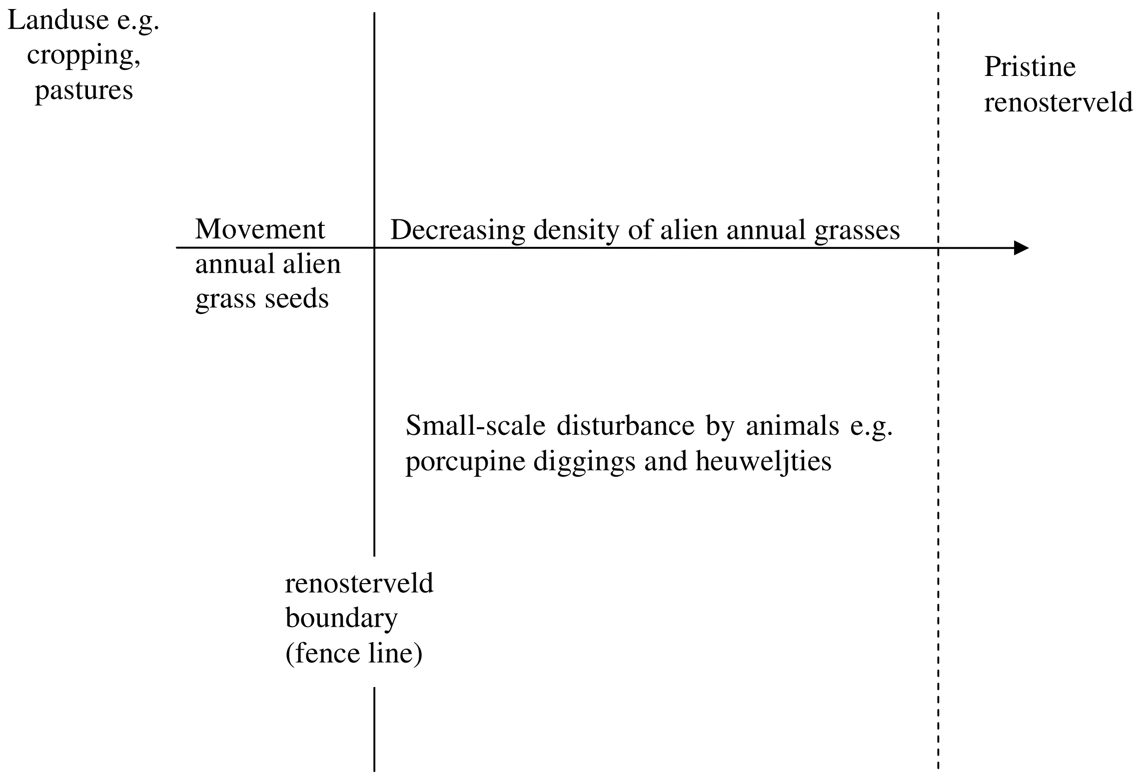

Figure 3.1: Hypothetical model of alien grass seed bank distribution in renosterveld fragment edges as influenced by adjacent agricultural inputs. Propagules from the adjacent agricultural field are moved via vectors such as wind or animals from the fields into the patches.

3.4.2 Seed bank sampling

The objective of this chapter was to determine the species present in each treatment seed bank, thus gaining insight into the regeneration potential and dispersal of the seed bank.

The seed banks were sampled after the first rains (15-22 May 2005) this meant sampling occurred with the first flush of grasses in winter 2005. The top 20 mm (or two centimetres) of soil were removed within a 160 mm by 270 mm quadrate at three points along the edge of the quadrate (refer fig. 3.2). Samples were dried and sieved through a 1 mm sieve. The samples were subsampled and placed in 160 mm x 270 mm trays with a standard depth of 20 mm. Trays were watered and kept moist in a greenhouse without temperature control. Trays were randomly rotated on a weekly basis. Once seedlings had emerged they were removed and identified to genus level at least. The number of individuals of each species within each sample was recorded.

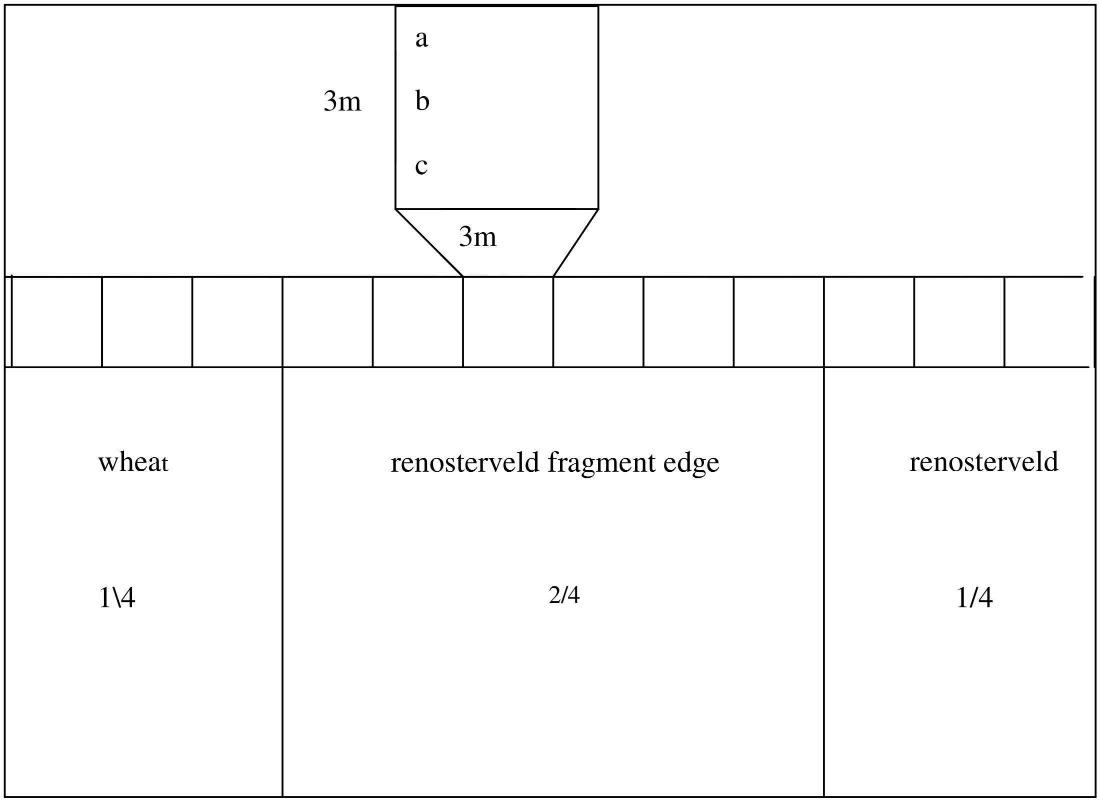

Figure 3.2: Transect design for sampling alien grass seed bank across a gradient from wheat farming through fragment edges into pristine renosterveld. Each quadrate was 3 m x 3 m. Within each quadrate a soil sample is taken for seed bank. Alien and indigenous grass cover was estimated as a proportion of total vegetation cover.

3.4.3 Analysis

Data were processed in Microsoft Excel. Data showed a normal distribution (Kent & Coker 1992, Wheater & Cook 2000). For each of the sites indigenous and alien species cover was averaged as a percentage of total vegetation in three divisions of the transects; quadrates 1-4 were near the fence line, quadrates 5-8 in a transition area and quadrates 9-13 were situated in renosterveld beyond the invasion front. Least squares regressions tested for significant correspondence between measured seed bank densities of indigenous and alien annuals against distances from the centers of renosterveld fragments. An analysis of variance tested the statistical significance of the regressions. One way analysis of variance tested variation in distance from the agriculture field edge inwards for the following: 1) percentage similarity between annual, alien, invasive grass seed bank and above ground cover; 2) number of annual, alien, invasive grass species in the seed bank and above ground cover.

3.5 Results

3.5.1 Alien and indigenous grass species

Alien grasses were clearly most dense on the fence line zone and decreased in cover for the transition zone and renosterveld zone (figure 3.3). Figure 3.3 also illustrates how indigenous grasses are consistently dense across the transects.

Fifteen indigenous grasses and thirteen alien species were encountered across the three study sites (Table 3.1). The indigenous grasses *Merxmuellera stricta, Melica racemosa, Ehrharta capensis, Ehrharta calycina, Helictotrichon turgidulum* were not found across all three sites. The remaining ten indigenous species were found across all the sites. Just over half of the alien species were found in all three sites. *Avena fatua, Briza maxima, Briza minor, Cynodon dactylon, Poa Annua, Bromus diandrus* and *Lolium perenne* were found at all three sites indicating how broad their range is, while *Agrostis stolonifera, Brachypodium distachyon, Bromus catharticus, Phalaris arundinacea* and *Vulpia muralis* were confined to only one site and *Bromus hordeaceus* was found at two sites. Of the thirteen alien species (Appendix 3.1) seven were annual species and four are perennial. Of the fifteen indigenous species (Appendix 3.2) only one species is an annual, *Ehrharta longiflora,* five species are of little economic value and the remaining eight hold some value to grazing.

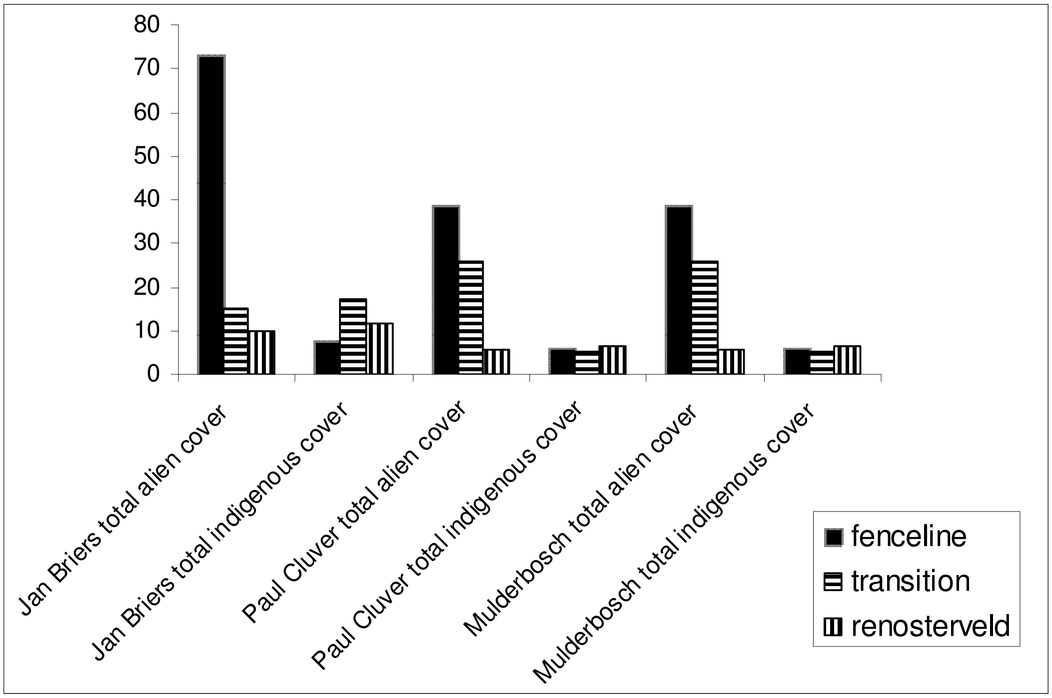

Figure 3.3 Distribution of alien and indigenous cover for each of the zones for all the sample sites.

Table 3.1: Indigenous and alien grass species located across study sites. X indicates presence.

Indigenous grass species	**Jan Briers Louw**	**Paul Cluver**	**Mulderbosch**
Melica racemosa Stapf.		x	
Ehrharta capensis Thunb.	x		x
Ehrharta calycina Sm.	x		x
Ehrharta longiflora Sm.	x	x	x
Ehrharta triandra Nees ex Trin.	x	x	x
Helictotrichon turgidulum Stapf.	x	x	
Koeleria capensis Steud Nees.	x	x	x
Pentaschistis curvifolia (Shred.)Stapf	x	x	x
Pentaschistis pallida (Thunb.)H.P. Linder	x	x	x
Merxmuellera stricta (Schrad.) Conert p	x	x	
Themeda triandra Forssk	x	x	x
Tribolium hispidum (Thunb.) Desv.	x	x	x
Tribolium uniolae (Lif) Renvoize	x	x	x
Alien grass species			
Agrostis stolonifera Roth		x	
Avena fatua L.	x	x	x
Brachypodium distachyon (L.) P.Beauv.	x		
Briza maxima L.	x	x	x
Briza minor L.	x	x	x
Bromus hordeaceus L.		x	x
Bromus diandrus Roth	x	x	x

Bromus catharticus Vahl	x		
Cynodon dactylon (L.) Pers.	x	x	x
Lolium perenne L.	x	x	x
Phalaris arundinacea L.		x	
Poa annua L.	x	x	x
Vulpia muralis (Kunth) Nees		x	

3.5.2 Distribution of alien and indigenous grass species

Jan Briers Louw Nature Reserve (JBR) had the highest alien grass cover of the three sites (Table 3.2). Alien grass cover was much higher near the fence line. The most dominant annual invasive near the fence line was *Bromus diandrus* (Table 3.2). *Cynodon dactylon* and *Lolium perenne,* both perennial grasses, were the most dominant alien grass species (Table 3.2). Indigenous grasses increased in cover into the patch and then decreased. More abundant species were the perennials *Helictotrichon turgidulum* and *Merxmuellera stricta* (Table 3.2). Paul Cluver (PCWE) and Mulderbosch (MWE) Wine Estates had comparatively lower densities of total grass cover. *Lolium perenne* was the most dominant perennial alien invasive at PCWE followed by *Phalaris arundinacea* near the fence line (Table 3.3). The most common annual alien species were *Vulpia muralis* and the *Briza* spp. At MWE, *Avena fatua* and the *Briza* spp. were the dominant annual alien invasive grass and *Lolium perenne* was the most abundant perennial grass (Table 3.4).

Indigenous grasses at PCWE were at consistently low densities throughout the patches (Table 3.3). *Merxmuellera stricta* and *Pentaschistis pallida* were the most abundant species. In JBR and MWE the indigenous grasses were at slightly lower densities near the fence line where the alien grasses are at the highest density (Table 3.2 and 3.4). The dominant indigenous grasses at MWE and JBR vary but were generally dominated by *Ehrharta spp.*

Table 3.2: Jan Briers Louw Geometric Tortoise reserve: Alien and indigenous grass species distribution and projected canopy cover (%) in three pooled groups quadrates 1-4 near the fence line, quadrates 5-8 a transition area, quadrates 9-13 renosterveld beyond invasion front.

Alien species	**quadrates 1-4**	**quadrates 5-8**	**quadrates 9-13**
Zone	**fence line**	**transition**	**renostervled**
Avena fatua	3.75	2.50	5.20
Brachypodium distachyon	0.00	3.03	2.00
Bromus diandrus	19.25	0.25	0.67
Bromus pectinatus	1.17	1.67	0.80
Cynodon dactylon	31.83	0.00	0.00
Lolium perenne	17.33	7.42	1.33
total alien cover	**73.33**	**14.86**	**10.00**
Indigenous species			
Ehrharta calycina	0.56	1.00	0.97
Ehrharta capensis	0.08	0.86	1.40
Ehrharta longiflora	0.00	0.83	0.32
Helictotrichon turgidulum	2.33	1.08	0.75
Koeleria capensis	0.00	0.42	4.47
Pentaschistis curvifolia	0.00	0.00	0.58
Pentaschistis pallida	0.00	0.17	0.42
Merxmuellera stricta	3.00	9.42	0.4
Themeda triandra	0.00	0.25	0.13
Tribolium obliterum	0.42	0.17	0.00
Tribolium hispidum	1.08	1.92	1.42
Tribolium uniolae	0.33	1.08	0.58
total indigenous cover	**7.81**	**17.19**	**11.43**
total percentage grass cover	**81.14**	**32.06**	**21.43**

Table 3.3: Paul Cluver Wine Estate. Alien and indigenous grass species distribution and cover in three pooled groups quadrate 1-4 near the fence line, quadrate 5-8 a transition area, quadrate 9-13 renosterveld beyond invasion front. Cover is a percentage of total surface area in each quadrate.

Alien grass species	**quadrate 1-4**	**quadrate 5-8**	**quadrate 9-13**
Zone	**fence line**	**transition**	**renosterveld**
Agrostis stolonifera	0.42	0.50	0.53
Briza maxima	3.42	2.75	0.73
Briza minor	1.33	3.33	2.80
Bromus hordeaceus	0.39	0.17	0.00
Bromus diandrus	1.33	0.08	0.00
Lolium perenne	16.08	2.17	0.07
Phalaris arundinacea	8.67	12.08	0.67
Poa annua	1.50	2.33	0.07
Vulpia muralis	5.44	2.5	0.93
total alien cover	**38.58**	**25.92**	**5.80**
Indigenous grass species			
Helictotrichon turgidulum	0.17	0.67	1.27
Melica racemosa	0.42	0.92	1.80
Pentaschistis pallida	0.08	2.25	1.13
Merxmuellera stricta	4.33	3.58	0.00
Tribolium hispidum	0.08	0.00	0.00
Tribolium uniolae	1.25	0.83	0.00
total indigenous cover	**5.83**	**5.00**	**6.62**
total percentage grass cover	**44.42**	**30.92**	**12.42**

Table 3.4: Mulderbosch: Alien and indigenous grass species distribution and cover in three pooled groups quadrate 1-4 near the fence line, quadrate 5-8 a transition area, quadrate 9-13 renosterveld beyond invasion front. Cover is a percentage of total surface area in each quadrate.

Alien grass species	**quadrate 1-4**	**quadrate 5-8**	**quadrate 9-13**
Zone	**fence line**	**transition**	**fence line**
Avena fatua	12.00	3.33	3.00
Briza major	5.33	1.75	0.80
Briza minor	5.00	0.00	0.60
Bromus diandrus	2.50	1.00	0.00
Lolium perenne	13.33	0.00	0.00
total alien cover	**38.17**	**6.08**	**4.40**
Indigenous grass species			
Ehrharta longiflora	3.00	0.00	1.50
Ehrharta calycina	1.13	4.00	1.83
Ehrharta capensis	0.50	2.13	0.80
Koeleria capensis	0.00	0.25	0.00
Pentaschistis curvifolia	0.00	0.00	1.10
Pentaschistis pallida	0.38	0.83	1.30
Merxmuellera stricta	0.50	2.25	0.40
Themeda triandra	0.00	1.00	0.00
Tribolium hispidum	0.00	1.42	1.40
Tribolium uniolae	0.00	0.50	0.40
total indigenous cover	**5.50**	**12.38**	**8.83**
total percentage grass cover	**43.67**	**18.46**	**13.23**

Alien grass cover decreased significantly with distance away from the fence line in JBR, r =-0.6, p=0.00004 (Figure 3.3). Alien grass cover decreased significantly with distance away from the fence line in PCWE, r=-0.67, p=0.000003 (Figure 3.4). Alien grass cover had a nearly significant decreasing trend in MWE, r=-0.32, p=0.0532 (Figure 3.5).

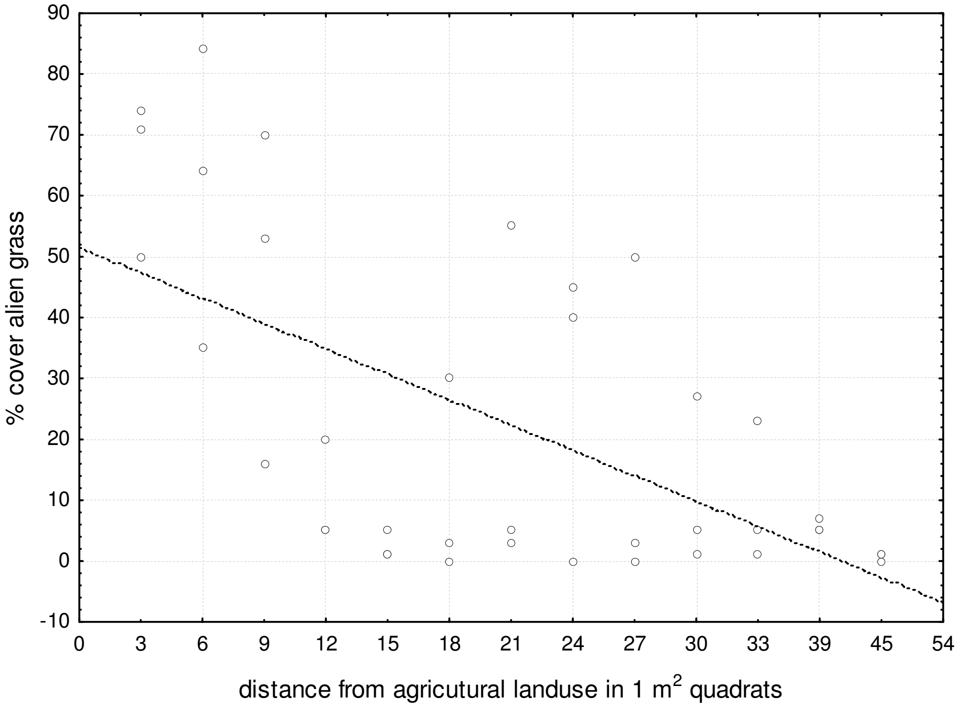

Figure 3.4: Jan Briers Louw Geometric Tortoise Reserve: Distribution (percentage of total area) of alien grass cover from the fence line into the vegetation patch.

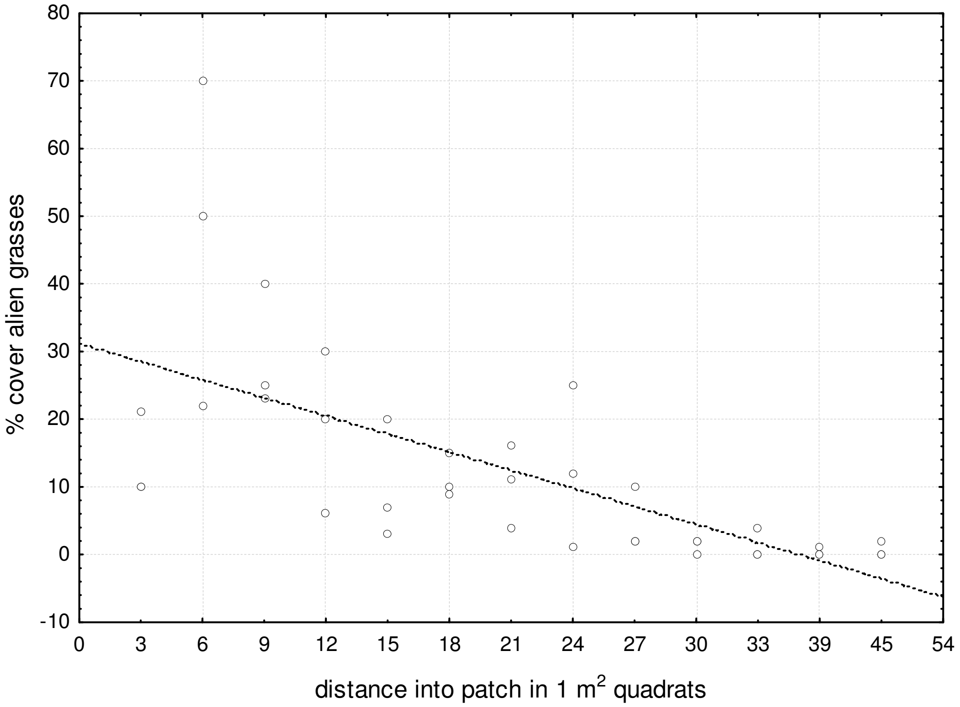

Figure 3.5: Paul Cluver Estate: Distribution (percentage of total area) of alien grass cover from the fence line into the vegetation patch.

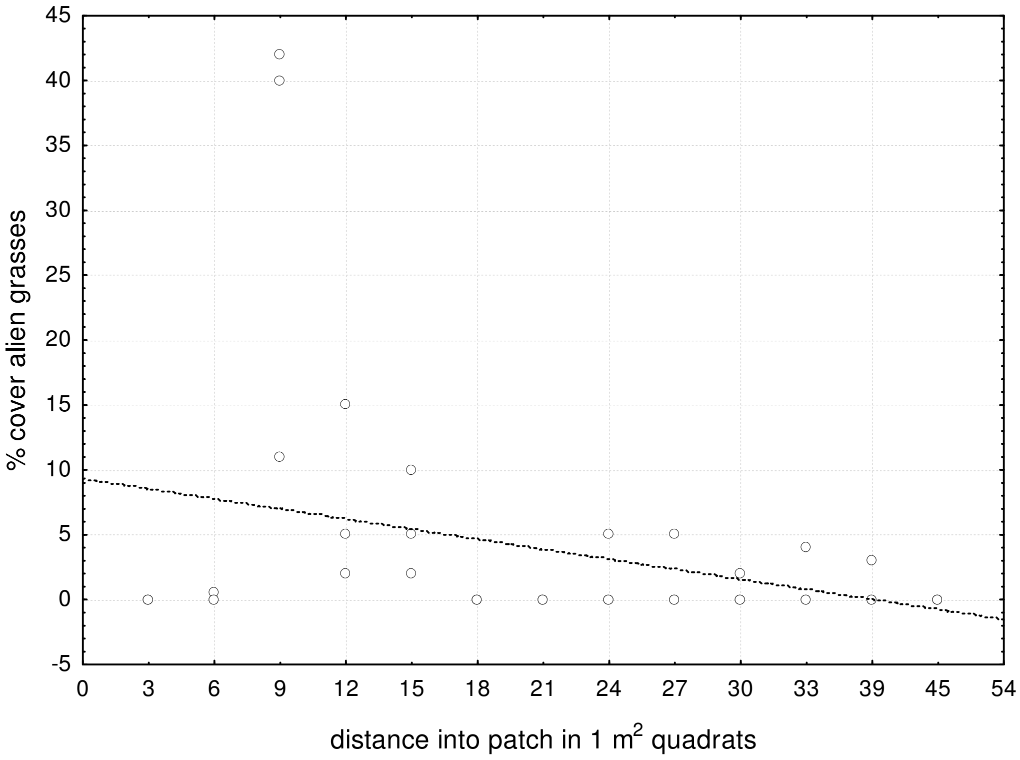

Figure 3.6: Mulderbosch: Distribution (percentage of total area) of alien grass cover from the fence line into the vegetation patch.

3.5.3 Distribution of alien grass seed bank

Annual alien invasive seed bank at PCWE significantly decreased from the fence line into the patch, unlike JBR and MWE (Table 3.5).

Seed bank density was the number of alien invasive grasses that emerged in each soil sample along the transects and was considered here to be an index of seed bank density for this group. There was no significant relationship between seed bank density and alien invasive cover at in JBR, r = 0.1749, p = 0.2870 (Figure1, Appendix 3.3). Points a and b are where there was a seed bank present but not evident in above ground biomass. The sample points were in an area where soils were compacted and open. If these points are removed r = 0.5669, p = 0.0003.

PCWE had a significant relationship between alien grass seed bank distribution and above ground cover r = 0.4103, p = 0.0095 (Figure 2, Appendix 3.3).

MWE did not have a significant relationship between seed bank distribution and above ground cover r = -0.0417, p = 0.8010. The invasion front at this site ended within six meters of the fence line, consequently statistical analysis does not yield significant results (Figure 3, Appendix 3.3).

Table 3.5: Relationship between distance from the fence line and density of the alien annual seed bank.

Statistic	r^2	r	p
Jan Briers Louw	0.0069	0.0829	0.6631
Mulderbosch	0.1579	-0.3973	0.1275
Paul Cluver	0.2438	-0.4937	0.0048

3.6 Discussion

This study assessed the alien and indigenous grass species composition of three sites. Alien invasive grass distribution, density and germination across a gradient from agricultural and grazing fields into natural veld were found to have patterns corresponding to different variables (for further detail refer chapter 2). The alien grasses can outcompete the indigenous grasses for space, nutrients, light and water once they have established in this band (Van Wyk and Oudtshoorn 1999). There was however variation on this result when sites were analyzed separately. Alien grass seed bank was only significantly related to above ground alien cover in one of the sites.

Both perennial and annual alien grasses were present across the range of sites. The annuals were predominately of European and Mediterranean origin. The perennial alien grasses were from Europe, Asia and northern Africa. The most common alien grasses were the same as those found to be widespread by Duvenhage (1993), *Avena fatua*, *Briza maxima*, *Briza minor*, and *Lolium perenne. Bromus pectinatus* was an exception and it was *Bromus diandrus* which was more common in this study. These species are originally from fire-adapted and grazed systems around the Mediterranean. They are often introduced as contaminants of crop seed and thereafter transported on the hair of animals or via their dung. Shiponeni (2003) proved that alien invasive grasses are effectively transported via animal dung in renosterveld environments. Other alien grass species found in wetter areas and near areas of nutrient enrichment include *Pennisetum clandestinum*, *P. setaceum* and *P. macruorum*. Europe and the Mediterranean are largely the source of naturalized alien grasses for southern Africa

(60%). The remaining species were from central and southern America, Africa, Asia, North America and Australasia (Milton 2004).

Annual grasses complete their life cycle within a year whereas perennials are long-lived and can survive burning and grazing (Milton 2004). Perennials are also capable of vegetative reproduction in addition to seeding. Annual grasses are adapted to quickly take advantage favourable conditions and disturbances. This could range from increased fire frequency, to heavier grazing pressure or alterations to soil nutrient content. All of these disturbances are features of the renosterveld environments. Annual seed banks can be stored in the landscape for approximately a year until a suitable combination of environmental variables allows them a competitive advantage (Dowling 1996). Many of the alien species are adapted for dispersal by animals and have barbed awns which attach to the pelts of animals. Animals can move from the agricultural fields where the seeds are present in the crops, to natural vegetation (Shmida and Ellner 1983). The annual grasses *Briza*, *Bromus*, *Lolium*, *Poa* and *Vulpia* are dispersed on herbivores pelts (epizoochorically), and *Briza*, *Lolium* and *Poa* through herbivore digestive systems (endozoochorically) in renosterveld systems (Shiponeni and Milton 2006).

Another major dispersal mechanism for grass species is wind. The landscape in which renosterveld is located is conducive to this being a more efficient vector allowing seed to spread further. Large tracts of land are ploughed up and barriers to movement of seed destroyed. Patches of vegetation that suffer from a high grazing intensity have an altered structure. This is often sparser and allows seed to travel further into patches. These alien annual grasses emerge from the seed bank where conditions favour them. The alien annual grasses are observable as an invasion front on the edges of remnant renosterveld patches. They are also common on heuweltjies. The heuweltjies are sites of increased animal activity through termite activity and animal digging/ foraging. This increase in physical disturbance combined with a concentration on nutrients creates favourable colonization sites for opportunistic species such as alien annual grasses.

3.6.1. Alien and Indigenous grass species

Indigenous grasses increased from the fence line into the patch at all sites. These plants would be in direct competition to the alien invasive grasses and are adapted to natural conditions of this environment. The added anthropogenic disturbance features give the alien invasive species a competitive advantage.

Lolium perenne featured strongly in the landscape. It is frequently observed on roadsides and on farms. Germination of invasive *Lolium perenne* has proven to be inversely related to biomass of surrounding vegetation (Milbau *et al.* 2005). This was also the case for the renosterveld sites in this study, and in general *Lolium perenne* occurred where there was less shrub cover. A decrease in germination success is possibly related to water and nutrient availability and temperature in gaps (Milbau *et al.* 2005). Again water would be more available where there is a lower above ground biomass. A strong positive relationship between light availability and growth of *Lolium perenne* was found (Milbau *et al.* 2005). This again concurs with the renosterveld study sites, there was more light available closer to the fence due to clearing of the taller shrubs. A higher above ground biomass could result in higher resource use below ground and therefore less available resources for invaders (Milbau *et al.* 2005). This could be true deeper into the patch where the nutrients are often of higher concentration and the above ground cover is far greater. Higher above ground biomass would increase competition for space and light.

3.6.2 Alien grass seed bank and above ground cover patterns

The distribution of the alien seed bank indicates the potential for invasion of alien annual grasses. The distance into the patch, to which the seed bank was located, is an indicator of how efficient dispersal was from the edge into the patch. Annual alien invasive seed bank and cover at PCWE decreased significantly with distance from the fence line, this would indicate that there was some barrier to dispersal decreasing the spread of propagules into the patch. Above ground cover and seed bank were significantly related for the PCWE. The decrease in propagule density could possibly explain the decrease in the above ground alien cover with distance into the patch. This was a site where there were the most disturbances by animal grazing and trampling. This higher degree of disturbance creates many sites that favour emergence of alien invasive grasses as they are able to utilize resources with greater efficiency than indigenous species.

This pattern is not as clearly evident with JBR and MWE, the seed bank was randomly distributed into these patches. Alien grass cover decreased with distance from the fence line, although not significantly. The relationship between seed bank and cover for MWE, was difficult to assess as the invasion front ended within six meters of the fence line. Thus there were not sufficient data points. The decrease in alien grass cover from the fence line was clearly visible but not statistically so.

At JBR, alien grass cover decreased significantly with distance away from the fence line, but was not correlated with seed bank density. The significant decrease in alien grass cover from the fence line into the patch suggests that there are features of the system near the fence line which promote germination of the alien grasses. Further into the patch where the seed bank was not significantly less there are significantly fewer alien invasive grasses. It appears that the first four meters into the reserve have been cleared at some point, this creates a space where there is a lot of light and moisture. These conditions stimulate germination and growth of opportunistic species such as alien annual grasses. Palatable alien grasses encourage a higher grazing intensity thus perpetuating the restriction of natural veld regeneration (Hobbs 2001, Holmgren *et al.* 2001). The alien grasses are highly dense in this region and are approximately a meter tall by the end of the growing season. A seasonality effect was observation with regards to the height of grasses and flowering times of indigenous annuals and geophytes. Alien grasses germinate and geophytes start growing at similar times, however by the time grasses are over a meter in height the geophytes have already flowered and set seed.

In Australian pastures a study was conducted to establish whether seed bank availability limits the distribution of seed bank limitation and the environmental conditions of the spread of the invasive species. The annual, alien invasive grasses used were *Heteropogon contortus* and *Pennisetum setaceum.* Treatments included two nutrient levels and two levels of disturbance. Greater seed production did not result in a greater abundance of alien grasses, few seeds were found. Most seeds were derived from the current year. The conclusion from this study was that recruitment by these grasses was more strongly influenced by water availability than by disturbance, nutrient and seed limitation (Goergen and Daehler 2002). These findings concur with some of the results found in this study.

The density and cover of alien grass species was found to be highest closer to urban edges in a study in northern Sydney, Australia. King and Buckney (2001) investigated the distribution of alien and native grass seed banks in relation to distance from urban edges and above ground vegetation cover. The seed bank did not reflect native or alien above ground cover. The results from this study indicate that invasive plants are restricted by suitable conditions. It was concluded that physical disturbance or nutrient enrichment would result in changes to the number of alien plants present in the vegetation, restricting them to suitable conditions. Thus even though alien species may be present in the seed bank, by preventing unnatural alterations to the environment the germination and success of these aliens can be avoided. In the renosterveld environment irrigation of land adjacent to renosterveld patches should be controlled and monitored in order to prevent moisture conditions more suited to the annual alien invasive grasses.

JBR had very little disturbance except on the heuweltjies where termite activity increases the nutrient levels and loosens the soils. This also encourages animals to forage there and they further disturb the soil creating microclimates for alien invasive species. The susceptibility of heuweltjies to annual alien grass invasion has been proven previously (Holmgren *et al.* 2001, Viellefosse 2001). Further into the patch the shrubs were old and provide a large cover of shade. It was also observed that they prevent rain from reaching the soil surface during light showers. Thus reducing the frequency with which moisture reaches the soil surface. Conditions are harsher and could prevent the alien annual grass seed bank from having a competitive edge over indigenous grass species. Indigenous grasses increased in cover into the patch and then decreased.

3.7 Conclusion

Results from this study indicated that there are a number of factors playing a role in the distribution of grasses within each site. Between site variation is great with different factors such as seed bank distribution, nutrient gradients and disturbance by animals playing a greater or lesser role in each. These patches need to be managed individually since there is such variability between them. A buffer zone for each would be of benefit by “soaking” up any edge effects.

3.8 References

Allessio Leck, M., Thomas Parker,V. and Simpson,R.L. (eds). 1989. Ecology of soil seed banks. Academic Press, London.

Chippindall, L.K.A. and Crook, A.O. 1976. 240 grasses of Southern Africa. Salisbury, Rhodesia.

D'Antonio, C.M. and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics*. 23. 63-87.

Dowling. I.M.1996. The ecology of *Vulpia. Plant Protection Quarterly*. 11. Supplement 1. 204-206.

Duvenhage, A.J. 1993. Die voorkoms van uitheemse kruidgewasse in die natuurlike plantegroei van die Stellenbosch omgewing. Unpublished M.Sc.Thesis, University of Stellenbosch.

Grabandt, K. 1985. Weeds of crops and gardens. CIBA-GEIGY (Pty) Limited. Johannesburg.

Goergen, E. and Daehler, C. 2002. Factors affecting seedling recruitment in an invasive grass (*Pennisetum setaceum*) and a native grass (*Heteropogon contortus*) in the Hawaiian islands. *Plant Ecology*. 161. 147-156.

Hobbs, R.J. 2001. Synergisms among habitat fragmentation, livestock grazing and biotic invasions in Southwestern Australia. *Conservation Biology*. 15(6). 1522-1528.

Hobbs, R.J. 1992. Disturbance, Diversity and Invasions; Implications for conservation. *Conservation Ecology*. 6 (3). 324.

Holmgren, M., Aviles, R., Sierralta, L., Segura, A.M. and Fuentes, E.R. 2000. Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients and fire. *Journal of arid environments*. 44 (2). 197-211.

King, S. A. and Buckney, R.T. 2001. Exotic plants in the soil-stored seed bank of urban bushland. *Australian Journal of Botany*. 49. 717-720.

Milbau, A., Nijs, I., de Raedemaecker, F., Reheul, F. and de Cauwer, B. 2005. Invasion in Grassland gaps: the role of neighbourhood richness, light availability and species complementarity during two successive years. Functional Ecology. 19. 27-37.

Milton, S, J. 2004. Grasses as invasive alien plants in South Africa. *South African Journal of Science*. 100. 69-75.

Thomas Parker, V. & Kelly, V.R. 1989. Seedbanks in California chaparral and other Mediterranean Climate shrublands. *Ecology of Soil Seedbanks.* (eds Allessio Leck, M., Thomas Parker, V. and Simpson, R.L.) Pp 347-384. Academic Press, Inc. San Diego, California.

Shiponeni, N.N. 2003. *Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa*. M.Sc. thesis, University of Stellenbosch.

Shiponeni, N.N. and Milton, S.J. 2006. Seed dispersal in the dung of large herbivores: implications for restoration of renosterveld shrubland old fields. *Biodiversity and Conservation*. 15. 3161-3175.

Van Oudtshoorn, F.1992. Guide to grasses of southern Africa. BRIZA publications Cc, Pretoria.

Van Wyk, E & Van Oudtshoorn, F. 1999. *Guide to grasses of Southern Africa*. Briza Publications, Pretoria.

Viellefosse, A. 2001. *The effects of nutrients on alien European grasses*. Unpublished BSc. (Hons) thesis, University of Stellenbosch.

Chapter 4

The role of nutrient enrichment in the competitive interaction between an annual invasive grass (*Avena fatua*) and herbaceous plants indigenous to South African renosterveld

4.1 Abstract

Nitrogen availability might play a role in successful invasion of indigenous Western Cape shrublands (renosterveld) by alien invasive annual grasses. To test the hypothesis that an increase in nitrogen would result in a greater increase in biomass for an alien annual grass than for various indigenous plant functional groups, *Avena fatua* was grown in competition with three indigenous species, an annual forb (*Dimorphotheca pluvialis*), a geophyte (*Oxalis purpurea*) and an indigenous perennial grass (*Tribolium uniolae*) at three levels of soil nitrogen. We found that the alien grass *Avena fatua* had significant increases in biomass when nitrogen was added, whereas the indigenous species did not. Alien grass competition significantly influenced performance of the annual and the indigenous grasses but did not affect the geophyte. Competitive interactions did not appear to be significantly affected by addition of nitrogen.

Keywords: greenhouse experiment; nitrogen; biomass.

4.2 Introduction

Many invasive species are colonisers adapted to take advantage of disturbed habitats (Hobbs and Huenneke 1992). Characterised by high population growth rates, short generation times, abundant seed production and highly effective seed dispersal (Rejmánek and Richardson 1996; Westman 1990) they are similar to early seral species. Annual invasive grasses in particular have evolved to produce large volumes of seed, and have rapid growth rates and fast germination times (Gustafson *et al.* 2004). Native species are similar to late seral species, able to persist at low nutrient levels and to out-compete alien species under these conditions (Wedin and Tilman 1990, Redente *et al.* 1992). Once these species have arrived they are often able to alter soils to further perpetuate themselves and to spread. In nutrient poor soils competition for nutrients is one of the more important mechanisms determining vegetation composition. Indigenous grasses and alien grasses have proven to respond differently to resources such as water, light and nitrogen (Naumburg and DeWauld 1999, Abbot and Roundy 2003, Brooks 2003). This can lead to competitive exclusion (Brooks 2003, Corbin and D'Antonio 2004). Alien invasive grasses can be expected to respond differently to indigenous grasses in the renosterveld environment when there is an increase in nutrients, water and light.

According to Tilman and Downing (1994) nutrient addition in large quantities could favour early successional species that are out-competed on less fertile soils by slower-growing perennials that use nutrients more efficiently. The primary macronutrients for plant growth are nitrogen (N), phosphorous (P) and potassium (K), and these are the most commonly added as fertilizers (Bandel *et al.* 2002). Increased nitrogen levels either through nitrogen fixing plants or fertilizers have proven to increase growth and abundance of annual grasses, thus allowing them to outcompete perennial species (Paschke *et al.* 2000, Yelenik *et al.* 2004).

Lower soil nitrogen usually results in a decreased plant biomass, this has been particularly noticeable in invasive species and early seral species (Huenneke *et al.* 1990, Redente *et al.* 1992). Invasive species and seral species have a high dependency on nitrogen while late seral species and native species have a low dependency. There have been opposing results for the effect of nitrogen in the biomass of grasses and forbs depending on the species growth strategy and whether it is a native species. Responses tend to differ in accordance with location and plant type. Native plant species that are adapted to low nitrogen environments have a lower biomass response with added nitrogen (Seastedt *et al.* 1991, Morgan 1994). Renosterveld species, such as perennial grasses, geophytes and annuals, especially those on the small patches that are not suitable for farming, can be expected to respond relatively slower than alien annual invasive grasses. The grasses will utilize added nitrogen more effectively. For example native forbs in serpentine grasslands reduced their biomass with an increase in nitrogen because of competition from alien grass species (Huenneke *et al.* 1990). Another study however in a native forb from a tall grass prairie increased in biomass with an increase in nitrogen (Seastedt *et al.* 1991).

Several studies have demonstrated that nutrients may play a role in the competitive interactions between native and alien species (Groves *et al.* 2003, Suding *et al.* 2004). In Australia native grasses proved to be less competitive when grown at increased nutrient levels than those introduced from Europe (Groves *et al*. 2003). Nutrient enrichment occurs across the landscape (carbon dioxide, phosphorous and nitrogen) and invasive species have responded more rapidly to this (Zavaleta 2006). Environmental eutrophication from farming processes could have a similar effect at a smaller scale. Clements (1983) suggested that alien plants are able to invade sandstone soils in the Northern Sydney region because of nutrient enrichment. Rapid dominance by an invasive species could indicate that it is able to take advantage of an alteration to resource levels. Increased nitrogen levels in regions where nitrogen was previously limiting may create different competitive dynamics favoring invasive species (Huennke *et al.* 1990, Sher and Hyatt 1999, Davis *et al.* 2000). Alien seeds beyond the nutrient enrichment gradient may be able to establish if nutrient levels increase or there is another form of disturbance that favors them.

The soils in the Cape Floristic Region of the Western Cape region of South Africa are generally nutrient poor. However fine-textured, shale-derived soils are slightly more fertile and support a shrubland type known as renosterveld (Cowling *et al.* 1986). Several forms of disturbance are present in the renosterveld environment. Natural disturbances include the activity of animals and fire while anthropogenic activities bring additional forms of disturbance such as grazing, altered fire regimes and crop production with associated ploughing, drift of fertilizers, pesticides and alien propagules. Depending on the environment a given type of disturbance can play a greater or lesser role in the community structure. By influencing soil nutrient and water variables, conditions for plant germination and growth are altered allowing different, better suited, or alien species to invade.

Alien annual grass species in renosterveld systems become invasive due to a synergy of interactions between the natural and anthropogenic disturbance characteristics of the community and the characteristics of the invading species (Mack *et al.* 2000, Lambrinos 2002, Shea and Chesson 2002, Ehrenfeld 2003). Nitrogen has been found to benefit alien annuals and potentially facilitates a decrease in native plant richness (Anderson and Inouye 2001). Available resources, environmental conditions and characteristics of the invader determine the strength of the impact that an alien plant can have (Mack *et al*. 2000, Shea and Chesson 2002).

The objective of this study was to gauge the role that nitrogen at different concentrations plays in the productivity of the alien annual grass *Avena fatua*. Secondly the objective was to gain insight into any competitive advantage this could give an alien invasive grass over an indigenous plant species.

4.3 Methods

4.3.1 Soil sample site: Jan Briers Louw Geometric Tortoise Reserve

The study of the responses and interactions of plant species when nitrogen was added to soils was carried out under controlled conditions in a greenhouse, using soils collected from renosterveld habitats. Since the intention was to test competitive dynamics of the invasive grass and native species in soil specific to the renosterveld environment, field soil was selected in order to retain the microbial activity found in the renosterveld soil habitats. Soil for a greenhouse experiment was sampled at the Jan Briers Louw Geometric Tortoise Reserve, located at 33 45’ 45” S and 18 50’ 07” E. The site is on a privately owned farm on the R312 southwest of Paarl. It comprises 28 ha of Lowland fynbos and renosterveld and is surrounded by old lands and ploughed fields some of which have been invaded by the leguminous Australian shrub *Acacia saligna.* Alien invasive grasses occur beneath these *Acacias*. There are areas that have not been burned or grazed in over 10 years along the fenceline of the reserve (Van Rooyen 2003). Heuweltjies are also found in the reserve. These nutrient rich mounds formed by termites are frequented by animals such as *Orycteropus afer* (Aardvark), *Sus scrofa* (Feral pig) and *Georychus capensis* (Mole rat) (Shiponeni 2002). Alien invasive grasses are present at a high density on heuweltjies. There are a range of small indigenous herbivores (hares, tortoises, small antelope, porcupine and other rodents) browsing the renosterveld in the reserve but at low intensity. The soils were sampled to a depth of 10 cm within a 25 x 16 cm surface area along the length of the transects for all sites described in chapters 2 and 3. The soils were sieved through a 1 mm sieve to remove as many seeds of non-target species as possible.

4.3.2 Greenhouse experiment

A “pot” experiment tested competitive relationships between an alien invasive grass species and an indigenous grass, geophyte and annual forb species under three levels of nitrogen (N). The experiment was conducted in a greenhouse from 25 July 2007 to 15 September 2007 and temperatures ranged from 15º C to 25º C. The alien grass used was *Avena fatua*, originally from the Mediterranean and/or Eurasia. This species is highly competitive, producing large numbers of seed that have a staggered germination (Grabandt 1985). It is common in disturbed areas such as gardens and roadsides (van Oudtshoorn 1999) and is a weed in irrigated cultivated landscapes. It is commonly found in damp areas and sandy soils (van Oudtshoorn 1999). The geophyte, *Oxalis purpurea*, is a bulbous perennial with short rhizomes leading to its bulbs and is capable of vegetative reproduction. It is stemless, with compound leaves borne in basal rosettes at ground level, and is widespread from Namaqualand to Caledon. *Tribolium uniolae* is an annual or perennial grass, and is common to winter rainfall areas such as the karoo and fynbos biomes (Watson and Dallwitz 1992). The annual forb, *Dimorphotheca pluvialis,* is a daisy common in the Namaqualand region of the Western Cape. Seeds of *A. fatua*, *T. uniolae* and *O. purpurea* were collected from the Stellenbosch area. *D. pluvialis* seed was purchased from a nursery. Each indigenous species was grown alone and in combination with ten *Avena fatua* plants under no, low and high nitrogen levels. *Avena fatua* was also grown alone at a density of 10 individuals under each nutrient condition. Each treatment was replicated seven times.

Nitrogen was added in the form of limestone ammonium nitrate (LAN) and nutrient levels were set at control (no N addition), low N (0.1 g per pot) or high N (0.2 g per pot). These levels were determined according to accepted farming practices (Bennie Diedericks pers comm.[2]). Watering commenced on 22 July 2006 at three minutes of fine spray twice a day. As temperatures increased, watering was adjusted accordingly. Pots were arranged in a fully randomised experimental design. Once germination had begun nutrients were added (4 August 2006). Progress was monitored twice a week. Plant height, colour and leaf size and condition was noted. Plants were harvested from 15/09/06 to 20/09/06 once there were some indications of senescence. Roots and shoots were separated, and following washing and drying, fresh roots and shoots were weighed. Any treatments where there was a mortality of plants were excluded as mortality could not be conclusively explained by competitive interactions. Plant material was then oven dried at 70ºC for 48 hours and thereafter dry shoot and root mass was determined.

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4.4 Analysis

A 2-way ANOVA tested for the significant effects of competition (presence of *A.fatua*) and level of nitrogen supply on the growth of each indigenous species. Data were collected for above and below ground biomass both dry and fresh. Analyses considered the effect of nitrogen on alien grass biomass, the effect of nitrogen on indigenous biomass, the interaction of alien presence and nitrogen and the impact of alien competition on above ground versus below ground biomass. The weighted mass means were used for analysis of the individually grown plants as there were mortalities in these pots. Thus the means were based on different sample sizes. The number of observations was used when weighting the calculations, giving an unbiased estimate of the weighted population mean. The plants grown in competition did not suffer any mortality and could therefore the data did not need to be weighted.

4.5 Results

Dry mass results had the same patterns as fresh mass, thus for simplicity fresh mass results are presented while dry mass results are included in Appendix 4.1. Results for above and below ground mass of the alien and native species were used as a measure of competitive interactions under a range of conditions. Notes on the progress of the experiment are given in Appendix 4.2. F ratios for fresh and dry mass are included in appendix 4.3.

4.5.1 Responses of *Avena fatua* to nitrogen and competition

The alien annual grass *Avena fatua* significantly benefited from addition of nitrogen, responding both above and below ground. The fresh root mass increased from a weighted mean of 23.15 g (control) to 32.16 g (high nitrogen) (figure 4.1), F=17.26, $p<0.001$ and the shoot fresh mass from a weighted mean of 12.57 g to 19.74 g, F=36.31, $p<0.001$) (figure 4.2). The leaves of plants receiving nitrogen supplements were also a deeper shade of green, while the plants in lower nitrogen were more yellow (figure 4.3 A, B).

There was no significant competitive affect from the indigenous grass species on the root or shoot biomass of *Avena fatua* under the range of nitrogen concentrations (figures 4.3 C, 4.4 and 4.5). *Avena fatua* shoot mass is higher without competition but not significantly so.

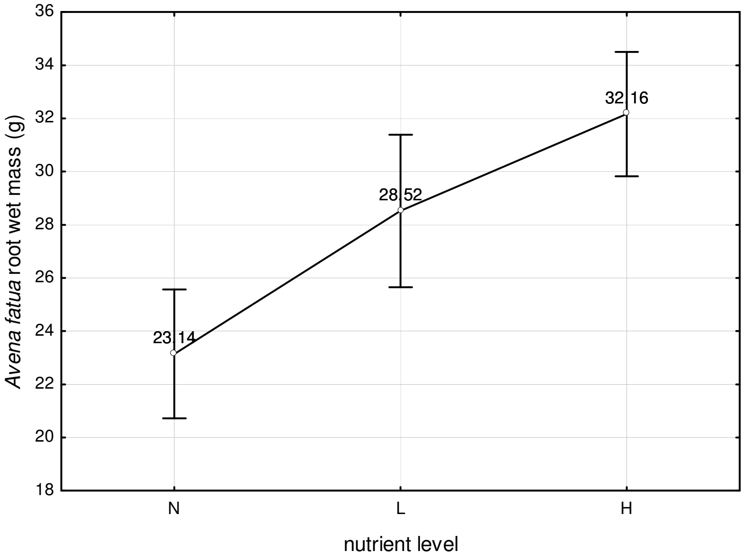


Figure 4.1: *Avena fatua* weighted mean root mass under three nutrient levels none (N), low (L) and high (H).

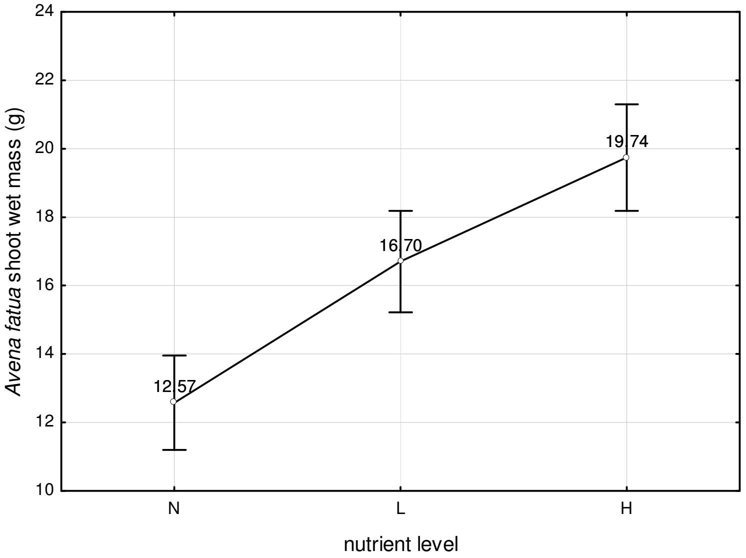


Figure 4.2: *Avena fatua* weighted mean shoot mass under three nutrient levels none (N), low (L) and high (H).

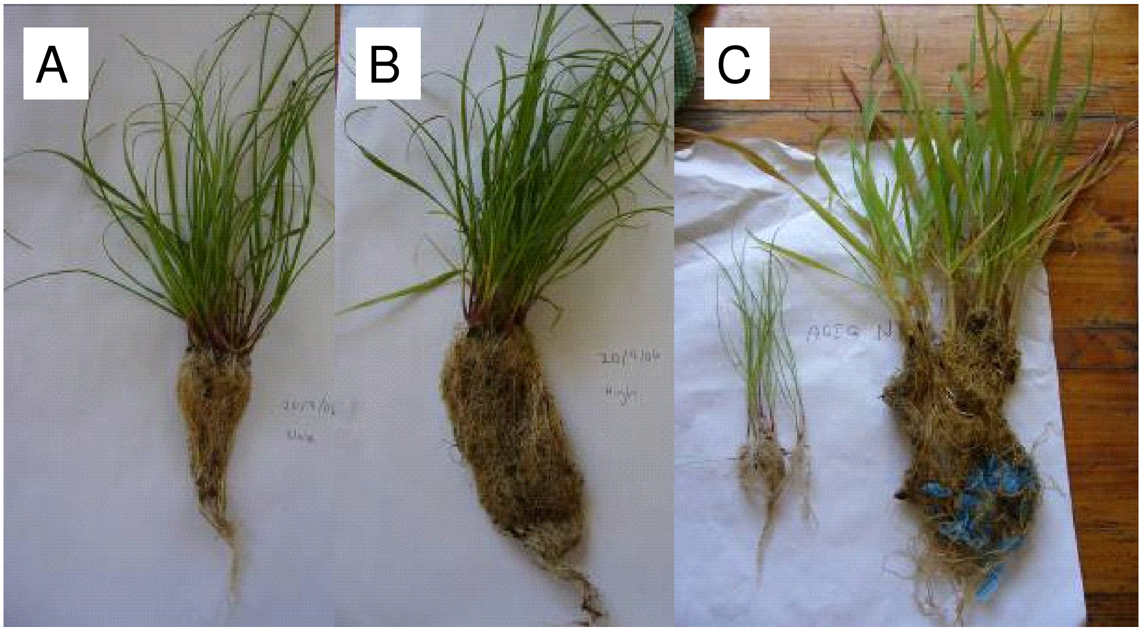


Figure 4.3: Response of *Avena fatua* to nitrogen and competition. (A). *Avena fatua* grown with no added nitrogen, (B). *Avena fatua* under high nitrogen conditions, (C). *Tribolium uniolae* (left) and *Avena fatua* (right) grown in competition with no nitrogen added.

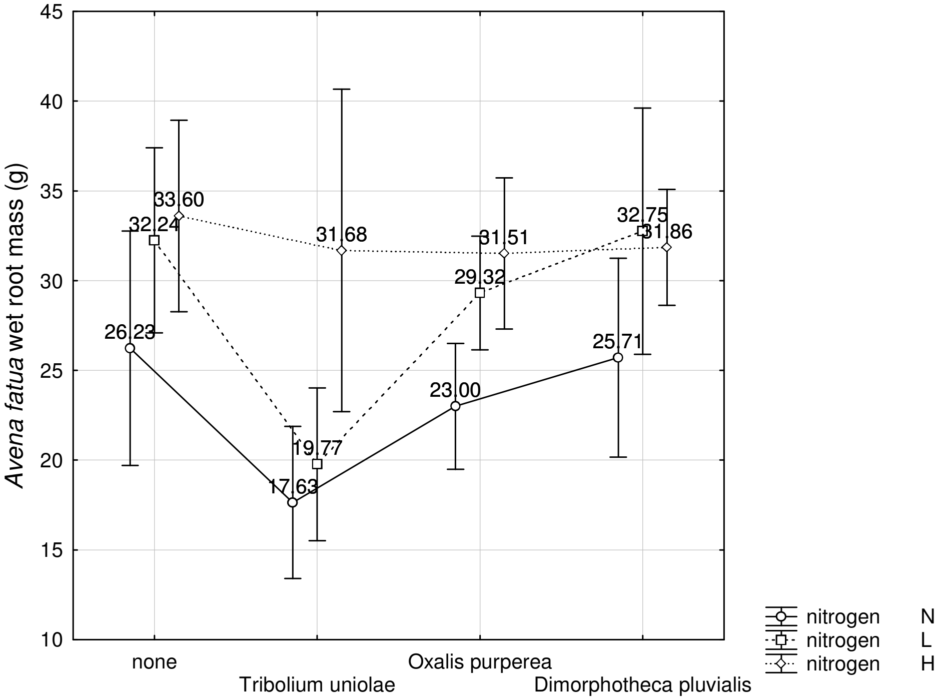


Figure 4.4: *Avena fatua* fresh root mass in competition with each of the indigenous species under no, low and high nitrogen conditions F=1.2, p=0.13.

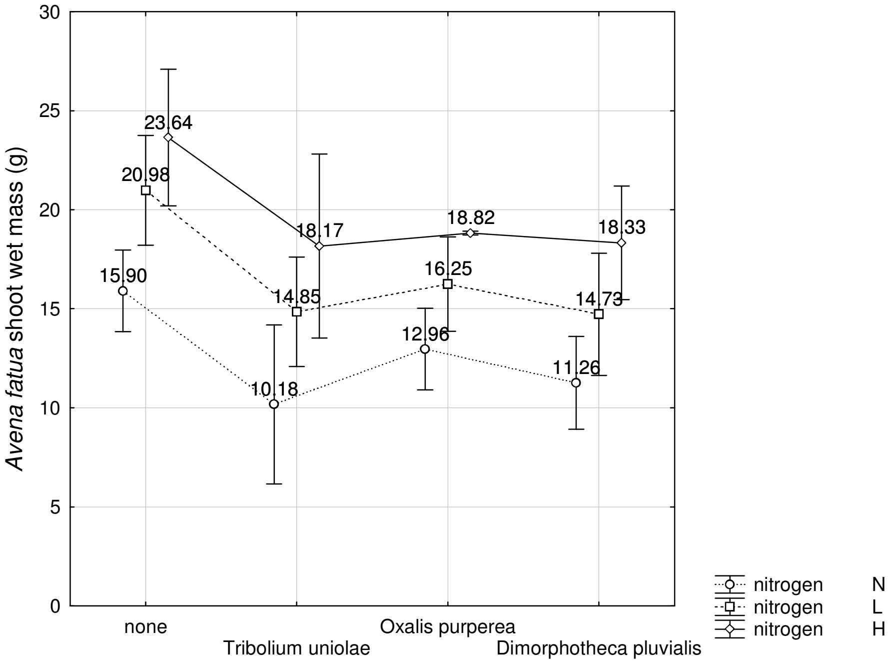


Figure 4.5: *Avena fatua* fresh shoot mass in competition with each of the indigenous species under no, low and high nitrogen conditions, F=0.27, p=0.98.

Table 4.1: ANOVA results for nutrient affect on indigenous plant species fresh mass *Dimorphotheca pluvialis*, *Oxalis purpurea* and *Tribolium uniolae*.

	Dimorphotheca pluvialis		*Oxalis purpurea*		*Tribolium uniolae*	
	F	p	F	P	F	p
fresh root mass	0.14	0.87	2.4	0.11	1.08	0.36
fresh shoot mass	0.6	0.56	0.6	0.33	0.66	0.53
Dry root mass	0.14	0.87	3.01	0.64	2.04	0.16
Dry shoot mass	1.04	0.37	1.18	0.34	1.17	0.33

Table 4.2 a and b: Means (unweighted) and standard deviation for the above and below ground fresh and dry mass of indigenous plant species and alien grasses grown in competition (comp) and alone. The three nitrogen levels are none (N), low (L) and high (H).

a) **Species**		*T. uniolae*		*T. uniolae*		*T. uniolae*		*O. purpurea*		*O. purpurea*		*O. purpurea*		*D. pluvialis*		*D. pluvialis*		*D. pluvialis.*	
	nitrogen level	N	N	L	L	H	H	N	N	L	L	H	H	N	N	L	L	H	H
	state	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	none
	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
Avena fatua **roots fresh mass**	**mean**	17.63	26.23	19.77	32.24	31.68	33.61	23	26.23	29.32	32.24	31.51	33.61	25.71	26.23	32.75	32.24	31.86	33.61
	std dev	4.58	7.06	4.6	5.57	9.72	5.77	3.79	7.06	3.42	5.57	4.55	5.77	5.99	7.06	7.42	5.57	3.48	5.77
Avena fatua **shoots fresh mass**	**mean**	10.18	15.9	14.85	20.98	18.17	23.64	12.96	15.9	16.25	20.98	18.82	23.64	11.26	15.9	14.73	20.98	18.33	23.64
	std dev	4.34	2.23	2.99	3	5.02	3.73	2.23	2.23	2.58	3	0.1	3.73	2.53	2.23	3.34	3	3.1	3.73
Avena fatua **roots dry mass**	**mean**	4.15	5.39	3.69	6.18	7.2	6.21	4.73	5.39	8.27	6.18	7.67	6.21	6.28	5.39	7.37	6.18	6.05	6.21
	std dev	1.43	1.86	0.69	0.98	2.4	1.29	1.39	1.86	1.85	0.98	1.76	1.29	1.41	1.86	2.04	0.98	1.5	1.29
Avena fatua **shoots dry mass**	**mean**	2.2	4.07	3.59	5.68	4.48	5.97	2.69	4.07	3.88	5.68	4.23	5.97	2.9	4.07	3.66	5.68	4.3	5.97
	std dev	0.54	0.58	0.76	1.06	1.29	0.75	0.56	0.58	0.42	1.06	0.28	0.75	0.5	0.58	0.74	1.06	0.76	0.75

b)	nitrogen level	N	N	L	L	H	H	N	N	L	L	H	H	N	N	L	L	H	H
	state	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	alone	comp	none
indigenous roots fresh mass	**mean**	0.03	2.21	0.25	3.1	0.29	3.68	0.2	0.17	0.09	0.29	0.17	0.41	0.03	1.78	0.04	2.11	0.11	1.73
	std dev	0.01	1.1	0.13	1.9	0.08	2.43	0.12	0.15	0.08	0.29	0.19	0.29	0.01	1.47	0.02	1.65	0.13	1.23
indigenous shoots fresh mass	**mean**	0.03	2.85	0.31	2.85	0.53	3.45	0.13	0.15	0.03	0.13	0.06	0.45	0.15	11.76	0.24	15.12	0.6	17.54
	std dev	0.01	0.8	0.11	1.18	0.2	1.36	0.06	0.14	0.03	0.19	0.11	0.92	0.06	10.52	0.15	8.77	0.37	10.23
indigenous roots dry mass	**mean**	0.12	0.37	0.04	0.77	0.06	0.74	0.08	0.06	0.04	0.08	0.08	0.15	0	0.31	0.01	0.35	0.02	0.29
	std dev	0.02	0.16	0.02	0.62	0.04	0.34	0.09	0.07	0.04	0.08	0.11	0.12	0	0.24	0	0.27	0.02	0.2
indigenous shoots dry mass	**mean**	0.17	0.68	0.07	0.62	0.17	0.79	0.01	0.02	0	0.02	0.01	0.06	0.02	1.4	0.04	1.9	0.07	2.25
	std dev	0.06	0.12	0.02	0.25	0.12	0.25	0.01	0.02	0	0.03	0.01	0.12	0.01	1.02	0.05	1.07	0.04	1.22

4.5.2 Responses of renosterveld plant species to nitrogen and competition

Addition of nitrogen did not yield any significant increases in mean fresh or dry mass of indigenous plant species (Table 4.1). The indigenous species did not utilize the increase in available nitrogen unlike the alien grass *Avena fatua*.

Dimorphotheca pluvialis had a higher standard deviation, both above and below ground, when grown without competition than when grown with competition from *Avena fatua*.

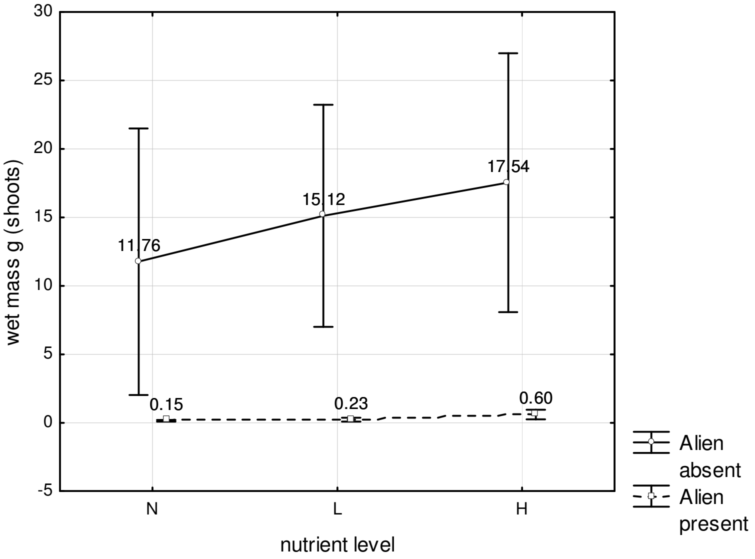


Figure 4.6: Unweighted mean shoot mass of *Dimorphotheca pluvialis* with aliens present and aliens absent under three nutrient levels (F=0.52, p=0.6).

The competitive affect of *A. fatua* on *D. pluvialis* was highly significant. Weighted root fresh mass (1.87 g to 0.06 g) and weighted shoot fresh mass (14.81 g to 0.33 g) of *D. pluvialis* was depressed (F=32.27 (roots) and 45.18 (shoots) p<0.005). Competition also seemed to decrease the variability in the mass of *D. pluvialis* (table 4.2). Nitrogen had no significant effect on *D. pluvialis* mass without competition (F=32.67, p=0.89) and variability of root and shoot mass was large. The combined effect of nutrients and competition was not significant (shoots: F=0.52, p=0.6 roots: F=0.18, p=0.89) (figure 4.6) although there was far less variance of the root and shoot mass under competition and increased nitrogen compared to those individuals with only competition or added nitrogen. Competition from *A. fatua* reduced the above ground biomass of *D. pluvialis* significantly more than it reduced the below ground biomass (F=43.24, p<0.001). The number of inflorescences produced by *D. pluvialis* was far greater without competition, and responded positively to nitrogen addition in the presence and absence of competition (Table 4.2).

Table 4.3: Reproductive output of *D. pluvialis* with and without competition from *Avena fatua* at three levels of nitrogen addition.

Nitrogen level	N	mean number of inflorescences with competition	N	mean number of inflorescences without competition
None	7	0.57	7	2.29
Low	7	0.71	7	6.6
High	7	1	7	8.29

Avena fatua depressed the fresh root mass of the geophytes significantly, reducing the weighted mean from 0.29 g to 0.15 g (F=5.21, p<0.05) and shoot mass from 0.15 g to 0.08 g (45.18, p<0.001). Variance was lower with competition from *A. fatua* than when *O. purpurea* was grown alone.

4.5.3 Responses of renosterveld plant species to nitrogen and competition

Nitrogen addition increased above ground weighted mass of *O. purpurea* from a mean of 0.15 g to 0.45 g (table 4.2). However there was high variability and this was not a significant result (F=0.7, p=0.5).

In combination with alien grass there was no significant combined effect on root or shoot mass of native species although again a trend indicating a possibility of it. Where there was no nitrogen added the masses of native species with and without competition were similar (root mass 0.2 g without competition and 0.17 g with (appendix 4), shoot mass 0.13 g with competition and 0.15 g without) and they diverged as the nitrogen level increased (mean root mass 0.11 g with competition and 1.73 g without (appendix 4), mean shoot mass 17.54 g without competition and 0.06 g with, figure 4.7). This divergence was not significant however because of high variability (F=0.61, p=0.55). There was a significant difference between the competitive effect on the above ground biomass and below ground biomass, the above ground biomass being more greatly affected, F=30.25, p<0.001.

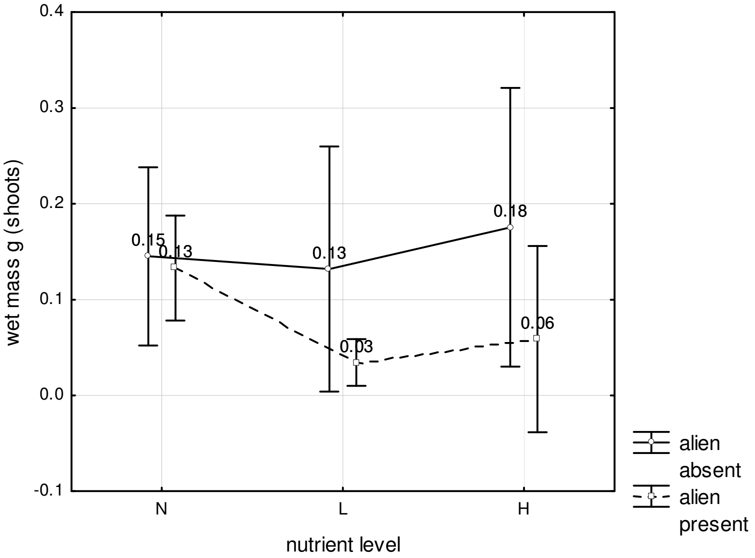


Figure 4.7: Unweighted mean shoot fresh mass of *Oxalis purpurea* with and without *Avena fatua* under three nutrient levels (F=0.7, p=0.5).

The competitive affect of the aliens on weighted mean root fresh mass of *Tribolium uniolae* was highly significant (F=46.29, p<0.001), and the variance in mass much lower than when *T. uniolae* was grown without *A. fatua*, with the mean dropping from 3 g to 0.19 g. Weighted mean fresh shoot mass of *T. uniolae* with and without *Avena fatua* dropped from 3.05 g with *A. fatua* to 0.29 g when *A. fatua* was not present (F=121.48, p<0.001). There was no significant effect on root fresh mass for the interaction of nutrients and alien grass (F=0.72, p=0.49, figure 4.8).

Where aliens were present there was a lot less variance and where they were absent the variance was far larger. There was a nearly significant result for the interactive effect of competition and nutrients for the shoots (F=2.81, p=0.073). The variance of the indigenous grass mass was quite large therefore this was not a clear result.

Shoot fresh mass of *T. uniolae* again showed a significant competition effect from a mean of 3.05 g to 0.29 g. The depressive effect on the shoots was highly significant (F=121.48, p<0.001). There was a slight trend for increased fresh mass (weighted mean from 1.44 g to 2 g) with additional nitrogen but high variance rendered this a non-significant result (F=1.76, p=0.19). The nutrient affect on dry shoot mass showed a trend but it was not a significant nutrient effect (F=2.6, p=0.09). The affect of competition on above and below ground biomass was not significantly different, F=0.27, p=0.6.

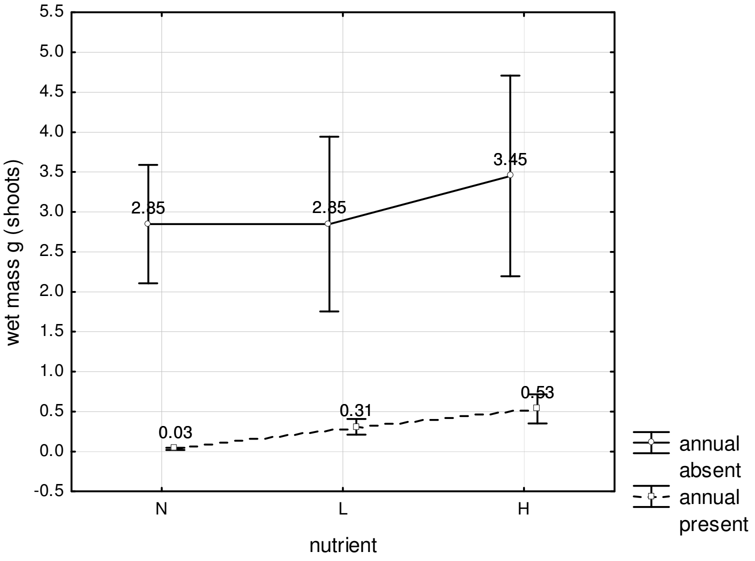


Figure 4.8: Unweighted mean shoot fresh mass of *Tribolium uniolae* with and without *Avena fatua* under three nutrient levels (F=0.72, p=0.49).

4.6 Discussion

This study aimed at gauging the role that nitrogen plays, in the competitive interactions, between the alien annual grass *Avena fatua* and each of three indigenous plant species, at different nitrogen concentrations. Results from our study supported a very clear, competitive effect of alien grasses on an indigenous grass and an indigenous annual. The biomasses of these two indigenous species were significantly depressed, however the geophytes did not respond in the same way. There was some evidence that competition by the alien plant was exacerbated by nitrogen.

Nutrient addition frequently results in the dominance of a few species and therefore decreases diversity (Tilman 1993, 1997). For example fertilization of Californian serpentine grassland reduced species richness and resulted in dominance of few alien species (Huenneke *et al.* 1990). When fynbos soils are enriched by fixation of nitrogen by the alien leguminous tree *Acacia saligna*, the nitrogen cycling regime is altered, alien weedy grass species increase and prevent post-revegetation of the natural fynbos following clearing of *A. saligna* (Yelenik *et al.* 2004).

In the Netherlands, fertilizing has resulted in a gradual loss of species particularly those of low stature (Kleijn and Snoeijing 1997). Many renosterveld geophyte, annual and grass species, such as those used in this study, are of low stature and are thus vulnerable to the same effects. *Avena fatua* is far taller than any of these and with its faster growth rate and earlier germination, it is able to outcompete these species for light and space.

A study in Australia (Groves *et al.* 2003) investigated seven grass species in monoculture and mixtures along a nutrient gradient. The species included native and alien perennials, as well as alien annual species. The native grasses performed poorly in the mixed stands under increased levels of nutrients. Australian native perennial grasses, were unable to compete with the introduced annual and perennial species under increased nitrogen and moisture conditions. In this experiment fresh and dry mass of the indigenous perennial grass *Tribolium uniolae* did not significantly increase with addition of nitrogen, although the trend was positive. There was no significant synergistic interaction of the nutrients and competition on above or below ground biomass, although there was a trend for this in the below ground biomass. *A. fatua* developed extensive root systems, increasing significantly in biomass with an increase in nitrogen. The decrease in the below ground biomass of the indigenous species might have been caused by below-ground competition for water and nutrients other than nitrogen, or by above-ground competition for light. A reduction in light availability causes a shift in biomass allocation from roots to shoots, with resulting etiolated shoots and stunted root development in plant species with high light requirements (e.g. Milton 1982). This concurs with the field study of Groves *et al.* (2003). Numerous other studies have concluded that, with high nitrogen availability, alien grasses are able to produce more biomass and outcompete native grasses that are adapted to low nutrient conditions (McGraw and Chapin 1989, Rice and Nagy 2000, Brooks 2003, Defalco *et al*. 2003).

A study in south-eastern Australia investigated whether increased N levels gave the alien perennial grass *Nasella trichotoma* a competitive advantage over native Australian grasses (Badgery *et al.* 2005). All four native grasses used were competitive with the alien at low nitrogen, but only one was competitive at high nitrogen levels. Similarly the indigenous *T. uniolae* was unable to compete at higher levels of nitrogen, although the competitive effect of *A. fatua* was significantly overwhelming with or without addition of nitrogen. Competition alone from *A. fatua* significantly depressed *T. uniolae* biomass above and below ground. *N. trichotoma* is able to accumulate biomass faster than the native species and thus able to utilize increased nutrient levels at a faster rate. *A. fatua* germinated a week prior to the indigenous grass and gained biomass at a much faster rate, thus agreeing with the findings of Badgery *et al.* (2005). *A. fatua* clearly benefits significantly from nutrient enrichment in renosterveld soils where the indigenous grass *T. uniolae* does not. Only at high densities were the native grasses able to be competitive with *Nasella trichotoma* at all nitrogen levels. The study in Australia concluded that high native perennial grass density or biomass is essential for native grasses to compete with *N. trichotoma*. Native renosterveld grasses do not increase in biomass as rapidly as annual alien invasives, thus they would be unable to outcompete alien grasses. It was observed that in the study sites they do not occur densely. A potential management strategy for these patches would be to sow high densities of indigenous grass seed.

A study in the United States of America tested the hypothesis that alien have higher growth rates than native grasses, where nitrogen and light availability are high in a greenhouse experiment (Hunter and Omi 2006). Nitrogen and light treatments and their interactions on dry weight proved to significantly benefit the alien grass. Native grass dry weight was consistently lower than dry weight of the other plants in all treatments except where no nitrogen was added. This again concurs with the results from this study, the native grasses are not as significantly benefited by addition of nitrogen.

Dimorphotheca pluvialis was significantly impacted by competition from *A. fatua*. The annual had a far lower above and below ground biomass in competition regardless of the nitrogen level. The competitive impact was far more profound than the nutrient effect. The presence alone of alien seed and no water stress, gives the alien annual grass a significant advantage. *Oxalis purpurea* below ground biomass was significantly affected by competition, both below and above ground. The decrease in variance with competition again indicates that competition plays a major role in the growth of geophytes. Increased nitrogen resulted in a trend for an increase in biomass without competition, the high variance in this result indicates that nitrogen is not a strong driver of the success of these plants. A study in a Mediterranean dwarf shrub community found that perennial and annual grasses, climbers, perennial forbs and geophytes did not respond significantly to addition of phosphorous or herbicide treatments (Henkin *et al.* 2006). The annual, *D .pluvialis* and geophyte *O. purpurea* were similarly non responsive to increased nitrogen. In another study grass *Deschampsia flexuosa* in the Netherlands has proven to be capable of outcompeting the shrubs *Calluna vulgaris*, *Erica tetralix* and.*Molinia caerulea* when nutrient availability has been increased (Aerts and Berendse 1988, Aerts *et al.* 1990)

Above ground biomass of *D. pluvialis* was more strongly influenced by nitrogen levels although still not significantly so. The higher variation in the biomass of *D. pluvialis* with nitrogen, indicates that there are other factors playing a role in determining the biomass of the plants. The significant reduction of biomass and variance when the alien grass is present indicates that it plays an overriding role. The number of inflorescences produced by the *D. pluvialis* plants nearly doubled from "no added nitrogen" to "high nitrogen with competition" while inflorescences increased nearly fourfold from "no nitrogen" to "high nitrogen without competition". *A. fatua* was clearly depressing reproductive output. Above ground biomass was affected by competition to a greater extent than below ground biomass.

In North–west Europe, dwarf-shrubs have been out competed by grasses and this has been attributed to nitrogen deposition (Britton *et al.* 2003). The interaction of the grass, *Deschampsia flexuosa* and the shrub *Calluna vulgaris* was examined. The pot experiment found that there were few significant effects of watering and nitrogen addition. The biomass of *C. vulgaris* was reduced when grown in competition with *D.*

flexuosa, while *D. flexuosa* was unaffected. There was no significant nitrogen effect on *C. vulgaris* with regard to biomass or percentage cover, there was however also no nitrogen effect for the alien grass. It was concluded that *D. flexuosa* is better able to take advantage of disturbance events and also that it accumulates biomass faster than *C. vulgaris* (Britton *et al.* 2003). This illustrates that in some environments fertilizing plays little or no role in invasion. In the renosterveld environment it appears that different plant types are affected differently and this particular alien grass is capable of benefiting from fertilizing.

4.7 Conclusion

The boundaries between community types are rich sources of spatial heterogeneity, related to a wide variety of biotic and abiotic edge effects. Fragmentation of natural vegetation by cropland in the Western Cape makes understanding their ecological function vital to management of fragments and corridors for species conservation. In order to understand these boundary functions, we need to know how environmental factors and vegetation vary under human influence and across multiple scales. This study examines the effect that fertilizing of agricultural fields has on performance of alien and indigenous plant species in adjacent fragments of natural vegetation. The large variance in performance of all three indigenous species when grown alone indicates that there is no consistent response to an increase in available nitrogen. They are not well adapted to nitrogen-enriched soils whereas *Avena fatua* is and this is reflected in the significant biomass response to nitrogen. Although the interactive effect of increased nitrogen and competition was not significantly affecting the biomass of the indigenous species, the advantage that nitrogen affords the alien grass is enough to detrimentally reduce growth of the indigenous plants. Competition of the alien grass for moisture and light could be playing a more important role in the growth and reproduction of the indigenous plant than the direct effect of nitrogen addition.

The management implications of the study are that *Avena fatua* can potentially out-compete indigenous plants where it receives sufficient water, even in the absence of nitrogen supplementation. Access of alien grasses to water can be limited by maintaining the indigenous vegetation cover. Use of herbicides and grazing animals around and in renosterveld fragments should therefore be avoided. It is also possible that the competitive effect of *A. fatua* and other alien invasive annual grasses could be reduced by better control of fertilizer on adjacent fields. This could be done by reducing fertilizer drift during application, and by diverting nitrogen-laden runoff water.

4.8 References

Abbot, L.B. and Roundy, B.A. 2003. Available water influences field germination and recruitment and recruitment of seeded grasses. *Journal of Range Management.* 56. 56-64.

Aerts, R. and Berendse, F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio.* 76. 63-69.

Aerts, R., Berendse, F., De Caluwe, H. and Schmidt, M. 1990. Competition in heathland along an experimental gradient of nutrient availability. *Oikos.* 57. 310-318.

Anderson, J.E. and Innouye, R.S. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs*. 71. 531-556.

Badgery, W.B., Kemp, D.R., Michalk, D.L. and King, W.M.C.G. 2005. Competition for nitrogen between Australian native grasses and the introduced weed *Nassella trichotoma*. *Annals of Botany*. 96. 799-809.

Bandel, A.V., James, B.R., John J. and Meisinger, J.J. 2002. Basic Principles of Soil Fertility II: Soil Properties Department of Agronomy, University of Maryland at College Park http://www.agnr.umd.edu/MCE/Publications/Publication.cfm?ID=151 (accessed 12/07/06).

Britton, A. and Marrs, R. Pakeman, R and Carey, P. 2003. The influence of soil-type, drought and nitrogen addition on interactions between *Cullana vulgaris* and *Deschampsia flexuosa*: implications for heathland regeneration. *Plant Ecology*. 166. 93-105.

Brooks, M.L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mohave Desert. *Journal of Applied Ecology*. 40. 344-353.

Clements, A. 1983. Suburban development and resultant changes in the vegetation of the bushland of the northern Sydney region. *Australian Journal of Ecology*. 8. 307-319.

Corbin, J. and C. M. D'Antonio. 2004. Effects of invasive species on soil nitrogen cycling: implications for restoration. *Weed technology*. 18. 1464-1467

Cowling, R.M., Pierce, S.M. and Moll, E.J. 1986. Conservation and utilization of South Coast Renosterveld, an endangered South African vegetation type. *Biological Conservation*. 37. 363-377.

Davies, M.A., Grime, J.P. and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology*. 88. 528-534.

Defalco, L.A., Bryla, V. Smith-Longozo and Nowak, R.S. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* susp. *rubens* (Poaceae) and two native species. *American Journal of Botany*. 90. 1045-1053.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6. 503-523.

Grabandt, K. 1985. Weeds of crops and gardens. CIBA-GEIGY (Pty) Limited. Johannesburg.

Groves, R.H., Austin, M.P. and Kaye, P.E. 2003. Competition between Australian native and introduced grasses along a nutrient gradient. *Austral Ecology*. 28. 491-498.

Henkin, Z., Sternberg, M., Seligman, N.G. and Noy-Meir, I. 2006. Species richness in relation to phosphorus and competition in a Mediterranean dwarf-shrub community. *Agriculture, Ecosystems and Environment*. 23. 277-283.

Hobbs, R.J and Huenneke, L.F. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology.* 6 (3). 324–337.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. and Vitousek, P.M. 1990. Effects of soil resources on plant invasion and community structure in a Californian serpentine grassland. *Ecology.* 7. 478-491.

Hunter, M.E. and Omi, P.N. 2006. Response of native and exotic grasses to increased soil nitrogen and recovery in a postfire environment. *Restoration Ecology*. 14(4). 587-594.

Kleijn, D. and Snoeijing, G. I. J. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical changes caused by low levels of herbicides and fertilizers. *Journal of Applied Ecology.* 34. 1413-1425.

Lambrinos, J.G. 2002. The variable invasive success of Cortaderia species in a complex landscape. *Ecology*. 83. 518-529.

Lonsdale W. M. 1999. Global patterns of plant invasions and the concept of invisibility. *Ecology.* 80. 1522-1536.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazazz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications.* 80. 1180-1186.

McGraw, J.B. and F.S. Chapin. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. Ecology. 70. 736-749.

Milton, S.J. 1982. Effects of shading on nursery grown *Acacia* seedlings. *South African Journal of Botany.* 48 (2). 245-272.

Morgan, J. P. 1994. Soil Impoverishment: A little-known technique holds potential for establishing prairie. *Restoration and Management Notes.* 12. 55-56.

Naumberg, E. DeWauld, L.E. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics and understory graminoid species presence and abundance. *Forest Ecology and Management.* 124. 205-215.

Paschke, M.W., McLendon, W.T. and Redente, E.F. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems.* 3. 144-158.

Redente, E.F., Friedlander, J.E. and McLendon, T. 1992. Response of early and late semiarid seral species to nitrogen and phosphorus gradients. *Plant and soil*. 140. 127-135.

Rejmánek, M. and Richardson, D.M**.** 1996. What attributes make some plant species more invasive? *Ecology.* 77. 1655-1661.

Rice, K.J. and Nagy, E.S. 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. *American Journal of Botany.* 87. 1699-1706.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia.* 87. 72-79

Shea, K and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution.* 1. 170-176.

Sher, A. A. and Hyatt, L. A. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biological Invasions* 1. 107-114.

Shiponeni, N.N. 2003. *Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa.* M.Sc. thesis, University of Stellenbosch.

Suding, K.N., LeJeune, K.D. and Seastedt, T.R. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia.* 141. 526-535.

Tilman, D. 1993. How productivity limits colonization and species richness in grasslands. *Ecology.* 74. 2179-2191.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in the grasslands. *Nature*. 367. 363-365.

Tilman, D. 1997. Community invisibility, recruitment limitation, and grassland biodiversity. *Ecology.* 78. 81-92.

Van Oudstshoorn. F. 1992. Guide to grasses of South Africa. Briza publications Cc. pp 216.

Watson, L., and Dallwitz, M.J. 1992. The grass genera of the world: descriptions, illustrations, identification, and information retrieval; including synonyms, morphology, anatomy, physiology, phytochemistry, cytology, classification, pathogens, world and local distribution, and references. Version: 28th November 2005.

Wedin, D. A., and D. Tilman. 1990. nitrogen cycling, plant competition, and the stability of tallgrass prairie. Pages 5-8 *in* D. D. Smith and C. A. Jacobs, editors. Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls, Iowa, USA

Westman, W. E. 1990. Managing for biodiversity: unresolved science and policy questions. *Bioscience.* 40. 26-33.

Yelenik, S.G., Stock, W.D. and Richardson, D.M. 2004. Ecosystem impacts of invasive *Acacia saligna* in South African fynbos. *Restoration Ecology.* 12 (1). 44-51.

Zavaleta, E.S. 2006. Shrub establishment under experimental global changes in California grassland. *Plant Ecology.* 184 (1). 53-56.

Chapter 5

Concluding remarks and recommendations

5.1 Key messages

This study has provided the following information on invasive annual grasses in renosterveld:

(i) Fertilizer gradients from agricultural land play a lesser role in the distribution of alien invasive annual grasses, and in indigenous vegetation composition, than does physical disturbance and grazing of the vegetation.

(ii) Indigenous renosterveld grass species distributions are generally unaffected by fence lines agriculture, while alien annual grass cover declines rapidly from fence lines into renosterveld patches.

(iii) The alien grass, *Avena fatua*, can out-compete indigenous species with sufficient water and does not necessarily require nitrogen enrichment to do so.

Minimisation of physical disturbance of renosterveld fragments, combined with better management of fertilization and irrigation on adjacent agricultural land could reduce the risk of alien annual grass invasion into fragments. Intact renosterveld appears to outcompete alien annual grasses for light and water, and improved management of agricultural supplements would prevent nitrogen rich runoff from entering natural vegetation fragments to the possible advantage of weedy grasses.

5.2 Expectations for the future

Global environmental change is driven strongly by agriculture, at our current rates of consumption and population expansion, 10^9 hectares of natural systems will be agriculture (Tilman *et al.* 2001). This is predicted to mean a 2.4 to 2.7 fold increase in nitrogen and phosphorous driven eutrophication of terrestrial, freshwater and marine systems. The past few decades have seen increases in nitrogen and phosphorous addition as well as irrigation and this is predicted to increase further. These projected increases will have severe environmental impacts. Nitrogen and phosphorous leakage from agricultural systems has proven to be problematic. Productivity in the majority of terrestrial habitats is governed largely by nitrogen (Vitousek 1982). Nitrogen deposition from agriculture and the use of fossil fuels is altering the nitrogen present in soils and thus decreasing species diversity, composition and function of these terrestrial environments. The drought resistance of plant communities has been proven to be more robust if the community is higher in diversity (Tilman and Downing 1994). Thus establishing methods of dealing with these increased nutrient conditions from a local, through to a global scale, is needed.

5.3 Current methods of controlling invasions and recommendations

Invasive annual grasses are a global problem and there has been much research into why, how and how these processes can be stopped or prevented. Cowling *et al.* (1986) suggested that South Coast renosterveld be rehabilitated as “grassy swards”. This concept developed as a result of historical evidence that renosterveld was dominated by the grass *Themeda triandra*. This serves a dual purpose as these grasslands would be catering for conservation and grazing purposes. However West Coast renosterveld has a far lower proportion of grasses and a great diversity of geophytes. Thus establishing grasslands would retard the success of these endemic plants.

Musil *et al.* (2005) examined the cost effectiveness of combinations of mowing, handclearing, light and intense burning and pre-emergent herbicide application. The conclusion was that mowing prior to seed maturation, using offcuts as fodder, was the most cost effective method. These are all treatments post invasion and are all costly to some degree. The most cost effective way to deal with invasion by alien annual grasses is to prevent them before they occur. Burning of invasive annual grasses has yielded poor results as a management tool (Brooks and Pyke 2001). Australia and South Africa have used livestock grazing before seed set as a control for annual alien invasive grasses, however unpalatable grasses remain and high intensity grazing damages the area (Musil *et al.* 2005). Mowing is a poor technique as recruitment of natives after mowing is very low. The grass litter layer in the mowed area is too dense for indigenous seedlings or geophytes to emerge (Musil *et al.* 2005). Sucrose addition has been used to counteract nitrogen enrichment as it increases soil microbial biomass, and has proven successful in semi-arid systems (Blumenthal *et al.* 2003; Alpert and Maron 2000). Pathogens targeting annual alien invasive grasses have also been experimented with (Hetherington and Auld 2000).

Simulations by Schippers and Joenje (2002) lead them to the conclusion that field boundary vegetation diversity would be best preserved if nutrient input was prevented, mowing and removal of the mowed vegetation occurred, annual disturbance was restricted to less than 20 % of the area and the boundary area was kept wider than any fertilizer drift. These measures would be well suited to west coast renosterveld preservation. The boundary area of renosterveld could be sown with indigenous *Themeda* species that have the potential to outcompete annual alien grasses. This grass could potentially “mop” up any excess fertilizer and water, thus protecting the renosterveld patch. This grass is also of value to grazing making it a much more attractive management tool for farmers.

Research into the use of shading on Australian acacias (problem plants in the South Western Cape) as a tool for removing them (Milton 1982), yielded interesting results. The conclusion drawn from this study was that, in the field, 90 % shading would be required to be an effective control. For the acacia species it is not competition for water, nutrients, pathogens or chemicals released by competitors that result in death, but the shading. The effect of shading on annual invasive grasses could be an interesting study. It is an ideal tool as it does not mechanically disturb the environment. It could also be a cheaper method than altering fertilizing and irrigation regimes of farmers.

In the severely threatened and diminishing west coast renosterveld an integrated approach is required. Active removal of annual alien grasses, in combination with preventing drift of fertilizer and irrigation from adjacent agricultural fields, are necessary to remove the invasive problem and prevent creating circumstances favouring reinvasion. Involving the local farmers is also vital to the survival of west coast renosterveld and creating awareness through work such as that of Sue Winter (Winter *et al.* 2005, 2007) is of great importance.

There is already much information available on how the effects of agriculture can be reduced. Proper use of chemicals and water, pest management techniques, use of cover crops and buffer strips between agriculture and natural vegetation, are vital to conservation of the fragmented renosterveld environment. Research is needed investigating nitrogen, phosphorus and water requirements of crops so that the addition of these is optimal for the natural environment and the crops.

5.4 References

Alpert, P. and Maron, J.L. 2000. Carbon addition as a countermeasure against biological invasions by plants. *Biological Invasions*. 2. 33-40.

Brookes, M.L. and Pyke, D.A. 2001. Invasive plants and fire in the deserts of North America. In Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. K.E.M. Galley and T.P. Wilson (eds). Pp. 1-14. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention and Management. *Miscellaneous Publication No 11*, Tall Timbers Research Station, Tallahassee, F.L.

Blumenthal, D.M., Jordan, N.R. and Russelle, M.P. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications*. 13. 605-616.

Cowling, R.M., Pierce, S. M. and Moll, E.J. 1986. Conservation and Utilization of South Coast renosterveld, an endangered South African vegetation type. *Biological Conservation*. 37. 363-377.

Hetherington, S.D. and Auld, B.A. 1996. Biological control of annual grass weeds-progress and prospects. *Plant Protection Quarterly*. 11. Suppl. 1. 215-216.

Milton, S.J. 1982. Effects of shading on nursery grown *Acacia* seedlings. *South African Journal of Botany.* 48 (2). 245-272.

Musil, C.F., Milton, S.J. and Davis, G.W. 2005. An empirical examination of different management strategies for managing alien invasive grass infestations in a South African West-Coast reserve. *South African Journal of Science.* 101. 337-344.

Schippers, P. and Joenje, W. 2002. Modelling the effects of fertilizer, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agriculture, Ecosystems and Environment*. 93. 351-365.

Tilman, D. 1988. *Plant Strategies and the dynamics and structure of plant communities.* Princeton University Press.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature*. 367. 363-365.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth,R., Schindler, D., Schlesinger, W.H., Simberloff, D. and Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science*. 292. 281-284.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist.* 119. 553-572.

Winter, S.J., Esler, K.J. and Kidd, M. 2005. An index to measure the conservation attitudes of landholders towards Overberg Coastal Renosterveld, an endangered vegetation type in the Cape Floral Kingdom, South Africa. *Biological Conservation.* 126. 383-394.

Winter, S.J., Prozesky, H. and Esler, K.J. 2007. A case study of landholder attitudes and behaviour towards the conservation of Renosterveld, a critically endangered vegetation type in the Cape Floral Kingdom, South Africa. *Environmental Management*. 40. 46-61.

Appendix 2.1: Means and standard deviations for all transect variables. Jan Briers Louw Geometric Tortoise Reserve (JBR).

Quad	Alien grass cover	Indigenous grass cover	alien seed bank density	pH	Na cmol/kg	K cmol/kg	Ca cmol/kg	Mg cmol/kg	C %	Geophyte density	Shrub cover	Litter cover	Stone cover	Animal disturbance cover	Bare ground	Cryptogram cover	Soil water (g)	Soil density	mass % stones/sample
1	103.67	4.33	4.33	5.33	0.08	0.33	3.45	0.67	2.18	0.33	0.00	8.33	1.67	11.33	6.67	1.00	22.47	0.0016	30.33
	±12.06	±5.86	±1.53	±0.42	±0.01	±0.08	±0.55	±0.13	±0.25	±0.58	±0.00	±14.43	±0.58	±11.85	±2.89	±1.73	±19.23	±0.0002	±8.08
2	99.67	4.33	12.33	5.53	0.10	0.31	3.56	0.85	2.15	0.67	0.00	3.33	1.83	6.67	9.33	3.33	29.57	0.0016	15.67
	±9.07	±4.93	±7.37	±0.68	±0.03	±0.05	±0.14	±0.13	±0.22	±0.58	±0.00	±5.77	±1.26	±2.89	±1.15	±5.77	±13.05	±0.0002	±13.80
3	65.00	1.67	3.00	4.87	0.10	0.24	2.16	0.79	2.21	19.00	8.00	10.00	1.67	10.00	21.67	3.33	48.83	0.0013	15.33
	±39.61	±2.89	±2.65	±0.74	±0.02	±0.05	±0.74	±0.20	±0.44	±29.51	±6.93	±10.00	±1.15	±10.00	±24.66	±5.77	±55.62	±0.0001	±13.87
4	18.33	15.00	3.67	4.57	0.16	0.34	2.43	1.34	3.66	32.33	62.33	8.33	2.00	25.00	19.33	8.33	15.80	0.0015	0.00
	±10.26	±10.58	±1.53	±0.72	±0.10	±0.13	±1.49	±1.04	±1.47	±55.14	±24.68	±10.41	±1.00	±25.00	±8.14	±14.43	±9.10	±0.0000	±0.00
5	2.00	20.33	1.33	4.80	0.17	0.27	2.48	1.44	4.90	46.67	56.00	20.00	1.67	25.00	7.33	15.00	28.67	0.0014	10.00
	±3.46	±25.70	±0.58	±0.78	±0.04	±0.03	±0.63	±0.37	±2.15	±76.51	±18.73	±25.98	±0.58	±15.00	±4.62	±13.23	±20.88	±0.0001	±9.54
6	11.33	4.67	0.67	5.07	0.09	0.28	3.47	1.35	3.49	33.00	57.00	26.00	2.67	35.00	33.33	15.00	36.77	0.0014	18.67
	±14.01	±4.51	±1.15	±0.91	±0.03	±0.14	±2.20	±0.97	±0.84	±34.39	±16.09	±21.63	±2.08	±39.69	±20.82	±15.00	±33.30	±0.0001	±4.16
7	19.33	18.33	2.00	4.80	0.14	0.31	2.38	1.09	4.01	25.67	69.00	53.33	1.67	73.33	18.33	8.67	40.83	0.0014	15.67
	±26.86	±16.80	±1.00	±0.87	±0.09	±0.14	±1.55	±0.94	±2.25	±21.13	±31.43	±35.12	±0.58	±5.77	±7.64	±7.09	±40.50	±0.0002	±15.04
8	22.33	5.00	1.67	4.90	0.14	0.30	3.42	1.37	3.45	17.67	55.00	20.00	2.00	66.67	23.33	11.33	31.30	0.0013	22.67
	±22.50	±5.00	±1.53	±0.75	±0.07	±0.12	±0.77	±0.41	±0.65	±7.37	±44.44	±21.79	±1.00	±32.15	±20.21	±16.20	±32.72	±0.0001	±23.01
9	18.33	9.67	0.33	4.80	0.17	0.26	3.63	1.30	4.68	59.33	58.00	15.00	2.33	53.33	30.00	5.33	39.10	0.0014	21.67
	±25.74	±8.96	±0.58	±0.79	±0.09	±0.13	±2.44	±0.71	±3.58	±40.20	±13.11	±13.23	±0.58	±35.12	±18.03	±4.51	±48.52	±0.0002	±20.21
10	14.33	9.67	8.67	4.67	0.10	0.27	4.23	1.26	2.60	66.33	60.67	14.33	2.00	51.67	23.33	4.33	17.07	0.0014	52.67
	±12.90	±8.96	±9.61	±1.24	±0.05	±0.14	±5.99	±1.44	±1.36	±58.05	±25.50	±13.65	±0.00	±42.52	±23.09	±5.86	±8.02	±0.0000	±38.84
11	11.33	8.67	2.00	4.90	0.08	0.20	2.61	1.00	3.16	26.33	46.00	46.67	4.33	38.33	28.33	0.67	27.70	0.0014	8.67
	±5.69	±14.15	±2.65	±0.96	±0.03	±0.02	±1.33	±0.32	±1.46	±29.16	±22.87	±37.86	±4.93	±12.58	±16.07	±1.15	±12.25	±0.0000	±9.02
12	13.33	2.33	2.33	4.97	0.08	0.29	3.16	1.02	3.39	74.00	67.00	20.00	10.00	22.50	25.00	5.00	36.27	0.0015	21.33
	±5.77	±2.52	±0.58	±0.71	±0.02	±0.07	±1.19	±0.16	±0.65	±47.29	±31.10	±14.14	±0.00	±3.54	±21.21	±5.00	±10.63	±0.0000	±3.06
13	0.00	1.00	11.00	4.60	0.06	0.14	1.24	0.52	2.58	34.33	62.33	27.50	5.00	0.00	20.00	10.00	40.67	0.0015	40.33
	±0.00	±1.73	±17.35	±0.87	±0.01	±0.06	±0.23	±0.17	±0.08	±39.80	±17.21	±3.54	±4.24	±0.00	±7.07	±13.23	±8.51	±0.0002	±34.56

Appendix 2.2: Means and standard deviations for all transect variables. Paul Cluver Wine Estate (PCWE).

quad	Alien grass cover	Indigenous grass cover	Alien seed bank density	pH	Na cmol/kg	K cmol/kg	Ca cmol/kg	Mg cmol/kg	C %	Geophyte density	Shrub cover	Litter cover	Stone cover	Animal disturbance cover	Bare ground	Soil water (g)	Soil density	mass % stones/sample
1	23.67	1.33	9.00	6.47	0.61	0.33	8.79	1.95	2.75	4.67	0.00	25.00	10.00	0.00	60.00	0.09	0.0014	22.00
	±13.05	±2.31	±13.08	±0.47	±0.07	±0.16	±2.05	±0.55	±0.67	±1.15	0.00	±0.00	±5.00	0.00	±21.79	±0.01	±0.0003	±19.29
2	52.00	0.67	8.33	6.07	0.72	0.36	7.81	1.72	2.78	3.00	0.00	2.50	5.00	0.00	13.33	0.07	0.0016	27.00
	±31.10	±1.15	±10.41	±1.27	±0.48	±0.15	±3.25	±0.79	±0.55	±2.00	±0.00	±3.54	±0.00	0.00	±14.43	±0.02	±0.0001	±24.27
3	45.33	12.67	59.63	5.73	0.27	0.42	5.04	1.79	3.67	4.00	22.33	2.67	8.33	0.00	7.33	0.11	0.0014	10.00
	±12.10	±15.95	±41.09	±1.06	±0.11	±0.23	±0.47	±0.89	±2.12	±4.00	±16.17	±2.08	±2.89	0.00	±6.81	±0.01	±0.0002	±10.00
4	28.00	9.67	31.90	5.30	0.32	0.42	4.26	1.99	3.00	27.67	11.33	16.67	4.00	15.00	11.50	0.10	0.0014	8.67
	±11.36	±8.96	±14.60	±1.31	±0.04	±0.15	±1.41	±0.55	±1.52	±20.50	±8.08	±20.82	±1.73	±21.21	±12.02	±0.02	±0.0002	±10.97
5	13.67	13.67	12.10	5.60	0.37	0.33	4.95	1.97	3.27	39.00	25.00	9.33	5.00	45.00	11.67	0.10	0.0014	34.33
	±8.62	±10.26	±11.68	±1.47	±0.17	±0.03	±1.89	±0.65	±1.47	±32.42	±10.00	±13.65	±0.00	±63.64	±11.55	±0.01	±0.0001	±32.25
6	36.67	2.33	18.67	5.53	0.37	0.36	5.19	1.85	3.00	28.33	36.00	31.67	5.00	40.00	6.50	0.12	0.0014	29.67
	±4.04	±2.52	±17.04	±1.62	±0.06	±0.14	±2.82	±0.66	±1.55	±39.58	±20.66	±25.66	±0.00	±56.57	±2.12	±0.02	±0.0001	±33.29
7	26.00	7.67	15.33	5.17	0.32	0.55	3.93	2.21	3.96	31.00	40.67	46.67	0.00	25.00	7.33	0.09	0.0015	2.00
	±13.45	±4.16	±13.65	±0.81	±0.14	±0.15	±0.30	±0.10	±0.51	±38.57	±46.88	±20.82	0.00	±35.36	±6.81	±0.03	±0.0001	±3.46
8	27.00	6.00	29.73	5.17	0.33	0.70	5.20	2.82	5.05	28.33	23.00	28.33	0.00	45.00	15.67	0.10	0.0014	10.33
	±27.62	±6.00	±24.06	±1.00	±0.11	±0.26	±1.24	±0.70	±0.61	±22.14	±30.41	±10.41	0.00	±63.64	±21.13	±0.01	±0.0001	±12.34
9	11.00	4.67	11.47	5.07	0.32	0.91	5.99	3.01	5.21	32.00	48.00	26.33	0.00	50.00	1.67	0.10	0.0013	23.33
	±7.81	±4.16	±16.52	±0.64	±0.11	±0.19	±2.44	±1.17	±1.41	±25.94	±41.58	±3.21	0.00	±20.00	±0.58	±0.02	±0.0001	±12.70
10	5.00	5.67	3.83	4.97	0.27	0.87	4.24	2.65	4.94	23.33	58.67	30.00	2.50	46.67	3.00	0.10	0.0013	12.33
	±3.00	±5.13	±3.33	±0.72	±0.04	±0.19	±0.65	±0.25	±1.43	±26.86	±21.39	±5.00	±3.54	±33.29	±1.73	±0.01	±0.0000	±8.02
11	7.33	6.33	4.67	4.90	0.18	0.74	4.39	2.42	5.45	32.00	46.00	30.00	0.00	55.00	3.50	0.10	0.0014	12.33
	±6.43	±6.51	±4.04	±0.95	±0.05	±0.14	±0.20	±0.07	±2.19	±29.61	±30.79	±20.00	0.00	±21.21	±2.12	±0.02	±0.0001	±10.79
12	1.67	1.33	9.43	4.90	0.27	0.73	5.41	3.24	7.20	26.33	53.00	56.67	0.00	37.50	3.50	0.12	0.0013	13.00
	±1.53	±1.53	±14.64	±0.79	±0.02	±0.10	±1.07	±0.45	±2.60	±21.50	±12.77	±20.82	0.00	±3.54	±2.12	±0.02	±0.0001	±11.27
13	1.67	2.00	4.07	4.87	0.28	0.66	5.26	3.19	6.12	32.33	58.00	46.67	0.00	45.00	4.00	0.11	0.0011	8.33
	±2.08	±3.46	±1.21	±0.83	±0.09	±0.17	±0.44	±0.47	±0.54	±29.54	±25.36	±15.28	0.00	±27.84	±5.29	±0.02	±0.0002	±14.43

Appendix 2.3: Means and standard deviations for all transect variables. Mulderbosch Wine Estate (MWE).

quad	Alien grass cover	Indigenous grass cover	alien seed bank density	pH	Na cmol/kg	K cmol/kg	Ca cmol/kg	Mg cmol/kg	C %	Geophyte density	Shrub cover	Litter cover	Stone cover	Animal disturbance cover	Bare ground	Cryptogram cover	Soil water (g)	Soil density	mass % stones/sample
1	0.00	0.00	0.00	6.43	0.10	1.04	9.30	2.90	4.11	33.33	0.00	40.00	40.00	0.00	8.33	8.33	0.04	0.0015	21.00
	0.00	0.00	0.00	±0.87	±0.07	±0.88	±4.52	±2.32	±1.26	±57.74	0.00	±8.66	±5.00	0.00	±5.77	±7.64	±0.03	±0.0001	±18.25
2	0.00	0.00	0.00	6.10	0.06	0.61	6.40	1.83	4.71	6.67	0.00	13.33	40.00	0.00	36.67	10.00	0.05	0.0014	34.67
	0.00	0.00	±1.82	±0.90	±0.01	±0.13	±2.04	±1.11	±3.15	±11.55	0.00	±14.43	±21.21	±0.00	±25.17	±10.00	±0.02	±0.0001	±9.50
3	27.00	1.67	2.47	5.80	0.13	0.71	7.90	2.68	7.15	15.00	32.67	100.00	0.00	0.00	0.00	0.00	0.04	0.0013	78.00
	±14.73	±2.89	±4.27	±0.56	±0.04	±0.15	±0.96	±0.01	±4.69	±13.45	±42.83	±0.00	0.00	0.00	0.00	0.00	±0.01	±0.0001	±105.73
4	7.67	1.67	1.87	5.23	0.21	0.99	6.78	3.53	10.46	19.00	73.33	43.33	0.00	0.00	3.50	2.50	0.04	0.0012	8.67
	±12.42	±0.58	±2.27	±0.76	±0.14	±0.16	±4.23	±1.52	±8.83	±17.69	±5.77	±28.87	0.00	0.00	±2.12	±3.54	±0.03	±0.0002	±15.01
5	2.33	3.33	5.53	5.00	0.16	0.86	4.57	2.31	6.85	24.00	85.67	60.00	0.00	0.00	2.50	1.00	0.03	0.0012	39.00
	±2.52	±5.77	±5.27	±1.14	±0.04	±0.41	±1.40	±1.20	±1.44	±5.20	±10.26	±49.24	0.00	0.00	±0.71	±1.41	±0.01	±0.0000	±28.93
6	0.00	2.00	0.73	5.07	0.22	0.85	5.56	2.74	8.27	14.67	101.00	91.67	1.67	0.00	0.00	0.00	0.02	0.0012	28.67
	0.00	±3.46	±0.64	±1.16	±0.09	±0.29	±2.08	±1.18	±4.37	±17.62	±7.81	±2.89	±2.89	0.00	0.00	0.00	±0.01	±0.0002	±11.37
7	0.00	1.67	0.00	5.10	0.18	0.71	4.16	2.32	6.32	20.33	85.67	76.67	6.67	17.50	12.50	2.50	0.04	0.0008	33.67
	±0.00	±2.89	±0.00	±0.87	±0.09	±0.13	±1.47	±0.71	±1.12	±10.60	±23.12	±15.28	±11.55	±24.75	±17.68	±3.54	±0.04	±0.0007	±12.86
8	2.33	4.00	1.74	5.17	0.14	0.67	4.46	1.97	6.13	13.33	101.00	37.50	30.00	10.00	15.00	0.00	0.03	0.0011	29.67
	±4.04	±6.08	±1.51	±0.81	±0.07	±0.21	±1.85	±1.03	±2.92	±4.04	±20.30	±3.54	±27.84	±14.14	±14.14	±0.00	±0.02	±0.0001	±8.74
9	1.67	2.67	1.67	4.93	0.14	0.61	3.20	1.81	4.96	14.00	74.33	30.00	11.67	2.50	10.00	0.00	0.03	0.0012	17.67
	±2.89	±2.52	±2.89	±0.75	±0.06	±0.10	±1.22	±0.50	±0.39	±2.65	±16.86	±36.06	±12.58	±3.54	±14.14	±0.00	±0.02	±0.0001	±17.04
10	0.67	5.00	0.40	5.20	0.08	0.62	3.58	1.89	5.20	24.00	85.67	45.00	8.33	2.50	2.50	28.33	0.03	0.0012	39.33
	±1.15	±8.66	±0.69	±1.04	±0.02	±0.21	±0.48	±0.50	±0.64	±11.14	±32.72	±42.72	±14.43	±3.54	±3.54	±40.72	±0.01	±0.0001	±13.87
11	3.33	1.67	0.00	5.07	0.10	0.52	2.70	1.73	5.27	31.00	73.00	28.33	2.50	6.67	2.50	1.00	0.02	0.0012	20.67
	±5.77	±1.53	±0.00	±0.99	±0.02	±0.05	±0.54	±0.03	±1.79	±19.05	±27.62	±10.41	±3.54	±7.64	±3.54	±1.41	±0.02	±0.0001	±0.58
12	1.00	1.67	0.80	5.07	0.14	0.87	4.71	2.36	6.53	28.00	48.33	80.00	8.33	11.67	1.00	2.50	0.04	0.0011	43.67
	±1.73	±2.89	±1.39	±0.98	±0.03	±0.32	±1.71	±0.51	±1.75	±37.04	±11.02	±0.00	±14.43	±11.55	±1.41	±3.54	±0.03	±0.0001	±12.10
13	0.00	11.00	0.33	4.67	0.12	0.78	7.27	2.43	8.33	18.33	39.33	60.00	0.00	12.50	7.50	0.00	0.04	0.0010	26.33
	0.00	±17.35	±0.58	±0.64	±0.05	±0.27	±4.53	±0.89	±5.82	±27.47	±26.27	±17.32	0.00	±17.68	±10.61	±0.00	±0.02	±0.0002	±11.93

Appendix 2.4: Correlation matrix for all environmental, physical and chemical variables. AGC-alien grass cover, IGC-indigenous grass cover, ASB-alien seed bank, GD-geophyte density, SHC-shrub cover, Na-sodium, K-potassium, Ca-calcium, Mg-magnesium, C-carbon, LC-litter cover, SC-stone cover, AD-animal disturbance, BG-bareground, SW-soil water, SD-soil density, S-percentage stones/sample. The PCA axis 1 and 2 accounted for 42 and 11 variation of environmental, physical and chemical characteristics respectively.

	PCA 1	PCA 2	AGC	IGC	ASB	GD	SHC	pH	Na	K	Ca	Mg	C%	LC	SC	AD	BG	SW	SD	S
PCA 1		-0.68**	-0.71**	NS -	-0.33*	0.54**	0.83**	-0.70**	NS	NS	-0.32*	NS	0.49**	0.48**	-0.33*	0.45**	NS	NS	-0.50**	NS
PCA 2	-0.68**	NS	NS	NS	0.50**	NS	-0.71**	NS	0.35*	-0.58**	NS	-0.47**	-0.72**	-0.66**	NS	NS	NS	0.33*	0.654**	NS
AGC	-.71**	0.88**	NS	NS	0.32*	-0.40*	-0.62**	NS	NS	-0.43**	NS	-0.46**	-0.55**	-0.46**	NS	NS	NS	NS	0.54**	NS
IGC	NS	NS	0.32*	NS	NS	NS	NS	-0.36*	NS	-0.37*	-0.36*	NS	NS	NS	NS	0.44**	NS	NS	NS	NS
ASB	-0.33*	0.50**	-0.40*	NS	NS	NS	-0.35*	NS	0.37*	NS	NS	NS	NS	-0.33*	NS	NS	NS	NS	NS	NS
GD	0.54**	NS	-0.62**	NS	NS	NS	0.33*	-0.46**	NS	NS	NS	NS	NS	NS	NS	0.47**	NS	NS	NS	NS
SHC	0.825**	-0.71**	NS	NS	-0.35*	0.33*	NS	-0.63**	NS	NS	-0.38*	NS	0.52**	0.46**	NS	NS	NS	NS	-0.58**	NS
pH	-0.70**	NS	NS	-0.36*	NS	-0.46**	-0.63**	NS	0.45**	NS	0.72**	NS	NS	NS	0.55**	-0.45**	NS	-0.40*	NS	NS
Na	NS	0.35*	NS	NS	0.37*	NS	-0.33*	0.45**	NS	NS	0.49**	NS	NS	NS	NS	NS	NS	-0.43**	NS	NS
K	NS	-0.58**	-0.43**	-0.37*	NS	NS	NS	NS	NS	NS	0.55**	0.87**	0.78**	0.58**	NS	NS	-0.57**	-0.71**	-0.52**	NS
Ca	-0.32*	NS	NS	-0.36*	NS	NS	-0.38**	0.72**	0.49**	0.55**	NS	0.64**	0.35*	NS	0.33*	NS	NS	-0.63**	NS	NS
Mg	NS	-0.47**	-0.46**	NS	NS	NS	NS	NS	NS	0.87**	0.65**	NS	0.76**	0.52**	NS	NS	-0.47**	-0.78**	-0.47**	NS
C%	0.49**	-0.72**	-0.55**	NS	NS	NS	0.52**	NS	NS	0.78**	0.35*	0.76**	NS	0.71**	NS	NS	-0.49**	-0.50**	-0.69**	NS
LC	0.48**	-0.66**	-0.46**	NS	-0.33*	NS	0.46**	NS	NS	0.58**	NS	0.52**	0.71**	NS	NS	-0.36*	NS	NS	NS	0.4*
SC	-0.33*	NS	NS	NS	NS	NS	NS	0.55**	NS	NS	0.33*	NS	NS	NS	NS	-0.36*	NS	NS	NS	NS
AD	0.45**	NS	NS	0.44**	NS	NS	NS	-0.45**	NS	NS	NS	NS	NS	NS	-0.39*	NS	NS	NS	NS	NS
BG	-0.31	NS	NS	NS	NS	NS	NS	NS	NS	-0.57**	NS	-0.47**	-0.49**	-0.39*	NS	NS	NS	0.43**	NS	NS
SW	NS	0.33*	NS	NS	NS	NS	NS	-0.4*	-0.43**	-0.71**	-0.63**	-0.78**	-0.50**	-0.33*	NS	NS	0.43**	NS	0.38*	NS
SD	-0.50**	0.65**	0.54**	NS	NS	NS	-0.58**	NS	NS	-0/02**	NS	-0.47**	-0.69**	-0.62**	NS	NS	NS	0.38*	NS	NS
S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.40*	NS	NS	NS	NS	NS	NS

*correlation is significant at the 0.01 level (2 tailed)

**correlation significant at the 0.05 level (2 tailed)

Appendix 3.1: Characteristics of the most common alien grass species. Information sourced from (Van Wyk and van Oudtshoorn 1999, Grabandt 1985 and Chippindall and Crook 1976).

alien grass species	common name	type	Use	distribution in South Africa	origin	habitat
Agrostis stolonifera	Creeping bentgrass	perennial	little grazing value	grassland, savanna		wet areas, sourveld, sometimes a weed
Avena fatua	Common wild oats	annual	used for hay	Savanna and fynbos parts of the southern Cape	Europe, western and central Asia and North Africa	common weed in disturbed areas eg gardens, cultivated lands, roadsides
Brachypodium distachyon	purple false brome	perennial			southern Europe, northern Africa, south western Asia	
Briza major	Large quaking grass	annual	palatable but not for high productivity	Mainly restricted to the western Cape	Mediterranean	gardens, agricultural weed, roadsides
Briza minor	Small quaking grass	annual	palatable but not for high productivity	Mainly restricted to the western Cape	Mediterranean	gardens, agricultural weed, roadsides disturbed areas, moist areas, grassland and fynbos
Bromus hordeaceus	Soft brome	annual			Europe	
Bromus diandrus	Ripgut brome	annual	serious weed, awns damage wool and animals mouths	Common in fynbos, the western and eastern Cape	Mediterranean and Europe	disturbed areas, cultivated places, gardens, roads and moist places
Bromus catharticus	Rescue grass	annual	weed in lucerne, orchards and vineyards, palatable, average	grassland, fynbos and Nama-Karoo	Europe, Australia and America	disturbed areas, gardens, cultivated lands, roadsides

alien grass species	**common name**	**type**	**Use**	**distribution in South Africa**	**origin**	**habitat**
			grazing			
Cynodon dactylon	Couch grass	perennial	good lawn grass and soil stabilizer however potential to be a serious weed good pasture grass	Widely distributed through Africa grassland, savanna, nama karoo, fynbos	Europe	favours fertile, dryer soils often in areas of disturbance and increased nitrogen roadsides
Lolium perenne	Perennial rye grass	perennial	good fodder grass, cultivated in winter pastures, palatable	Western, Northern and Eastern Cape	Europe, north west Africa and temperate areas of Asia	disturbed areas eg old lands, roadsides and gardens, variety of soils, roadsides, disturbed areas, uncultivated lands
Phalaris arundinacea	Red canary grass	perennial			Asia	wetlands, disturbed areas
Poa annua	Annual blue grass	annual	low grazing value	Widely distributed in the Western and Eastern Cape as well as the Eastern areas of South Africa	Europe, Asia and the Mediterranean	wet areas, disturbed, gardens, roadsides, shade fynbos, grassland, savanna
Vulpia muralis	Wall fescue	annual			Europe	moist or dry and open

Appendix 3.2: Characteristics of the most common indigenous species. (Van Wyk and van Oudtshoorn 1999, Grabandt 1985 and Chippindall and Crook 1976).

indigenous grass species	common name	type	Use	distribution in South Africa	Habitat
Melica racemosa	Staggers grass	perennial	important veld grass	Western, southern and eastern cape. The fynbos, grassland and nama karoo.	slopes between rocks or in semi shade, along wooded edges and dune forests
Ehrharta calycina	Common calycina	C3 perennial or annual	good grazing grass, drought resistant	Western and southern Cape. The succulent karoo, fynbos savanna	disturbed sandy ground in arid areas but also in other vegetation especially where disturbance has taken
Ehrharta capensis		C3 perennial		Fynbos and karoo	Mountains and koppies
Ehrharta longiflora	Oat-seed grass	C3 annual	can be considered a weed, little economic importance	Western Cape, Namaqualand	semi disturbed soils, fruit orchards, grows in the shadow of shrubs and rocks and in disturbed moist areas
Ehrharta triandra		C3			
Helictotrichon turgidulum	Small oats grass	perennial	Reasonably valuable, remains green in winter, variable grazing value	Western Cape, grasslands/savanna	higher rainfall areas, grows in most soils, sometimes thick on road verges, disturbed areas, sandy soils
Koeleria capensis	Koleria	C3 perennial	Moderately palatable	tropical Africa, Southern and East Africa	high altitude grasslands or high rainfall wet areas
Pentaschistis curvifolia	Tassel grass	C3 perennial	average grazing	fynbos	variety of habitats, sandy soils
Pentaschistis pallida	Dune grass	C3 perennial	Poor grazing good soil stabilizer	South western parts of Western Cape	Disturbed places e.g. roadsides, limestone derived soils

indigenous grass species	**common name**	**type**	**Use**	**distribution in South Africa**	**Habitat**
Merxmuellera stricta	Cape Wire Grass	C3 perennial	No grazing value	South Africa and Lesotho	Mountainous areas, all soil types
Themeda triandra	Red grass	C4 variable perennial	good veld grass, palatable	widespread in Africa, grassland, savanna, nama karoo, fynbos	climax montane grassland, found on all soil types
Tribolium hispidum		C3 perennial	low grazing value	South western parts of Western cape	
Tribolium uniolae	Hair grass	C3 perennial	low grazing value	South western parts of Western cape	disturbed areas like road reserves

Appendix 3.3

Seed bank and above ground alien cover.

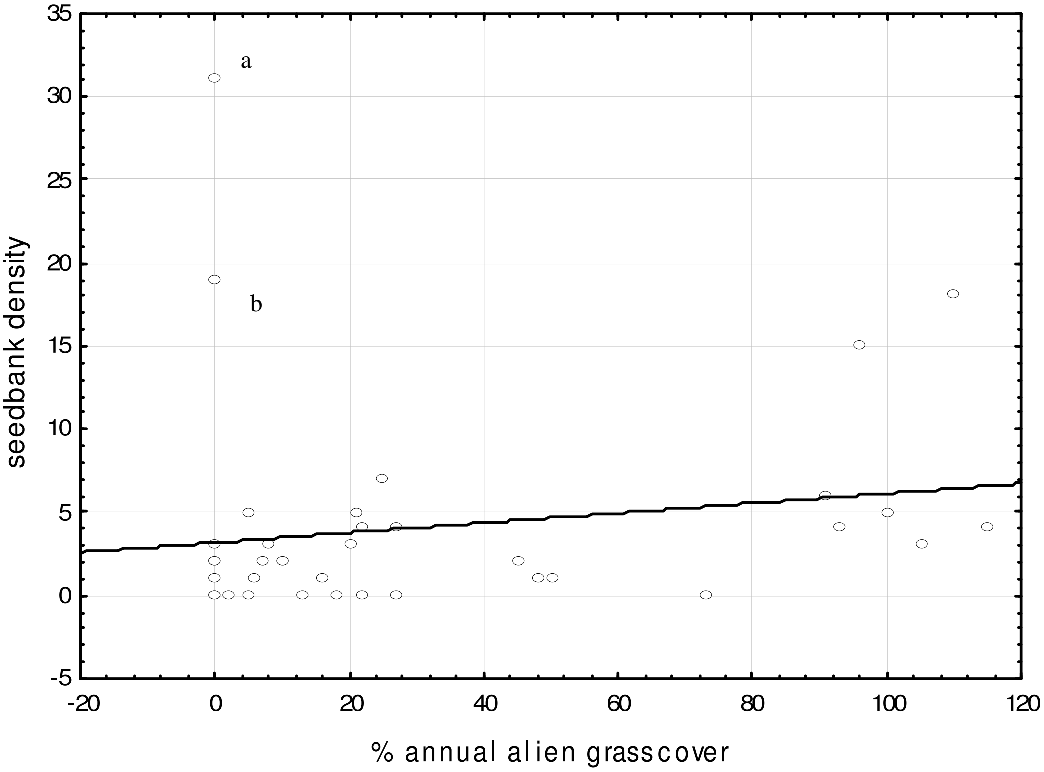


Figure 1: JBR: Relationship between alien grass seed bank and above ground alien grass cover. Points a and b are where there was a seed bank present but not evident in above ground biomass. The sample points were in an area where soils were compacted and open. If these points are removed r = 0.5669, p = 0.0003.

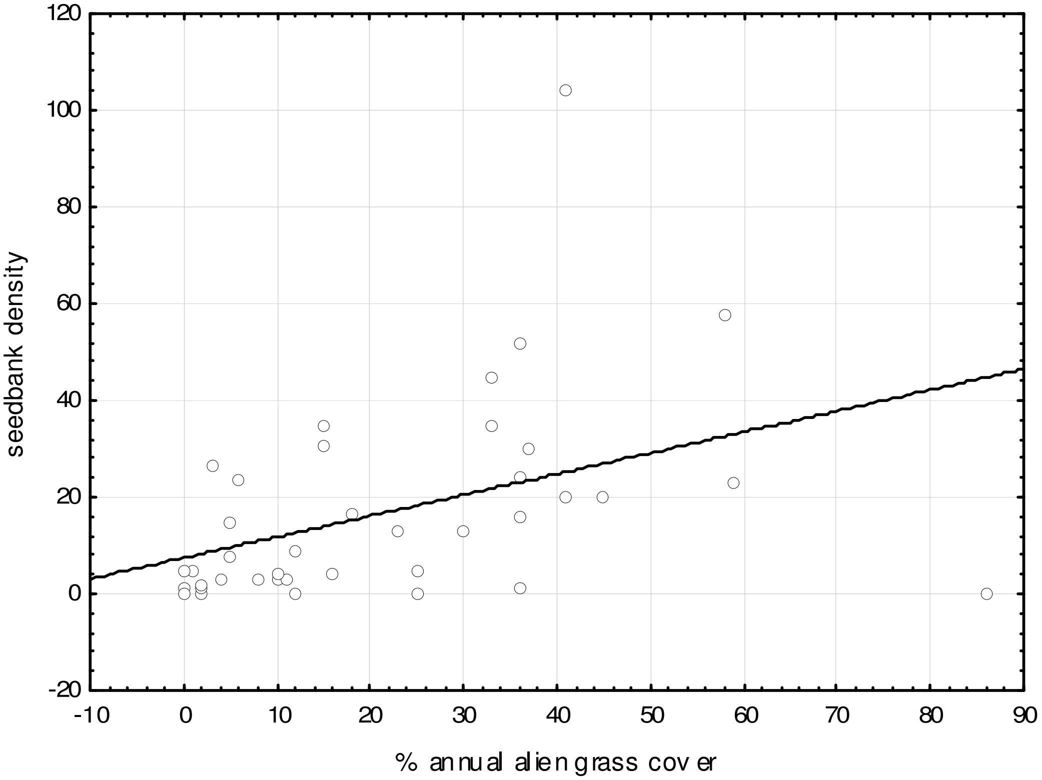
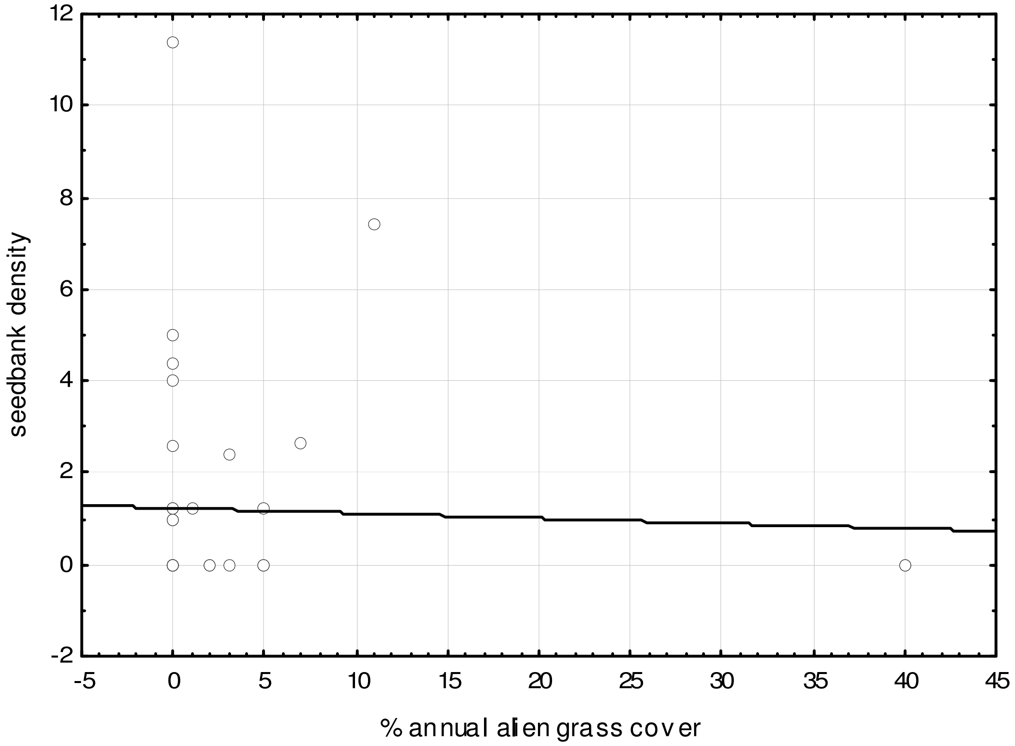


Figure 2: PCWE: Relationship between alien grass seed bank and above ground alien grass.



cover.

Figure 3: MWE: Relationship between alien grass seed bank and above ground alien grass cover.

Appendix 4.1

Dry mass results for pot experiment.

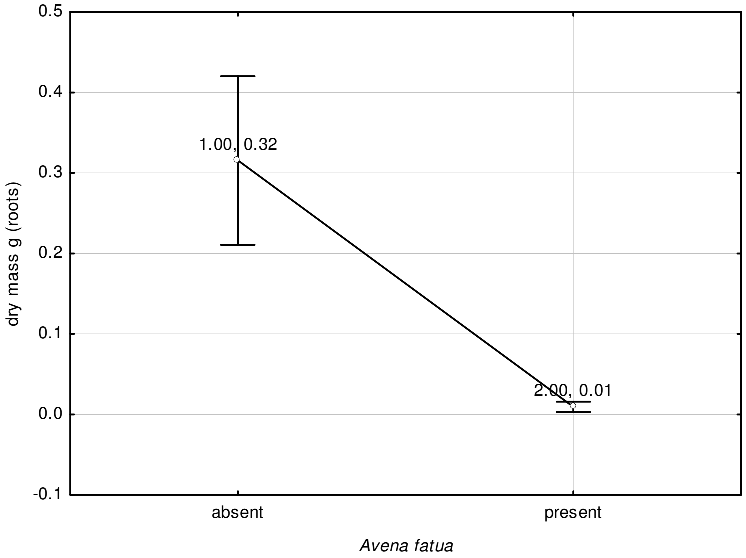


Figure 1: *Dimorphotheca pluvialis* weighted mean dry root mass with and without *Avena fatua*. F(1,36)=33.74, p<0.005.

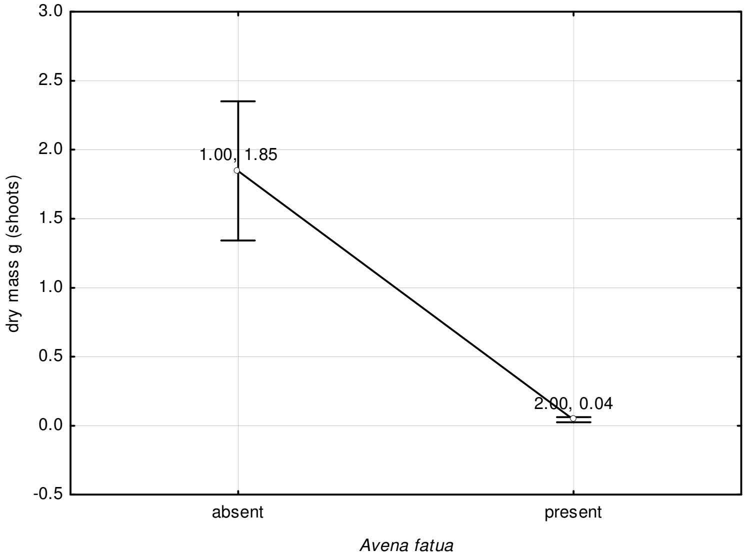


Figure 2: *Dimorphotheca pluvialis* weighted mean dry shoot mass with and without *Avena fatua* F(1, 36)=55.626, p<0.001.

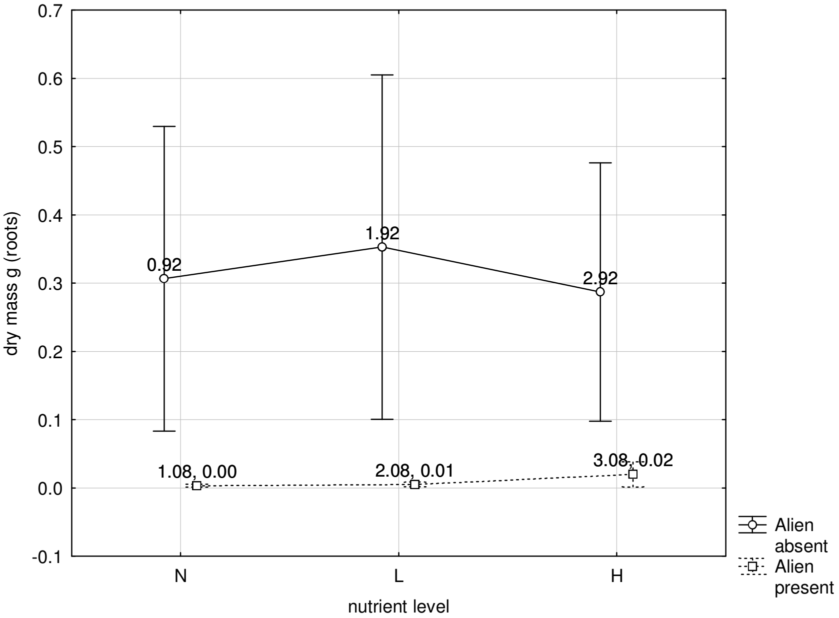


Figure 3: Weighted mean dry root mass of *Dimorphotheca pluvialis* with aliens present and aliens absent under three nutrient levels: F(2, 36)=.19700, p=.82207.

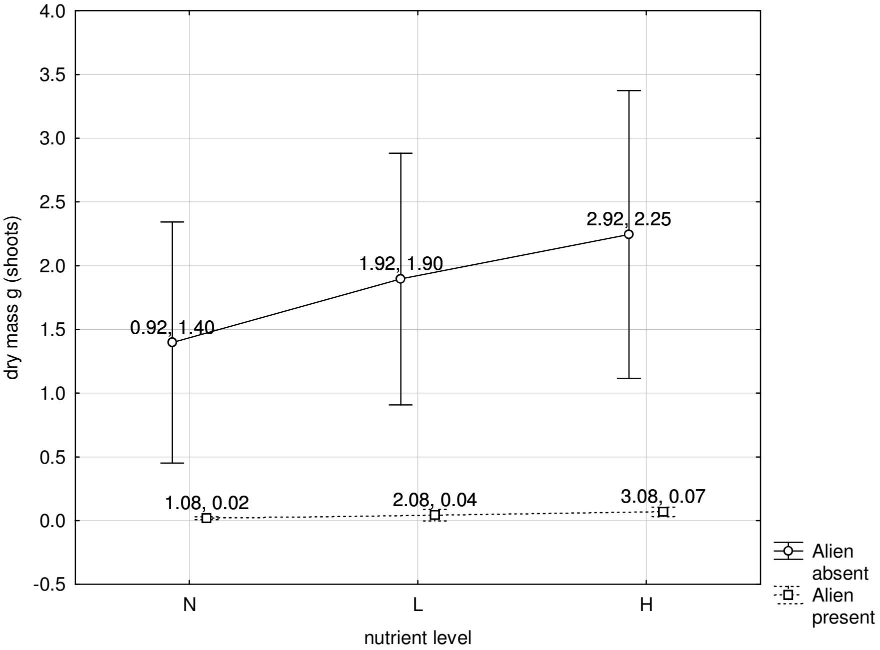


Figure 4: Weighted mean dry shoot mass of *Dimorphotheca pluvialis* with aliens present and aliens absent under three nutrient levels: F(2, 36)=.91997, p=.40770.

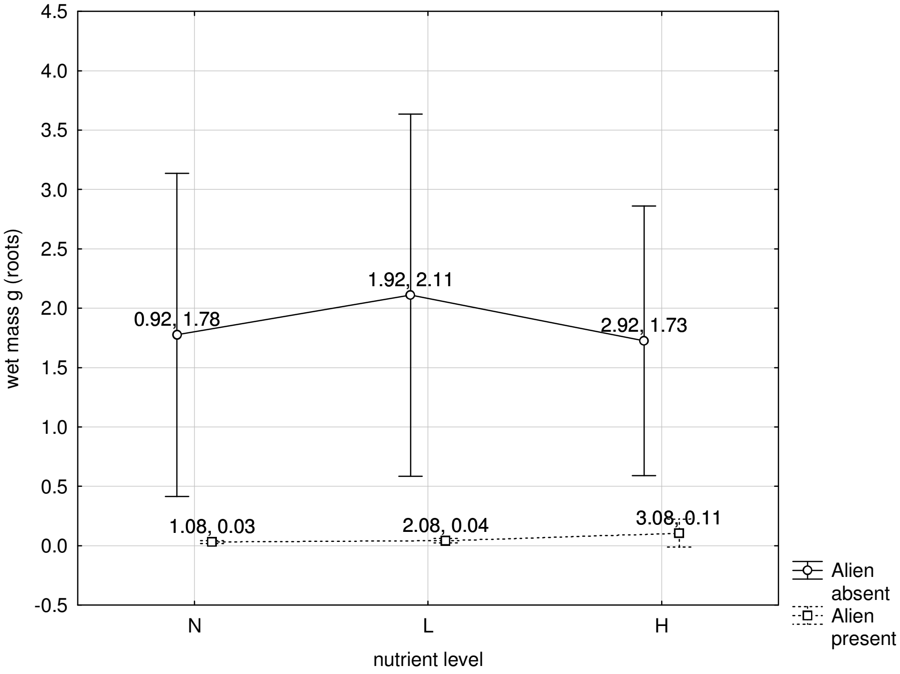


Figure 5: Weighted mean fresh root mass of *Dimorphotheca pluvialis* with aliens present and aliens absent under three nutrient levels:: F(2, 36)=.17640, p=.83900.

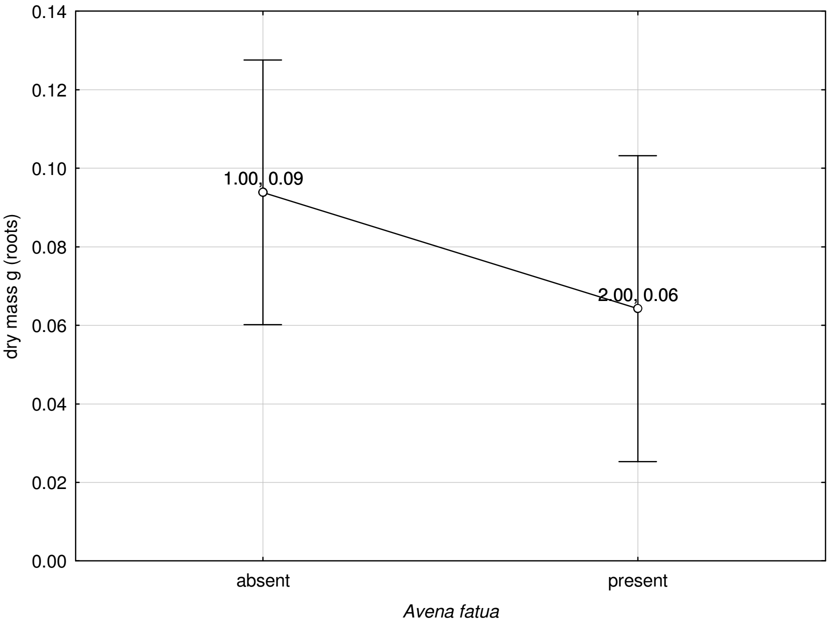


Figure 6: Weighted mean dry root mass of *Oxalis purpurea* with *Avena fatua* present and absent: F(1, 48)=1.4205, p=.23918

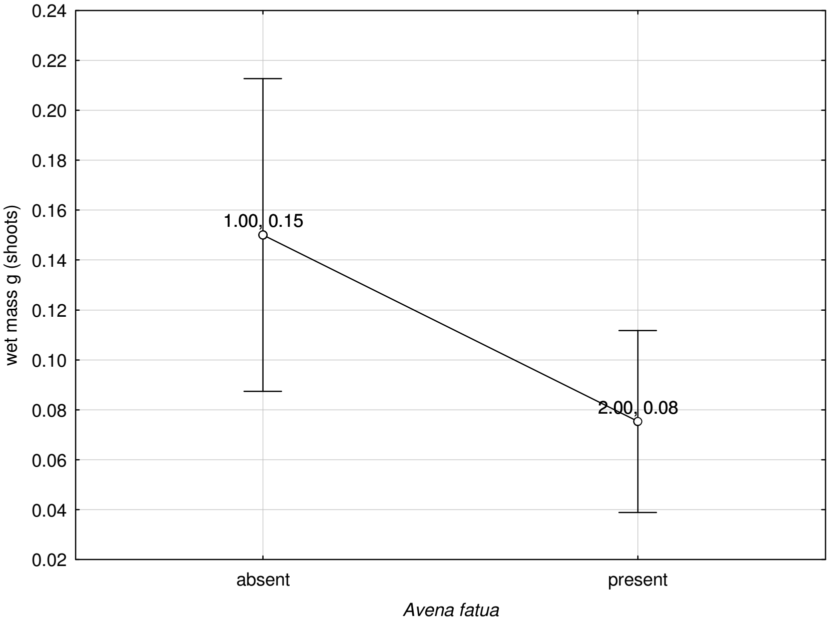


Figure 7: Weighted mean fresh root mass of *Oxalis purpurea* with *Avena fatua* present and absent: F(1, 47)=3.3443, p=.07379

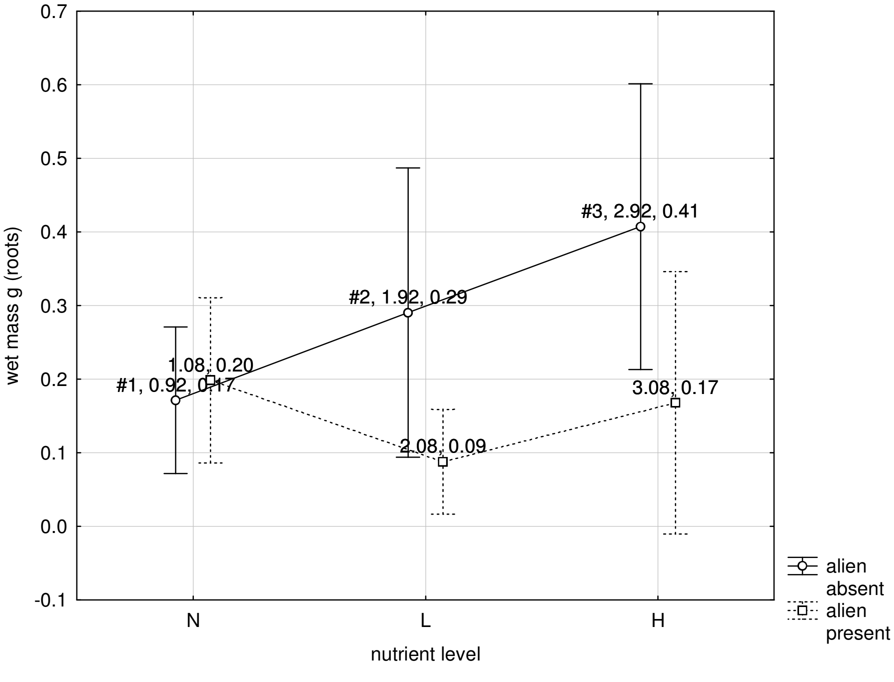


Figure 8: Weighted mean root fresh mass of *Oxalis purpurea* with and without *Avena fatua* under three nutrient levels: F(2, 48)=1.8960, p=.16124.

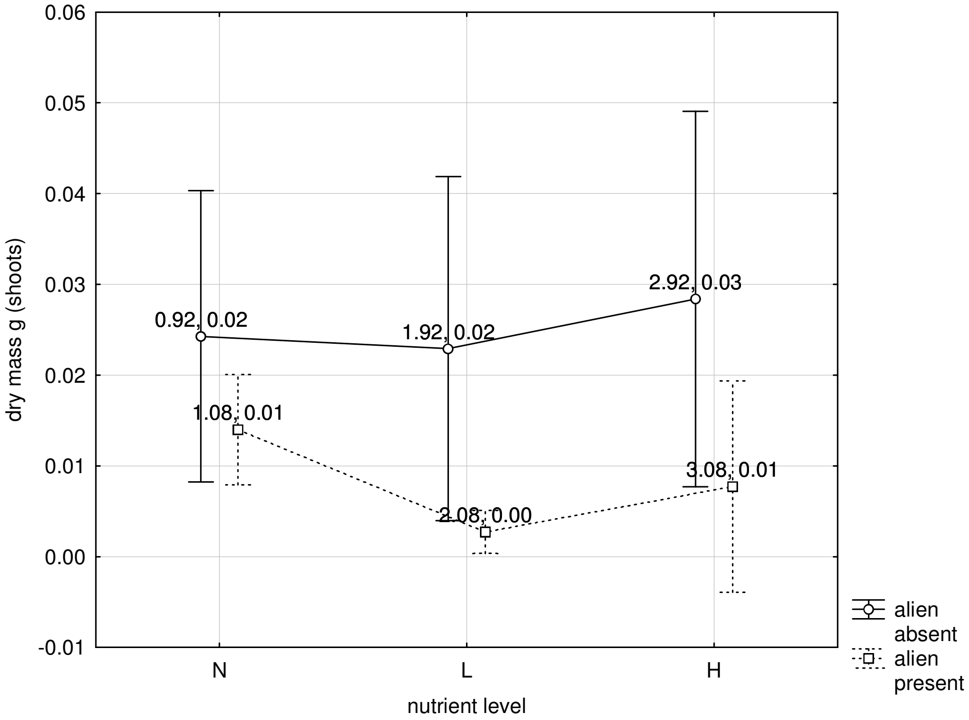


Figure 9: Weighted mean shoot dry mass of *Oxalis purpurea* with and without *Avena fatua* under three nutrient levels: F(2, 47)=.30701, p=.73711.

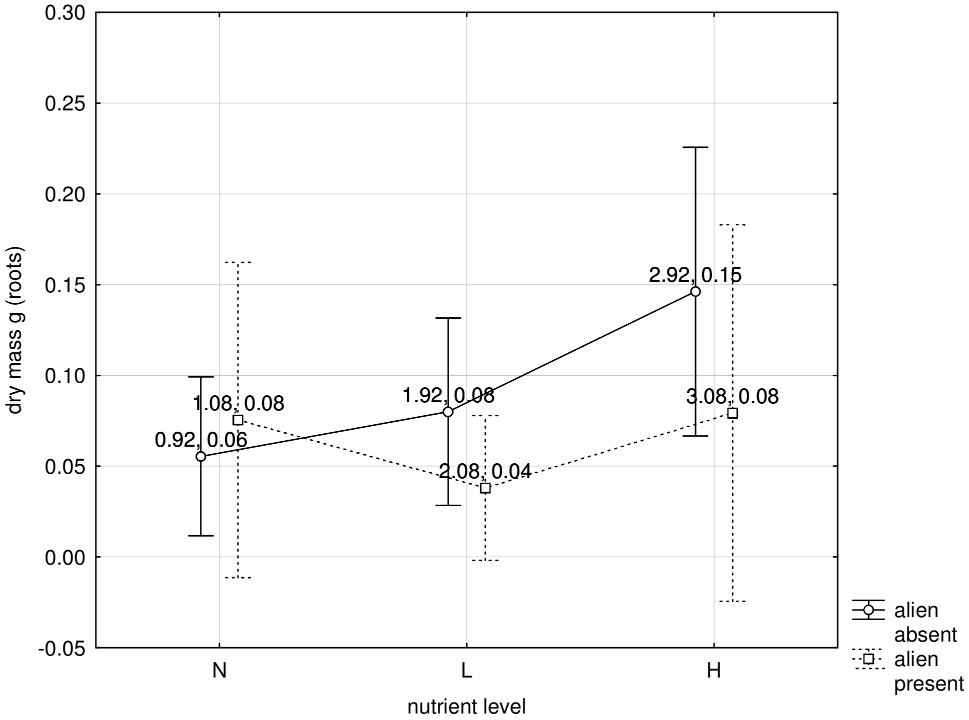


Figure 10: Weighted mean root dry mass of *Oxalis purpurea* with and without *Avena fatua* under three nutrient levels: F(2, 48)=1.0793, p=.34795

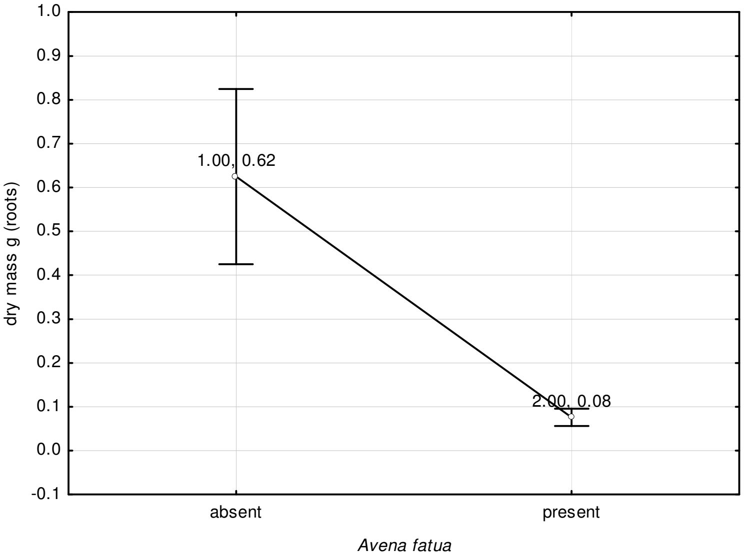


Figure 11: Weighted mean dry root mass of *Tribolium uniolae* with *Avena fatua* present or absent: F(1, 36)=36.205, p=.00000

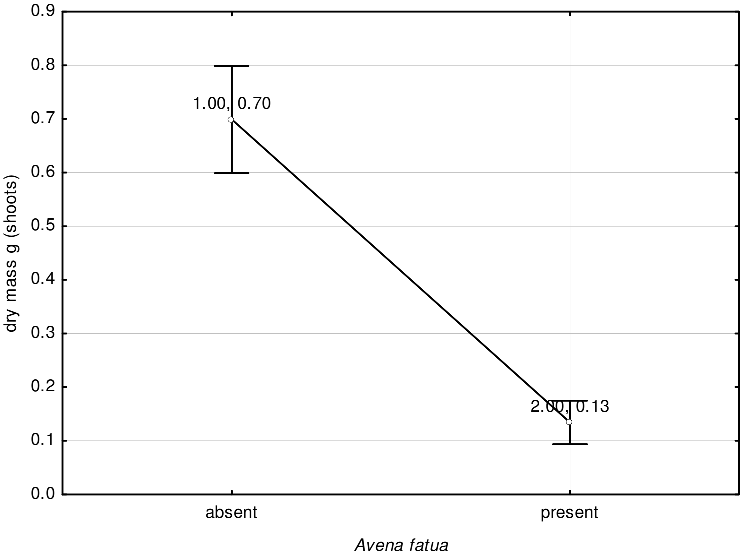


Figure 12: Weighted mean dry shoot mass of *Tribolium uniolae* with *Avena fatua* present or absent: F(1, 36)=125.25, p=.00000.

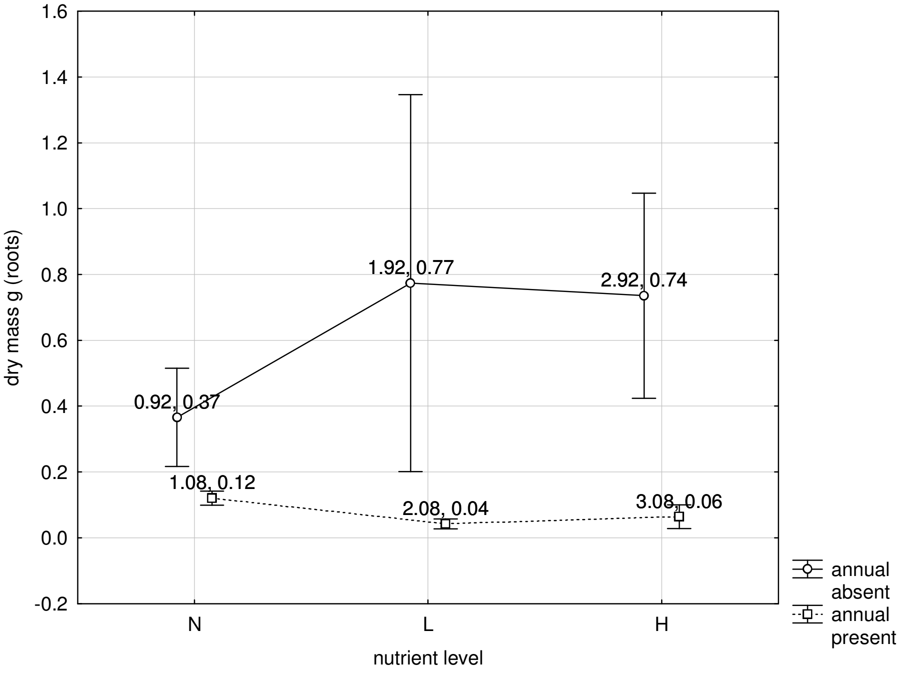


Figure 13: Weighted mean dry root mass of *Tribolium uniolae* with *Avena fatua* present or absent: F(2, 36)=2.8104, p=.07342.

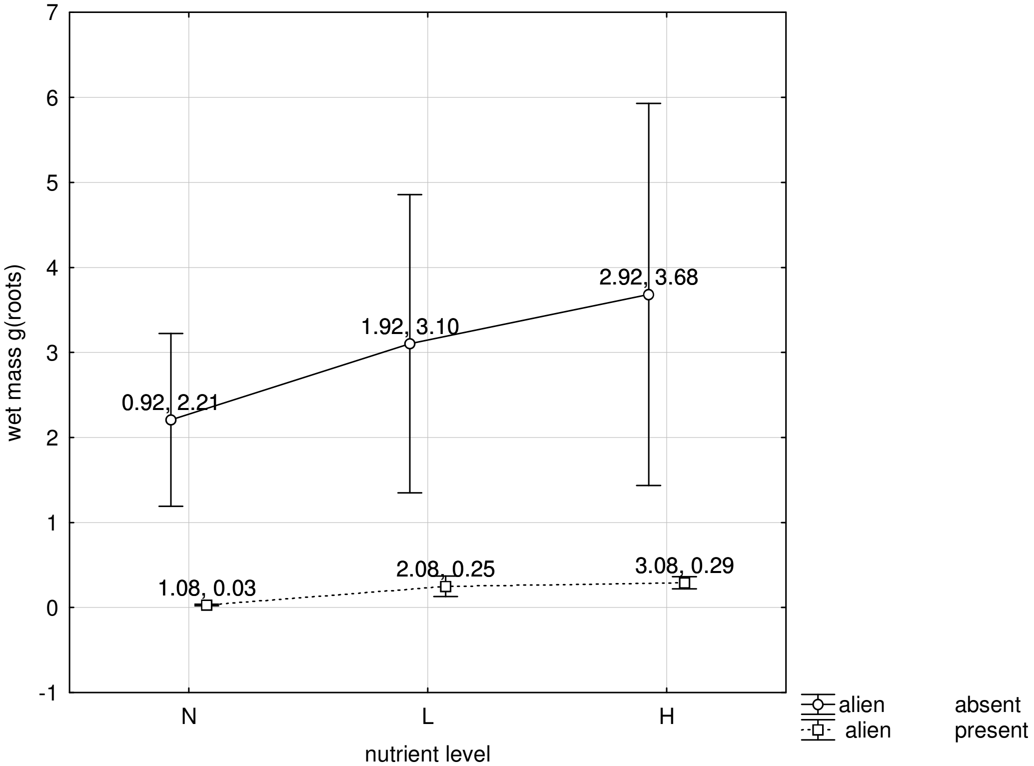


Figure 14: Weighted mean root fresh mass of *Tribolium uniolae* with and without *Avena fatua* under three nutrient levels: F(2, 36)=.72402, p=.49173

Appendix 4.2

Experiment progress

Monitoring of greenhouse experiment. *Avena fatua* emerged four days prior to indigenous grasses and growth was much more rapid. *Dimorphotheca pluvialis* only emerged ten days after *Avena fatua.* The geophytes *Oxalis purpurea* were the last to emerge fifteen days later and were still emerging towards the end of the greenhouse experiment.

2 Aug	6 Aug	9 Aug	12 Aug	15 Aug	17 Aug	22 Aug	5 Sept	13 Sept
Alien grasses emerged. nitrogen added.	Alien grass height: 2 cm. Indigenous grass height: 0.5 cm.	Alien grass height: 5 -15 cm. Indigenous grasses emerged, height: 1-2 cm. Alien grasses weeded to 10 per pot. Indigenous grasses weeded to 10 per pot.	Alien grass height: 12 -18 cm. Indigenous grasses height: 2 cm. annual height: 2 cm. geophytes height: 1 cm.	Indigenous grass height: 4 cm.	Geophytes present in all pots.	Alien grass height: 20-30 cm. Indigenous grass height: 7 cm.	Alien grasses height: 30-32 cm. Indigenous grass height: 15 cm Alien grasses with no N yellowing. Few geophytes in alien grasses died.	Indigenous grass height: 20 cm. Alien grasses yellowing in no N, less so in low N and still green in high N. Some dimorphotheca started to yellow. More oxalis emerged.

Appendix 4.3

Fresh mass f-ratios

Species		Competition	Nitrogen	Competition x Nitrogen
Dimorphotheca pluvialis	shoots	$F_{(1, 36)}$ = 45.18, p=0.00	$F_{(2,36)}$ =0.70, p=0.50	$F_{(2,36)}$ =0.52, p= 0.60
	roots	$F_{(1,36)}$ =32.27, p=0.00	$F_{(2,36)}$ =0.12, p=0.88	$F_{(2,36)}$ = 0.18, p=0.84
Oxalis pupurea	shoots	$F_{(1,47)}$ =3.54, p=0.07	$F_{(2,47)}$ =0.63, p=0.54	$F_{(2,47)}$ = 0.61, p=0.55
	roots	$F_{(1,48)}$ = 5.21, p=0.03	$F_{(2,48)}$ =1.22, 0.30	$F_{(2,48)}$ =1.90, p=0.16
Tribolium uniolae	shoots	$F_{(1,36)}$ =121.48, p=0.00	$F_{(2,36)}$ =1.76, p=0.19	$F_{(2,36)}$ =0.206, p=0.49
	roots	$F(_{1,36)}$ =46,29, p=0.00	$F_{(2,36)}$ =1.52, p=0.23	$F_{(2,36)}$ =0.72, p=0.49

Dry mass f-ratios

Species		Competition	Nitrogen	Competition x Nitrogen
Dimorphotheca pluvialis	shoots	$F_{(1,36)}$ =55.62, p=0.00	$F_{(2,36)}$ =1.16, p=0.32	$F_{(2,36)}$ =0.92, p=0.41
	roots	$F_{(1,36)}$ =33.74, p=0.00	$F_{(2,36)}$ =0.98, p=0.91	$F_{(2,36)}$ =0.20, p=0.82
Oxalis pupurea	shoots	$F_{(1,47)}$ =7.71, p=0.00	$F_{(2,43)}$ =0.41, p=0.67	$F_{(2,47)}$ =0.31, p=0.74
	roots	$F_{(1,48)}$ =1.42, p=0.24	$F_{(2,48)}$ =1.86, p=0.17	$F_{(2,48)}$ =1.08, p=0.35
Tribolium uniolae	shoots	$F_{(1,36)}$ =125.25, p=0.00	$F_{(2,36)}$ =2.60, p=0.09	$F_{(2,36)}$ =0.42, p=0.66
	roots	$F_{(1,36)}$ =36.20, p=0.00	$F_{(2,36)}$ =1.38, p=0.26	$F_{(2,36)}$ =2.81, p=0.07