

**FACTORS AFFECTING ALIEN GRASS INVASION
INTO WEST COAST RENOSTERVELD
FRAGMENTS**

By

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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.

Abstract

With only 1.76% conserved West Coast Renosterveld remaining it is crucial to prioritize the conservation and management of this fragile vegetation type. Because of its occurrence on fertile soils, renosterveld has been cleared for cultivation and other agricultural use and is thus fragmented to a critical point. These remaining fragments are subject to extensive edge effects and the exact parameters of a viable fragment must still be determined. The extent of alien grass species invasion into remnant renosterveld patches was determined using data collected using the line-intercept method. Sampling included three different management treatment areas adjacent to old lands: 1) a recently burned area, 2) a grazed area and 3) an unburned/ungrazed area providing a control sample. Additionally all small-scale soil disturbances along the lines were recorded.

*Results showed that *Briza* spp., *Bromus* spp. and *Avena fatua* were the most significant invading alien grass species. There was a significantly high variation between alien grass cover in each treatment, with the grazed area containing the highest overall level of alien grass invasion. The control area, with the exclusion of fire and animal activity, showed minimum alien grass invasion. Edge effects were apparent in all treatments, but were lowest in the control area, where percentage alien grass cover significantly decreased after a distance of fifteen meters into the remnant patch. A weak positive correlation between the occurrence of alien grass and indigenous grass was found, as well as evidence of a weak association between alien grass cover and shrub cover. The possibility that small-scale soil disturbances could be an important contributing factor to alien grass invasion was supported by the positive correlation between disturbances and percentage alien grass cover. A positive correlation was found between the occurrence of indigenous grass and small-scale soil disturbances, while shrub cover tended to be less associated with animal activity.*

It is concluded that the correct management regime could effectively control the excessive invasion of alien grass species into the remnant renosterveld patches. Grazing (including all animal activity and small-scale soil disturbances) was the main facilitator of alien grass establishment - even dominating the prominent consequences

of edge effects by facilitating alien grass establishment much deeper into the remnant patches. It could be assumed that a precise balance of low-pressure grazing and fire management should be established to enable the effective control of alien grass species while maintaining optimum biodiversity.

Keywords: renosterveld, alien grass, grazing, fire, management, small-scale soil disturbances

Uittreksel

Met slegs 1.76% oorblywende Weskus Renosterveld wat bewaar word, is die beskerming en effektiewe bestuur van hierdie bedreigde plantegroei 'n prioriteit. Die vrugbare grond waarop renosterveld voorkom, het veroorsaak dat dit uitgeroei word om eerder die kultivering van ekonomies produktiewe landbou gewasse moontlik te maak. Dus het renosterveld verminder en gefragmenteer tot 'n kritieke punt. Hierdie oorblywende klein areas bedek met renosterveld, is blootgestel aan ekstensiewe invloede van die omliggende areas en die presiese afmetings vir 'n effektiewe grote renosterveld fragment vir bewarings doeleindes, moet nog vasgestel word. Die mate van uitheemse gras spesie indringing in hierdie renosterveld fragmente is ondersoek deur die versameling van data deur die lyn-onderskep metode. Drie verskillende bestuursstelsels vir renosterveld is ondersoek om vas te stel wat die ergste graad van uitheemse gras indringing voorkom. Die studie het 'n 1) onlangs gebrande area, 2) 'n beweide area en 3) 'n kontrole area (wat nie gebrand of bewei is nie) ondersoek. Alle kleinskaalse grond-versteurings langs die lyne is ook aangeteken.

Die resultate het aangetoon dat Briza spp., Bromus spp. en Avena fatua, as uitheemse grasse, die belangrikste indringers was en dus die grootste bedreiging inhou. Daar was 'n beduidende hoë variasie tussen die mate van uitheemse gras bedekking aangeteken in elk van die bestuurs-stelsels. Die beweide area het die hoogste graad van uitheemse gras indringing getoon, terwyl die kontrole area (in die afwesigheid van vuur en weidings aktiwiteite) die meeste weerstand teen uitheemse gras indringing getoon het. Die invloed van die omliggende omgewing was ook duidelik sigbaar in al drie die bestuurs-stelsels, maar was duidelik minder in die kontrole area waar die persentasie

uitheemse gras indringing aansienlik verminder het na 'n afstand van vyftien meter in die renosterveld fragment in. 'n Swak positiewe korrelasie tussen die voorkoms van uitheemse grasse en inheemse gras spesies was aangeteken, asook bewyse van 'n swak negatiewe assosiasie tussen die uitheemse gras spesies en die inheemse bosse. Soos verwag, is daar bewyse gevind vir die teorie dat kleinskaalse grond-versteurings 'n belangrike fasiliterende faktor is vir uitheemse gras vestiging. Daar was 'n duidelike positiewe korrelasie tussen hierdie grond-versteurings en die persentasie uitheemse gras grondbedekking. Dieselfde positiewe assosiasie was gevind tussen die inheemse gras en hierdie kleinskaalse grond-versteurings, terwyl die inheemse bossie duidelik minder verbind was met die verskynsel.

Die gevolgtrekking is gemaak dat 'n korrekte bestuurs-plan die indringing van uitheemse grasse effektief sal kan beheer. Dier aktiwiteite (insluitende beweiding, grawe van gate, mier en termiet neste ens.), en dus kleinskaalse grond-versteurings, was die grootste fasiliteerders van uitheemse gras indringing en vestiging binne hierdie renosterveld stukke. Dit oorheers selfs die aansienlike effek wat invloede van die omringende omgewing op hierdie areas het, deur die uitheemse gras indringing selfs dieper in die fragmente in aan te help. Daar kan dus aangeneem word dat 'n presiese balans tussen lae-intensiteit beweiding (en dus fauna aktiwiteit) en veld brande vasgestel moet word vir die effektiewe beheer van uitheemse gras spesies terwyl die optimum bio-diversiteit terselfde tyd gehandhaaf word.

Sleutelwoorde: renosterveld, uitheemse grasse, beweiding, vuur, veldbestuur, kleinskaalse grond-versteurings

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Chapter 1

Introduction

Introduction

Renosterveld is an extremely endangered vegetation type of the Cape Floral Kingdom. It is closely related to Fynbos but lacks the constant presence of the characteristic plant families such as Proteaceae, Ericaceae and Restioaceae. The crucial difference between these vegetation types is the fact that renosterveld is situated on fertile soils as opposed to the leached, sandy soils preferred by fynbos. Because of the climate, rainfall and fertility of the soils, renosterveld has been cleared for agricultural activities in the past. The extent of this destruction was not stopped before almost all of the pristine areas were demolished. The result was isolated fragments of renosterveld left on areas that, primarily, could not be cultivated. The remaining patches have recently become priorities for conservation and research in order to obtain information on the dynamics of this vegetation type. There is little information about how to manage this veld type effectively, and currently it is still under threat from continuous agricultural expansion and mis-management. One of the main problems facing the remaining fragmented areas is the invasion of alien plant species. The remaining patches are small and therefore subject to extensive edge effects from the surrounding cultivated lands. Alien invasion in any vegetation type has severe effects on the biodiversity and dynamics of the specific indigenous vegetation and should be a major focus point in the conservation of the remaining small renosterveld fragments.

D'Antonio and Vitousek (1992) state that grasses are one set of invading species that, if sufficiently widespread, may effectively alter regional and even global aspects of ecosystem function. This study focuses on the invasion of alien grass species from surrounding cultivated lands and rehabilitating old lands under different management regimes (burning and grazing). The extent of invasion and identification of the alien species that pose the greatest threat would contribute knowledge and possibly a better understanding about the dynamics of renosterveld. It could provide the basis for

establishing best management practices for the effective conservation of the fragments that are left and also determine the precise parameters necessary to maintain a fragment in a pristine condition.

1.1 Introductory comments on thesis structure

The first chapter consists of a literature review to provide background information and an overview on what is currently known about renosterveld. The second chapter provides a description of the areas selected for the collection of data and examination of the current management regime, an area recently burned (and grazed by game), an area subject only to grazing (no recent fire) and a control area (neither burned nor grazed). It is followed by reports (discussed in Chapter 3) on plants recorded along line-intercept transects in the three differently managed West Coast Renosterveld fragments, respectively bordered by rehabilitating old lands (the burned and grazed remnants) and fertilised cultivation (the control area). From these results the extent of alien grass invasion into each of the fragments, subject to each treatment, could be evaluated to determine which management regime most effectively inhibits alien grass invasion. The extent of edge effects and thus the impact of the surrounding areas can also be seen and combined with the occurrence of small-scale soil disturbances and indigenous vegetation, to form a picture of what factors influence alien grass invasion into these remnant patches. The conclusions (discussed in Chapter 4) could contribute to the establishment of improved management regimes to minimise alien invasion while optimising biodiversity in these West Coast Renosterveld fragments and so ensure their survival.

The third chapter is written in paper format with formatting and layout in accordance with instructions to authors of *Diversity and Distributions* (for intended submission), so by design has some element of repetition with the more expansive literature review (Chapter 1) and study site chapter (Chapter 2). The thesis is also written for an intended audience of conservation biologists, conservation planners, private landowners, managers within conservation agencies, conservation extension officers and environmental policy makers.

1.2 Climatic and edaphic determinants of renosterveld

The Cape floral kingdom is concentrated in the region known as Capensis, which has been subdivided into two main formations, namely, the heathlands on oligotrophic soils which are fynbos and Mediterranean-type shrublands, and renosterveld and strandveld, found on the more fertile soils (Boucher 1983). West Coast Renosterveld is largely confined to Malmesbury Group shales, Cape Granite Suite and Klipheuwel Formation shales, which weather to form heavy clays and loamy soils. In drier areas it also occurs on Cape Granite Suite-derived soils (Low & Rebelo 1996). These soil types are found just north of Piketberg, to Somerset West, mainly on the lowlands and low hills. The area is typically Mediterranean with predominantly winter rainfall and hot, dry summers conducive to fires (Low & Rebelo 1996). Annual rainfall varies from 300 – 600 mm. Where annual rainfall is ≤ 250 mm, renosterveld is replaced by Succulent Karoo vegetation, while in areas where the rainfall is >600 mm it is replaced by Mountain Fynbos.

1.3 The floristic and structural features of renosterveld

Moll *et al* (1984) and Cowling & Heijnis (2001) distinguish between different types of renosterveld (according to location). This study is restricted to the Boland subtype of Coast Renosterveld as defined by Cowling & Heijnis (2001). West Coast Renosterveld differs from the South Coast Renosterveld in having a sparser grass cover, composed largely of C_3 genera (*Ehrharta*, *Pentaschistis*, *Merxmullera*, *Lasiochloa*, *Plagiocloa*, *Tribolium*, *Cymbopogon* and *Eragrostis*), a higher diversity of deciduous geophytes and annuals and the presence of *Eriocephalus africanus* and *Layserra gnaphaloides* as characteristic subdominants with *Elytropappus rhinocerotis* (Moll *et al* 1984) as a dominant. West Coast communities have a stronger fynbos influence and Boucher (1983) has suggested that West Coast Renosterveld is derived from mountain fynbos and strandveld elements. Fifty four percent of the species found in a broad-scale survey also occurred in Mountain Fynbos vegetation (Boucher 1983). Proteas, Ericas and Restios –typical of Fynbos – tend to be absent or very low in abundance. Renosterveld does share some endemic species with Fynbos and 1/3 of species endemic to the Cape Floral Kingdom are endemic to renosterveld (Low &

Rebello 1996). For its size, West Coast Renosterveld probably has the richest flora worldwide (McDowell & Moll 1992). C.A.P.E. (Cape Action Plan for the Environment) proclaimed Lowland Renosterveld to be 100% irreplaceable (Krug 2001) due to the fact that it has the highest recorded concentration of threatened plants, namely an average of approximately one species per square kilometer of remaining vegetation. The concentration of Red Data species is greatest in the remaining habitat because their ranges have been so reduced by intensive development (McDowell & Moll 1992).

A general description of renosterveld would be a mid-dense to closed (50 – 90% canopy cover) cupressoid and small-leafed, mid-high evergreen shrubs with regular clumps of broad-leafed tall shrubs as emergents (especially on heuweltjies). renosterveld is characterized by the dominance of members of the Daisy Family (Asteraceae), specifically one species – *Elytropappus rhinocerotis* (renosterbos) from which this vegetation type derives its name.

The overstorey is dominated by Renosterbos with subdominants of *Eriocephalus africanus* (wild rosemary), *Leysera gnaphalodes* (dune teabush), *Anthospermum aethiopicum* (jakkalsstert), *Athanasia trifucata*, *Felicia filifolia*, *Metalasia muricata* and *Stoebe spiralis* (Low & Rebello 1996). The understorey is essentially annual and herbaceous with perennial graminoids (Moll *et al* 1984). The general (above mentioned) perennial grass species are abundant with *Themeda triandra* (redgrass) and *Cymbopogon marginatus* (cape terpinetine grass) being the characteristic species. Management regimes consider the re-establishment of a vigorous *Themeda triandra* grassy sward to be the most effective long-term conservation strategy since utilization would be compatible with conservation. Assigning economic value to an otherwise ‘useless’ vegetation type would serve as an incentive for farmers to conserve remaining renosterveld patches on their land. Burning in autumn seems the optimum season of burn to re-establish grass dominance (Cowling *et al* 1986, Diemer 2000).

Acocks (1979) concluded the general species richness to be approximately four species per meter and a study done by Heydenrych and Littlewort (1995) on seven renosterveld hills in Darling, listed 420 indigenous species containing only seven Red Data Book species. Boucher (1983) analyzed the life history attributes of West Coast

Renosterveld flora based on a sample of 181 species from 133 plots (Table 1.1). The most prevalent plant families present in West Coast Renosterveld and the dominant genera within these families as recorded by Low & Rebelo (1996) and Holmes (2002) are given in table 1.2. Still, the largest part of the immense floristic value of renosterveld consists of the diversity of the geophytes found in this vegetation type. The high species richness of geophytes consists primarily of Iridaceae, Liliaceae, Oxalidaceae and Orchidaceae (Heydenrych 1995).

Table 1.1: *The floristic and structural features of West Coast Renosterveld (data from Boucher 1983)*

<i>Life/Growth form</i>	<i>Percentage cover</i>
Geophytes	22 %
Hemicryptophytes	13 %
Sprouting shrubs	27 %
Succulents	7 %
Seeders maturing in < 5 yrs	30 %
Seeders maturing in > 5 yrs	1 %
No of Red Data Book spp. in 7 280 km ²	187 (2.6 spp./km ²)

(*Percentage cover* portraying the percentages of species in the various life-history categories based on a floristic sample of 181 species)

Table 1.2: *The prominent Families and Genera from the various families found in West Coast Renosterveld (obtained from Low & Rebelo 1996, Holmes 2002)*

Family	Genus
Asteraceae	<i>Eriocephalus, Felicia, Helichrysum, Pteronia, Relhania</i>
Fabaceae	<i>Aspalathus</i>
Rubiceae	<i>Anthospermum</i>
Sterculiaceae	<i>Hermannia</i>
Thymelaeaceae	<i>Passerina</i>

1.4 Natural disturbance regimes of the past and its affects

Termites (heuweltjies), fire, grazing and their interactions

In the past South Coast Renosterveld, in particular, was allegedly dominated by grasses e.g. *Themeda triandra* (rooigras) and other tussock forming species that were replaced by higher shrub cover due to the establishment of European stock farmers (Low & Rebelo 1996, Cowling *et al* 1986). The transformation from migrating game and nomadic pastoralism of Khoi to sedentary pastoralism and crop cultivation of European farmers resulted in the elimination of much (bio)diversity and general change from grass-dominated to shrub-dominated elements (Tainton 1999). This notion is supported by current palynological studies on deposits, which show a very recent shift in dominance from Poaceae to Asteraceae pollen (Cowling *et al* 1986). Because of the high soil fertility it is probable that all herds of large game in the Fynbos biome occurred in renosterveld. Of the following species, *Equus zebra* (mountain zebra), *Equus quagga* (quagga), *Hippotragus leucophaeus* (bluebuck), *Alcelaphus buselaphus* (red hartebeest), *Taurotragus oryx* (eland), *Diceros bicornis* (black rhino), *Loxodonta africana* (elephant), *Syncerus caffer* (buffalo), *Panthera leo* (lion), *Lycaon pictus* (wild dog) and *Acinonyx jubatus* (cheetah), only *Equus zebra* (mountain zebra), *Panthera pardus* (leopard) and *Damaliscus dorcas dorcas* (bontebok) survived (Low & Rebelo 1996, Walker 1986). Even smaller fauna, such as the *Psammobates geometricus* (geometric tortoise) (Baard 1993, Baard 1995, Greig & De Villiers 1982) is suffering the consequences of the elimination of this unique vegetation type.

Bush clumps randomly scattered through renosterveld are associated with *Microhodotermes viator* termitaria, which have been present in the area for the last one million years (Boucher 1983). These clumps also cluster around rock outcrops and drainage lines, probably due to the more favourable, moist, local conditions (Boucher 1983). Clumps are dominated by typical Thicket Biome species, such as *Olea europaea* subsp. *Africana* (wild olive), *Rhus laevigata* (dune taibos) and *Euclea racemosa* (bush guarri) (Low & Rebelo 1996).

1.5 Conservation status and land-use

Renosterveld has been dramatically reduced from its prior extent. An original 512 266 ha of this vegetation type has been reduced to 29 502 ha (6%) (Figure 1.1) of which only 2 063 ha (0.4% of original area) was recorded as formally conserved by Parker in 1982. The statistics for West Coast Renosterveld showed that approximately 97% of this sub-type is transformed with a mere 1.76% conserved (Hoffman 1997, Holmes 2002, Low & Rebelo 1996) of which 80% is privately owned (McDowell & Moll 1992). Parker (1982) stated that forty one percent of the sub-continent's extinctions and 36% its endangered plants are concentrated in this region. Recent studies list West Coast Renosterveld (as well as South and South-west Coast Renosterveld) as one of the top ten priority conservation vegetation types (Reyers *et al* 2001). Specific statistics shows a total of 9% natural West Coast Renosterveld remaining of which 1.1% is degraded, 89.8% is transformed, 0.7% is protected and 8.1% is subject to road-effect. This clearly emphasize the need for the urgent establishment of secure reserves and correct management strategies to ensure the survival of the remaining species.

No renosterveld shrubland reserves are larger than 10 000 ha, only four of these reserves exceed 500 ha in size. Other vegetation types contain many reserves larger than 500 ha (Rebelo 1992). Fynbos 'islands' supported significantly fewer species than mainland sites of the same area, with up to 75% extinction on the smaller islands (Cowling *et al* 1997). The island effect disappeared at about 600 ha (Bond *et al* 1988, Cowling & Bond 1991). The species were apparently lost due to the change in the disturbance regime of these smaller areas. It was thus concluded that all reserves less than 500 ha will invariably require management to maintain species richness (Rebelo 1992). As renosterveld patches mostly fall into this category, it is crucial to determine how big these patches should be to comply to the minimum viable population size theory. This theory emphasizes the concept of a critical range of population sizes below which demographic, genetic, and environmental stochasticity strongly reduces a population's chances of long-term survival (Cantrell & Cosner 2001). Small, patch sized reserves may be feasible, provided that ecological processes shared between patches, such as fire regimes, water table dynamics and dispersal, are maintained and

thus connectivity is a crucial factor – absent because of impracticability in most cases (especially on farms). In general management authorities consider 500 – 1500 ha as the optimal-sized fire compartment and 5 000 ha as the minimum reserve size required. To maintain an even distribution of habitat age-classes and a minimum of 4 – 15 ha as a reserve size is needed to prevent species loss from fragmented areas (Cowling & Bond 1991). Road reserves form a large component of the potential area available for the preservation of Lowland Renosterveld shrubland. Within the Greater Cape Town metropolitan area, the road reserves alongside national roads alone amounts to more than 45 ha – a potential 10% increase in the area available for reserves. There seemed to be a resistance to the idea of road reserves in the Cape Floristic Region, with authorities favoring the maintenance of road verges as mowed grass parks (Rebello 1992), but recently the South African National Roads Agency has started to recognize the importance and possibility of road reserves (Van Rooyen pers. comm. 2002).

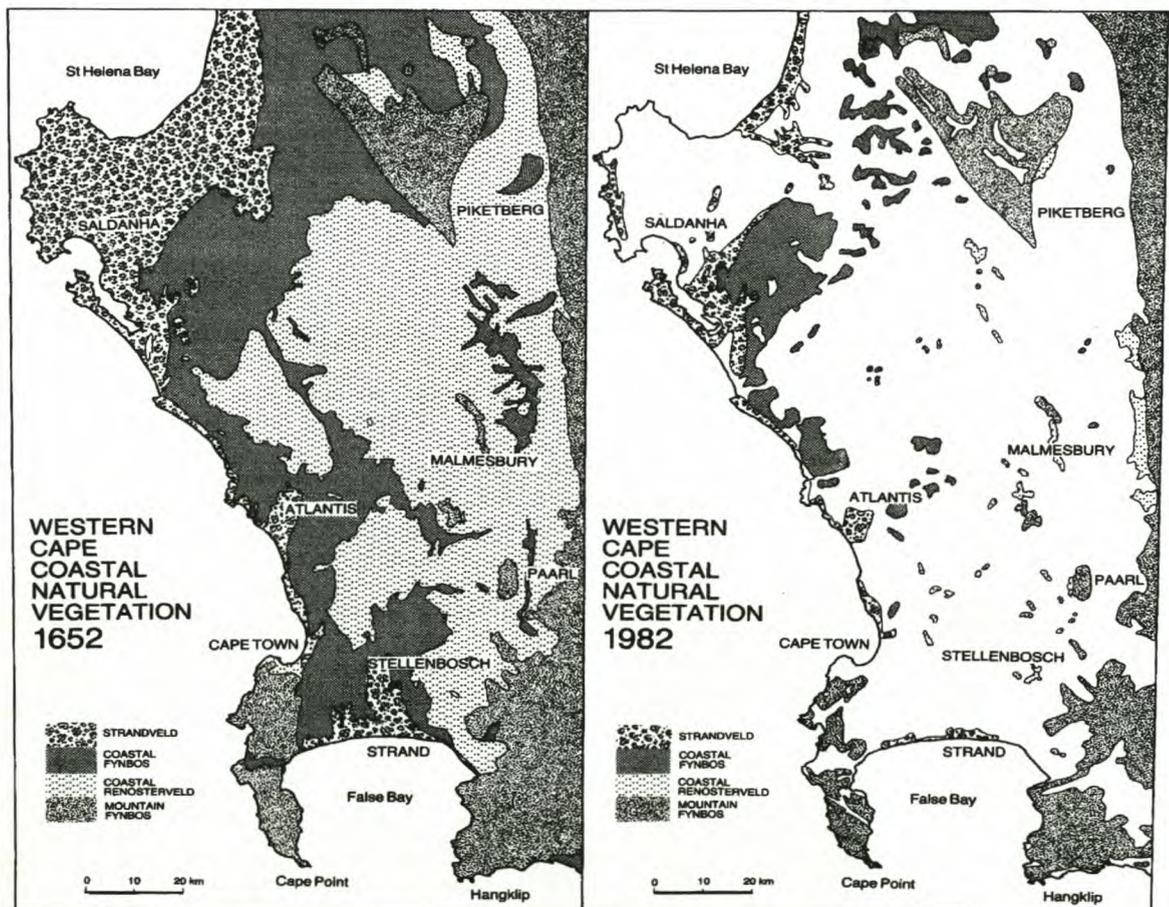


Figure 1.1: An illustration of the reduction in natural vegetation in the Western Cape Coastal Region from 1652 to 1982 (from Parker 1982)

The primary cause of the extensive annihilation of renosterveld is the cultivation of the fertile Malmesbury shales on which it is found. The area falls into the prime small-grain producing soils (Low & Rebelo 1996, Parker 1982). The fertile soils proved valuable for cultivation of wheat, oats and barley (60% of the total for the country is grown here), fruit, vines (particularly confined to this area), citrus, tobacco, lucerne and vegetables (Adamson 1938). Historically, the markets increased and transportation networks improved and so the focus on the grain-cropping industry shifted towards the clay-rich soils of the renosterveld. The West Coast lowlands were cleared earlier than those of the southwest and south coast (Hoffman 1997).

The additional invasion and subsequent shift in dominance to *Elytropappus rhinocerotis* (renosterbos) restricted the use of renosterveld as rangeland. Farmers considered *Elytropappus rhinocerotis* a weed, due to the fact that it has no grazing value, and owners were compelled to replace the natural vegetation with cultivated crops which, in short term, certainly yield greater economic rewards (Cowling *et al* 1986). Thus, due to the increasing pressure on land values and the necessity for economic productivity, the remaining fragments of renosterveld (Figure 1.1) are disappearing as steeper hillsides are coming under cultivation, river courses are altered and vlei (wetland) areas are drained. Patches of natural veld still remaining, are surrounded by cultivated lands and subject to injudicious management regimes (in terms of grazing and veld burning) which, among other, leads to alien plant invasions (Parker 1982). For this reason, this particular study could prove to be informative, as well as crucial, in assisting the preservation of these relic fragments.

1.6 Invasive alien plants

Most alien introductions were done in the period 1850 - 1900 due to the benefit that the species held for humans in terms of food, shelter, medicine, aesthetic enjoyment or cultural identity (Kowarik 1995). The introductions resulted in a significant proportion alien plant invasives in both natural and agro-ecosystems, spreading beyond the confines of their intended uses (Pyke & Knick 2003). Today, the impact

of these introductions on the reduction of global diversity, is only second to habitat destruction (Vasseur *et al* 2002).

Non-indigenous grasses are the biggest problem in the West Coast Renosterveld and the focus of this study. Presently the Mediterranean annual grasses, *Avena fatua* (oats), *Briza maxima* and *Briza minor* (quaking grass), *Bromus pectinatus* (japanese brome) and *Lolium perenne* (ryegrass) are widespread and common (Duvenhage 1993, Helme pers. comm. 2002). These grasses hybridize extremely rapidly and species are largely irrelevant. Additionally problem species include *Pennisetum clandestinum* (Kikuyu), *P. setaceum* and *P. macruorum* in wetter areas and near nutrient sources (farms, etc.), as well as the legume, *Trifolium angustifolium*. The African bunch grass, *Hyparrhenia hirta*, which is not indigenous in the winter-rainfall region of South Africa, is very invasive in some areas, but not so detrimental in the Swartland (Helme pers. comm. 2002). As for bulbs, *Oxalis pres-caprae* may be a problem in some places in the Overberg and Grabouw areas. In the Overberg, *Berkheya rigida* (an indigenous invasive) from ploughed lands poses a big problem, and in certain areas (only the Potberg lower slopes), *Acacia cyclops* and *Acacia saligna*. These species are only a problem in very limited areas of the Swartland, where they invade from the sandy fringes of true renosterveld patches. Other species invading from cultivated lands include *Rapistrum rugosum* (wildmostert), and *Echium plantagineum* (Swartland and Overberg) (Helme pers. comm. 2002).

Alien species infiltrate most, if not all, communities due to various factors, giving non-native species the competitive advantage over the indigenous species of a given area. Some of these plant characteristics include:

- Habitat factors – factors facilitating the establishment or dispersal of alien species such as soil moisture, structure or composition / high or low moisture availability or humidity / increased human activities / historical factors (the background of the area – including previous or surrounding land-uses)
- Biotic factors – increased or decreased competition, repellent characteristics for herbivores, more effective dispersal modes, further dispersal modes and the lack of natural enemies

- Demographic factors – larger seed crop size, faster growth rates, higher seed survival and maturity (D'Antonio & Vitousek 1992, Dean 1998, Kowarik 1995, Reichard 2001, Rejmanek 1995)

These factors come into play on a smaller scale, while on a broader scale, the ability of an alien plant to invade a region depends not only on attributes of the plant, but on characteristics of the habitat being invaded (Larson *et al* 2001, Pyke & Knick 2003). Fragmentation, representing one of these habitat characteristics, increases edge effects through the increased area to edge ratio of small fragments. Edge effects are usually all factors that change the physical environment (micro-climate, soil fertility, etc.) or biota (increased dispersal of introduced species, etc.). Together with disturbances, edge effects influence vegetation dynamics and composition of remaining natural vegetation and in such a way facilitate alien grass invasion.

Introduced species sometimes persist in small colonies, often in cultivation, for several generations before invasion is noticed. One explanation offered, is the so-called 'infection pressure' (With 2002). The hypothesis is that the introduced species would have to reproduce for sufficient generations locally for the population to reach a condition that allows spread from the point of introduction (Baker 1986). It is speculated that this could be connected to the founder effect, in that a population arising from one or a few initial seeds would require time before sufficient genotypic variation could evolve to permit colonisation of variable habitats. This fact could explain the percentage cover of alien grass species found under various management regimes, considering temporal factors. It could also be assumed that surrounding fertilised crops possibly accelerate the whole process and extent of alien grass invasion as they already contain genotypic variation needed for survival in that particular area. Fertilised crops also contribute to the invasion susceptibility of renosterveld remnants by providing a protected, nurturing environment for alien grass populations to pass through the initial phase of exponential growth to the stage where a problematic invasion would be facilitated. The other factors taken into consideration, possibly more prominent, would be some change in the environment, that is needed before the species' requirements for spread are met - the conditions required for spread occurring episodically and infrequently (such as fires, seasonal grazing etc.) (Hester & Hobbs 1992). Alien grasses were found to be a huge problem after fires, especially in the Swartland, as they rapidly out-compete the indigenous

species (Helme pers. comm. 2002). In conclusion, it is thus logical that alien invasions would be common in disturbed areas and that recent invaders are often rare in pristine communities (Williamson 1996).

Seeing that remaining renosterveld fragments are, without exception, exposed to extensive edge effects from surrounding pasture or cultivated lands, it could be deduced that the disturbance regime within these patches would be altered. This would influence the vegetation dynamics and composition and create a 'plant invasion window' for alien species to infiltrate. A characteristic feature of many successions seems to be dependence of invading species on just the right window in the successional sequence to enter the community and proliferate (Richardson *et al* 1992). A brief, initial period of dominance by weedy annuals has been observed by Holt *et al* (1995) as typical in recently abandoned old fields. On the other hand, negligent management of grazing creates the opportunity for competitive and easily established alien species to colonize the areas, especially those disturbed frequently or to a greater extent such as along the edges of remnant patches. Colonization through the patches occurs more rapidly along the edges and then the plants spread through local, within patch dispersal (Harrison *et al* 2001). Evidence to support this was found in a study done by Tyser and Worley (1992), where the alien plant species richness and abundance declined with increased distance into natural vegetation.

Initial establishment could also enhance the rate of succession, where established individuals sustain a dominance (in terms of competition for resources, etc.) over the natural successional species, and thus facilitate the establishment of other alien invasive species (Holt *et al* 1995). Many introduced plant species may even use mutualisms, such as animal-mediated seed dispersal and symbioses between plant roots and micro-biota, in their new habitat to overcome barriers to establishment and to become naturalized or invasive. Mutualistic relationships formed between alien grass species and other organisms (native or themselves) already established in the system, would also contribute to the enhancement of the invasion process (Richardson *et al* 2000). Alien species could even change the habitat conditions as to be less favorable for the indigenous species, for example by changing nitrogen dynamics, fire regimes or surface water resources (Le Maitre *et al* 2000). The higher seed production and dispersability of alien species would also provide them with a

competitive advantage over the indigenous species in the fragmented landscapes (Rouget *et al* 2001). Combined with the absence of any important natural enemies that control population growth (Richardson *et al* 1997) – it is not surprising that alien species flourish in disturbed or altered environments. Early stages of colonization is a critical phase in the invasion process and could predict the success or failure of introduced species to invade, as well as to represent the stage at which invasions could be managed (Higgins 1998). Further modeling studies are required to determine how invasion rates changes with increasing fragmentation.

Dukes (2002) found a negative relationship between species richness and the impact of invaders. Other studies infer that invasibility is positively correlated with the number of ‘empty niches’ (Pyke & Knick 2003, Richardson *et al* 2000, Vlok 1988). This suggests that declining biodiversity can reduce a community’s resistance to invasion. Although renosterveld contains a high level of species richness, the surrounding cultivated lands and subsequent increased level of propagule influx (Harrison *et al* 2001) could lead to a reduction in resistance against alien grass invasion and thus increase the impact of the non-native species within the fragments.

These invasive plant species have the potential to significantly alter ecosystem composition and functioning after invasion (D’Antonio & Vitousek 1992, Simons 1998). One of the most important consequences of alien invasion, proven by experiments, was found to be the significant reduction in regeneration of dominant woody species (Hobbs & Atkins 1991). Perennial indigenous grass species (Dyer & Rice 1997) and indigenous annuals and geophytes (Baard 1993, Cowling *et al* 1997, D’Antonio & Vitousek 1992) are also severely threatened by these alien annuals, but further studies are needed to determine the exact magnitude of this threat. Another consideration includes the threat to biological soil-crust communities. The previously crust-dominated interspace between perennial plants is often subject to these invasions (Belnap & Eldridge 2001). The dominance of alien grass species would thus illuminate the biological soil crusts and their role in the existing vegetation dynamics. This could have a possible effect on soil-moisture, temperature and structure, which could result in a further decline of indigenous species establishment and facilitation of the non-native grass species.

1.7 Factors influencing alien invasion:

1.7.1 Fragmentation and edge effects

Almost half of the remaining small, untillable islands of Renosterveld exists (Figure 1.1) on slopes greater than 20% where cultivation of virgin lands are prohibited by legislation, as well as the rockiness and potential water erosion (McDowell & Moll 1992). All the fragments remaining are a product of a disturbed environment (repeated short interval fires, overgrazing and collecting of firewood), shown by the overwhelming dominance of large areas by a few species with pioneering abilities (Boucher 1983).

When dealing with the influence of fragmentation on alien invasion and the vegetation dynamics, two aspects have to be considered:

- i) the spatial arrangement of fragments within a landscape, and
- ii) the factors affecting fragments, which arise from both within and around the individual fragments.

The first approach deals primarily with the description and qualification of the spatial arrangement of fragments in the landscape and the relation of this arrangement to the dynamics of the biota. This thus includes isolation, biogeographic considerations of fragment size, shape and position relative to other fragments, connectivity, etc. The second approach deals mainly with the processes arising from the isolation of a fragment and its subsequent interaction with the surrounding landscape and how these processes affect the biota. This thus considers edge effects and changes in landscape processes (Hobbs 2001).

Relevant to this study would be the consideration of the effect of the spatial configuration changes of patches on the physical, chemical and biotic fluxes across the landscape. Figure 1.2 illustrates the various types of interactions possible between relevant factors. Weed invasion, herbivory abundance and activity can be influenced both directly by changes in spatial configuration and indirectly by the resulting changes in landscape fluxes. It is also evident that the internal condition of individual fragments can be as important, or more important, than the spatial pattern of fragments (size and isolation) in determining biotic abundance and distribution – alien

grass species invasion included. Hobbs (2001) found a strong correlation between remnant size and condition. All small remnants in his study were heavily invaded by weeds, whereas most large remnants were in relatively good condition. This reflects the more general phenomenon that small remnants are more likely to be strongly influenced by the surrounding matrix and thus become degraded (Kemper 1997).

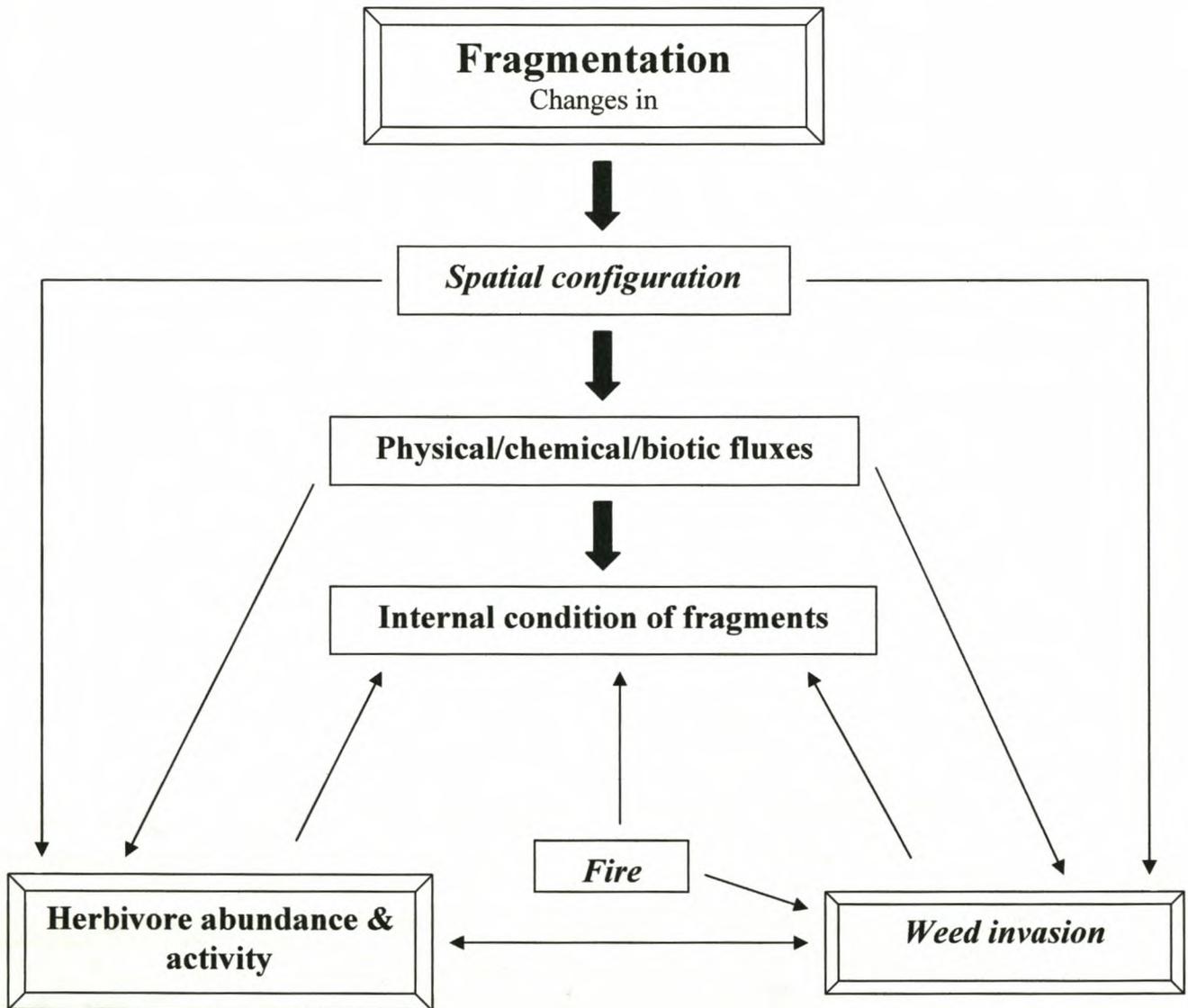


Figure 1.2: *Interrelationships among the direct effects of changing spatial configuration, altered landscape fluxes and changes to internal fragment condition, with particular reference to weed invasion, animal activity and fire (adapted from Hobbs 2001)*

The direct effects of agricultural activities on pristine veld, such as the case with renosterveld, includes destruction of the larger indigenous fauna, causing a continuous shrub canopy with consequential shading which leads to the depletion of herbaceous flora and increased termite activity. The replacement of indigenous fauna with livestock, and thus overgrazing in some areas, has led to soil erosion and a generally drier soil climate. Stages of degradation found in renosterveld, considered to be related to a general drier soil climate (dominance of scrub, to scrub, to low inedible dwarf shrubs, particularly succulents, to perennial herbs and finally to dominance by annuals) can also be seen under short interval burning regime coupled with overgrazing (Boucher 1983). All of this is leading to West Coast Strandveld flora (particularly the succulent component) becoming more conspicuous in areas currently supporting Coastal Renosterveld.

Disturbance of soil by tilling, the addition of fertilizers, chemical insecticides and herbicides have an extensive impact on natural diversity (Richardson *et al* 1992). Especially with 'strip ploughing' the narrow strips of natural vegetation left are exposed to cultivated land on either side and would be invaded by these pasture species from both sides. Studies have shown that even in rehabilitation of previously ploughed land directly adjacent to species-rich renosterveld, the re-established vegetation has a considerably smaller proportion of the original species composition (McDowell & Moll 1992). The increased use of 'dry-land' leguminous pastures entitles steep lands to be seeded with exotic species which may be 'fortified' by fertilizer treatment. It is doubtful whether natural diversity could be retained in the face of both competition with introduced pasture species and altered nutrient regimes (McDowell & Moll 1992). Techniques such as these promote the intrusion of alien grass and pasture species into the remaining renosterveld patches.

1.7.2 Natural disturbances

The disturbed nature of much of today's landscape provides growing conditions that are more suitable for a variety of exotic, disturbance-adapted plants than for the native species that originally inhabited the land. Anything that damages a healthy natural community is likely to open the way for invasive plants (Solecki 1997). Even for a

single ecosystem and disturbance event, effects vary at different trophic levels and occur over a wide range of biological levels. Most disturbances produce heterogeneous and patchy effects (evident with grazing & burning) and these effects themselves depend on the state of the community prior to disturbance. In general it was found that during disturbance succession is driven by exogenous factors (outside the community), while during disturbance-free periods, succession is primarily driven by endogenous factors. Thus the state of the community would determine the extent of the changes or effects the disturbance would have on the community (White & Pickett 1985).

The spatial scale of disturbances plays a fundamental role – smaller diggings or ant nests independently serving a much smaller number of individuals and species, but their impact figuratively aggregated could be equivalent functionally to fire or other larger scale disturbances. Small-scale disturbance agents (burrowing animals) could maintain opportunities for many short-lived species (annuals & biennials), while larger-scale agents (fire) could produce larger and longer-term disturbances. The potential for influence by small and short-term patch disturbances is much less in or surrounded by a system with high biodiversity. Higher biodiversity provides the increased capability of contributing at different seasons and different times in recovery of the disturbed area (Dukes 2002, Loucke *et al* 1985). Recurring disturbances create initial conditions for opportunistic species at intervals such that a relationship could be recognized between the species' life history and the average return time of the disturbance (Loucks *et al* 1985). Still, it is clear that disturbances have the largest effect in communities that were already more susceptible to invasion (Vieillefosse 2001).

1.7.2.1 Fire

Like fynbos, renosterveld is a fire-prone vegetation type with plant recruitment occurring predominantly after fire (Boucher 1995). The fire return interval of renosterveld is probably shorter than in Fynbos (<10 years) owing to the high grass coverage of the more fertile soils. The frequent burning of the vegetation at a cycle too short to allow regeneration of most plant species, promotes grass cover and is

often utilized to provide extra grazing (Rebello 1992). Vieillefosse (2001) stated that fire only affects the degree of invasion when combined with some other type of disturbance.

Fires create and cause various effects and responses resulting from variation in fire type, intensity, season of burning and predictability – all of these interlinked with each other (Christensen 1985). Disturbances, such as fire, typically open space in sessile communities, allowing the establishment of other individuals (Denslow 1985). The most significant effects of alien grasses on ecosystems result from interactions between grass invasion and fire (D'Antonio & Vitousek 1992). Holmes (2002) found that the herbaceous and other indigenous components of renosterveld experience reduced establishment success after fire, due to the competition and vigorous growth of alien annual grasses. This could be due to various factors, which facilitate the establishment of alien grass species. Above ground portions of most shrub species are killed during most fires, soil temperatures rise considerably, nutrient availability is enhanced, soil crusts are destroyed, physical and chemical soil properties are altered, soil moisture is lowered and seed predation is increased, to name some of the consequences of fire able to aid alien recruitment. The changes in not only physical components, but biological components (such as the dominance of flammable alien grass species opposed to indigenous species reluctant to burn) of areas frequently burned would ultimately change the existing fire frequency, intensity and type (D'Antonio & Vitousek 1992).

Surface soil temperatures could rise to 100°C, but the heat transfer down soil profiles quickly attenuates these high temperatures (Christensen 1985). This could mean that seeds buried deeper would more readily survive fire – a possible adaptation of some alien species to survive fires. The duration of these elevated soil temperatures depends on the rate of fire spread and the burning of residual material. The soil temperature, and thus microclimate, of recently burned areas are also affected. Studies have shown that recently burned areas have higher maximum and lower minimum temperatures, as well as considerably more variation in the air temperature 10 cm above ground. Such changes could potentially alter plant survival and growth.

Additionally, increased light availability may greatly influence alien and indigenous seedling and sprout growth – especially in moister areas (Christensen 1985).

Despite potential nutrient losses due to volatilization and increased runoff, nutrient availability has in general been found to be higher immediately following fire. It additionally is considerably more variable – the variation arises due to the local variation in fire intensity as well as uneven ash distribution (Christensen 1985, Simons 1998). Generally a burned area experiences increased nitrogen, phosphorous, calcium and magnesium availability. The pH level rises, stimulating microbe activity, which in turn plays a role in the nutrient-cycles (Kruger 1987, Marais 2000, Rundel 1983). These nutrient additions give alien grasses a competitive advantage over the indigenous species. Although *Bromus diandrus* and *Briza maxima* show serious weedy qualities globally on cultivated and disturbed lands (Gibbs *et al* 1990), Simons (1998) found that *Bromus diandrus* increasingly invaded areas infested with nitrogen-fixing *Acacia* infested areas. This contributes to the existing evidence, provided by heuweltjies as nutrient enriched sites (Vieillefosse 2001), that alien invasion is facilitated by nutrient enrichment. Interestingly, *Briza maxima* was found to invade more successfully after the establishment of a pioneer grass species and a subsequent annual fire cycle. Simons (1998) concluded that specific alien C₃ grasses might only pose a threat under specified conditions.

Due to insolation, increased surface soil heating would result in less available water in surface soil horizons in the first season following fire. This could lead to indigenous species seedlings not being sufficiently hydrated to germinate and ultimately favoring alien species, which are adapted to survive harsh conditions (Holmes 2002). Once sufficient leaf area, providing shade, is established – surface soil moisture availability may increase above pre-fire conditions. Thus, conditions for seedling germination and establishment may be most favourable in the second or third year following burning (Christensen 1985), at which stage alien species would already have established the competitive advantage in the ‘plant invasion window’ created.

Biochemical changes associated with burning may also influence the physical and hydrological properties of soil. Fire is thought to cause the downward migration of hydrophobic chemicals increasing surface soil wettability and the potential for surface

erosion – this playing an important role in post-fire vegetation patterns (Christensen 1985). Fire and its consequences also profoundly affect shrubland herbivore and small mammal populations and, thereby, the patterns of grazing and animal activity (Karr & Freemark 1985).

1.7.2.2 **Grazing**

Several studies have clearly indicated that alien invasion is much more prevalent in fragments that have been grazed by livestock for long periods (Hobbs 2001). Different vegetation types display different degrees of susceptibility to alien infiltration, but in all cases stock grazing significantly increases the level of invasion (Holmgren *et al* 2000, Savory 1986). It was also found that livestock grazing effectively increases edge effects by altering the physical and chemical properties of soil and increasing alien invasion much further into vegetation fragments than in ungrazed fragments (Karr & Freemark 1985).

Prolonged use of native vegetation for livestock grazing results in profound ecosystem changes, including altered vegetation structure and composition and changes in the physical and chemical properties of soil (Scott 1986, Stander 1988). The most obvious changes are in the understorey composition, with a reduction or removal of the native shrubs and herbaceous perennials (Hobbs 2001). Grazing animals could facilitate the dispersal, and thus invasion, of the non-native grass species by transporting the seeds entangled in their fur or in their dung to sites ideal for germination (Richardson *et al* 2000). Additionally trampling has a marked influence on soil structure, particularly in soils with relatively high clay content. It leads to significant reductions in litter and soil-crust cover and increased penetration resistance, which in turn leads to a reduction in water-infiltration rates and a less buffered soil microclimate. Another factor associated with animal activity that has an impact on the vegetation, is digging and burrowing (Kotanen 1995). The effects of digging and burrowing species in terms of soil turnover have been assessed in the past and it is apparent that their activity has a significant effect on soil properties (Hobbs 2001). This could thus contribute to the facilitation of alien species establishment in creating favorable conditions for the recruitment of alien seedlings, which could even

possibly be unfavorable for indigenous species. Digging activity moves soil, creates depressions and this provides safe sites for alien seedlings to aggregate and germinate (Kowarik 1995). Grazing, in general, has further, more subtle influences in fragmented systems (Hobbs 2001).

A summary of the effects of high and low intensity grazing regimes is given in Figure 1.3. High intensity grazing would signify a very high density of grazing animals, possibly higher than the optimal stocking rate for renosterveld. Low and Jones (1995) estimated that the carrying capacity of renosterveld was one Small Animal Unit (SAU) per 2 – 4 ha, depending on the season and annual rainfall (for cattle, one Large Animal Unit is equivalent to six SAU). The Nature Reserves studied in this project kept to the prescribed stocking rate of the natural renosterveld fragments and high levels of grazing would suggest a situation where there was a concentration of grazing and other animal activities. Low level grazing would thus apply when there is less animal activity, well within prescribed carrying capacity, and where the grazing animals are distributed over an extensive area. Figure 1.3 reveals the expected chain of events when certain factors come into play and what the result of this is in the management regimes examined in this study. In terms of grazing it would be expected that moderate animal activity would exclude excessive trampling or digging. No drastic alteration of the existing vegetation dynamics would occur, resulting in just the necessary fluctuation of vegetation and ecological components to strengthen the natural dynamics of the area and thus less opportunity for alien grass invasion. Excessive grazing, in small areas or over a greater area extent, would lead to the removal of the palatable species, changes in the vegetation composition and large scale trampling and digging thus altering the soil properties and dynamics. This disruption of the existing vegetation dynamics of the area, combined with the negative effects of island dynamics and edge effects already present in the fragment, would facilitate the establishment of alien grass species. In the long run the effects of the invading alien grass species would alter most previous vegetation dynamics that sustained the indigenous species to such an extent that only alien species could dominate the area. The same result would be seen with a fire cycle at a short return interval. Again certain species would fail to survive the demands of re-establishment at such a high frequency and changes in soil chemistry, moisture availability and all other existing vegetation dynamics they have adapted to. Fast growing species (such

as alien grass) and re-sprouting species would be favored. This, combined with the creation of vacant niche space and all the previous mentioned factors that fragments

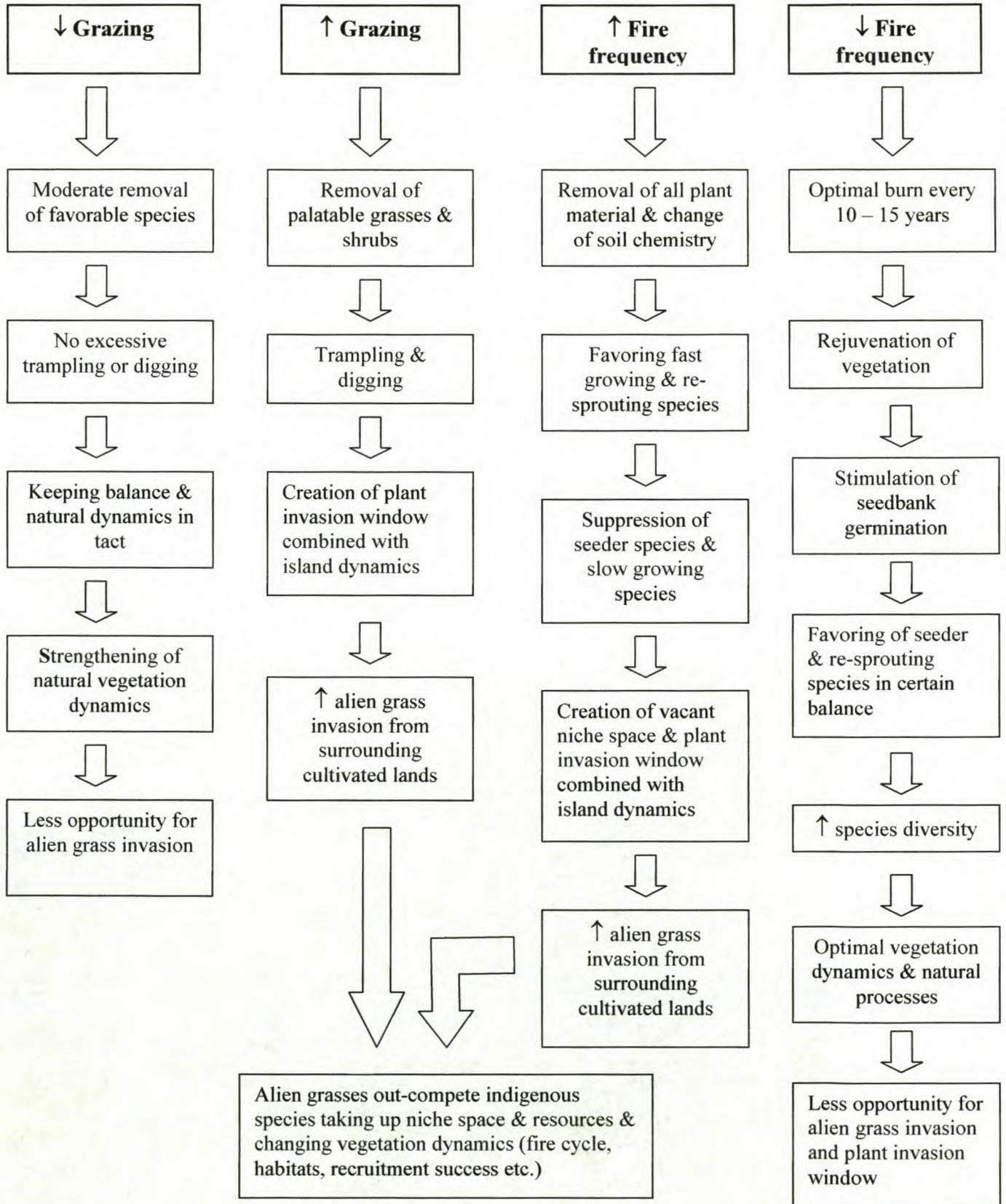


Figure 1.3: The effect of high (↑) and low (↓) fire or grazing regimes on the invasion of alien grass species into renosterveld fragments

are subjected to, would lead to increased alien grass invasion and the same conclusion reached with high grazing activity. The optimal fire cycle of 10 – 15 years would rejuvenate the vegetation, stimulate the seedbank germination and existence of re-sprouting and seeding species in equilibrium to maintain the high species diversity known in renosterveld. The maintenance of the existing vegetation dynamics and natural processes would leave less opportunity for the alien grass species to invade.

1.7.2.3 **Ants**

The role of large herbivores and birds in the widespread transport of small –seeded grasses is a well-recognised fact, but ants and termites are by far the most important invertebrate dispersers of seeds – especially short-distance dispersal. The most notable case would be the attraction of elaiosomes – ants collecting the seeds for the oily food bodies derived from the funicles – and discarding the seeds in their underground nests. Although alien grasses do not possess these oily food bodies, they still provide an effective food source for these invertebrates. Harvester ants, such as *Messor* species in South Africa, collect the most abundant seeds available and transport them over distances of 50 – 100 m to their nests (Milton & Dean 1993). By burying the seeds in their nests to maintain stores for later consumption, they provide protection from predators and fire, and may facilitate the formation of foci of small populations over the landscape. This in turn may speed-up the invasion process. When the ant nests are disturbed by predators, the viable seeds are released onto the organically enriched soils of the nest mound. In this way, the harvester ants facilitate the invasion of alien plants, including the European *Bromus* spp. (Richardson *et al* 2000).

1.7 Objectives of the study

The main objectives of this study were to:

- determine the extent of alien grass invasion into remnant West Coast Renosterveld patches,
- identify the major alien grass species posing a threat under a range of management regimes,
- determine which management regime (fire, grazing or absence of any active management) inhibits alien grass invasion most effectively,
- determine the effect of surroundings (fertilized crops and rehabilitating old lands on the extent of alien grass invasion into the fragments and provide an indication of the extent and degree edge effects impact on the remnant renosterveld patches,
- identify other factors facilitating alien grass invasion (such as small-scale soil disturbances or indigenous vegetation growth and establishment).

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Chapter 2

Study area

2.1 Elandsberg Private Nature Reserve

Elandsberg Private Nature Reserve is located approximately 25 km north of Wellington, directly south of the Voëlvlei dam, in the Western Cape. It is situated at 33° 27' S and 19° 03' E (3319AC Tulbagh) and extends over 3 606 ha. The Elandskloof mountain marks the eastern border of the reserve. The topography results in a well-drained area by run-off water from the mountains and in winter, with a higher rainfall, large floodplains form on the slightly lower sloped western portion of the reserve. There are also artificially built drainage systems in the reserve and runoff water collects into one large and several small dams (Diemer 2000, Shiponeni 2002).

Parts of the reserve have previously been used for agricultural purposes and are now slowly being re-colonized by renosterveld. These are referred to as old lands. These areas mark past ploughing activities, but are now incorporated into the reserve. The old lands, or fields, were cultivated for wheat from the late 1960's up until 1987 after which they were left abandoned from any agricultural activity (ploughing or livestock grazing). These fields are bounded by active agricultural cultivation to the west and thus provide a buffer zone between the farming area and the natural vegetation of the reserve to the north and east. The general description of the vegetation on these old lands, is an open grassy area, dominated by one of the perennial African lawn grasses, *Cynodon dactylon*, in summer. After the winter rainfall season, annual alien pasture grasses such as *Vulpia myuros*, *Briza maxima*, *Briza minor*, *Bromus diandrus*, *Bromus pectinatus*, *Lolium perenne* and *Poa annua* dominate. In the transition zone, between the natural vegetation and the old lands, there is some returning renosterveld vegetation and waves of *Elytrophapus rhinocerotis* encroaching into the field, mainly along the ploughed furrows that span the field and run parallel with the ecotone (Shiponeni 2002).

The area was used for livestock grazing until 1973 when it was stocked with re-introduced populations of antelope (Table 2.1) and partly cultivated for wheat and grain. Cultivation, of the area presently forming the reserve, ceased in 1987 when it was registered and proclaimed as a private nature reserve in 1988.

According to Acocks (1988) the vegetation at Elandsberg can be divided into 2 main types: Coastal Renosterveld and Mountain Fynbos. Renosterveld makes up the largest part of the reserve and Mountain Fynbos is mainly found along the mountains on the eastern border. Grassy patches are scattered throughout parts of the reserve (Diemer 2000, Shiponeni 2002). The Elandsberg reserve offered two ideal sample sites with different management histories to be evaluated in terms of the extent of alien invasion into pristine vegetation. There is sustained sheep and game grazing (Table 2.1) on the reserve including the old lands that have not been ploughed for the past 10 – 15 years. Table 2.1 provides a general idea on which animals are found in the reserve and what their feeding preferences are. This could be useful in evaluating which areas of the vegetation each species have the biggest influence and which species could be more effective in a specific management regime goal.

The mammalian grazers, browsers and other small herbivores roam freely in the reserve, using both the natural vegetation and the old ploughed lands. The re-introduced antelope now appear to be important in controlling the structure and composition of the vegetation and allegedly converted the old lands into *Cynodon dactylon* covered fields. Introduced feral pigs, *Sus scrofa*, dig up geophytes and open significantly large patches in the vegetation which provides safe recruitment sites for the establishment of alien and indigenous seedlings. Porcupines are responsible for similar disturbances.

In addition to herbivory and past agricultural activities, patchy fires influence vegetation patterns in Elandsberg Nature Reserve. The entire reserve was burned in 1982, followed by smaller patches burning in 1988, 1989 and 1999 separately (Diemer 2000). The grassy patches of the old lands were burned as recently as 2000. Elandsberg thus provided a recently burned and grazed area (burned in 1999), at the Slangkop gate along the side of the Vlei road, and a grazed area (which had not been

burned since 1982), along the Slangkop road, both adjacent to old lands that are undergoing passive rehabilitation (Figure 2.1 & Figure 2.2).

Table 2.1: *Herbivorous vertebrates of the Elandsberg Private Nature Reserve and their preferred forage* (Shiponeni 2002).

Species	Major feeding category or general sources of food
<i>Connochaetes gnou</i> (Black wildebeest)	Short grass grazer
<i>Connochaetes taurinus</i> (Blue wildebeest)	Grazer
<i>Damaliscus dorcas dorcas</i> (Bontebok)	Short grass grazer
<i>Equus burchelli</i> (Burchell's zebra)	Mixed feeder
<i>Equus zebra</i> (Cape mountain zebra)	Long-medium grass grazer
<i>Taurotragus oryx</i> (Eland)	Mixed feeder
<i>Oryx gazella</i> (Gemsbok)	Long grass grazer
<i>Pelea capreolus</i> (Grey rhebok)	Mixed feeder
<i>Alcelaphus buselaphus</i> (Red hartebeest)	Short grass grazer
<i>Antidorcas marsupialis</i> (Springbok)	Mixed feeder
<i>Orycteropus afer</i> (Aardvark)	Ants & termites
<i>Sus scrofa</i> (Feral pig)	Bulbs, corms, rhizomes & insects
<i>Georychus capensis</i> (Mole rat)	Bulbs, corms & rhizomes
Other rodents	Seed eaters, leaves & insects
<i>Struthio camelus</i> (Ostrich)	Soft annual plants, flowers & seeds
<i>Hystrix africaeausstralis</i> (Porcupine)	Bulbs, corms & rhizomes
<i>Psammobates geometricus</i> : <i>Chersine angulates</i> (Tortoises)	Soft annual plants & flowers

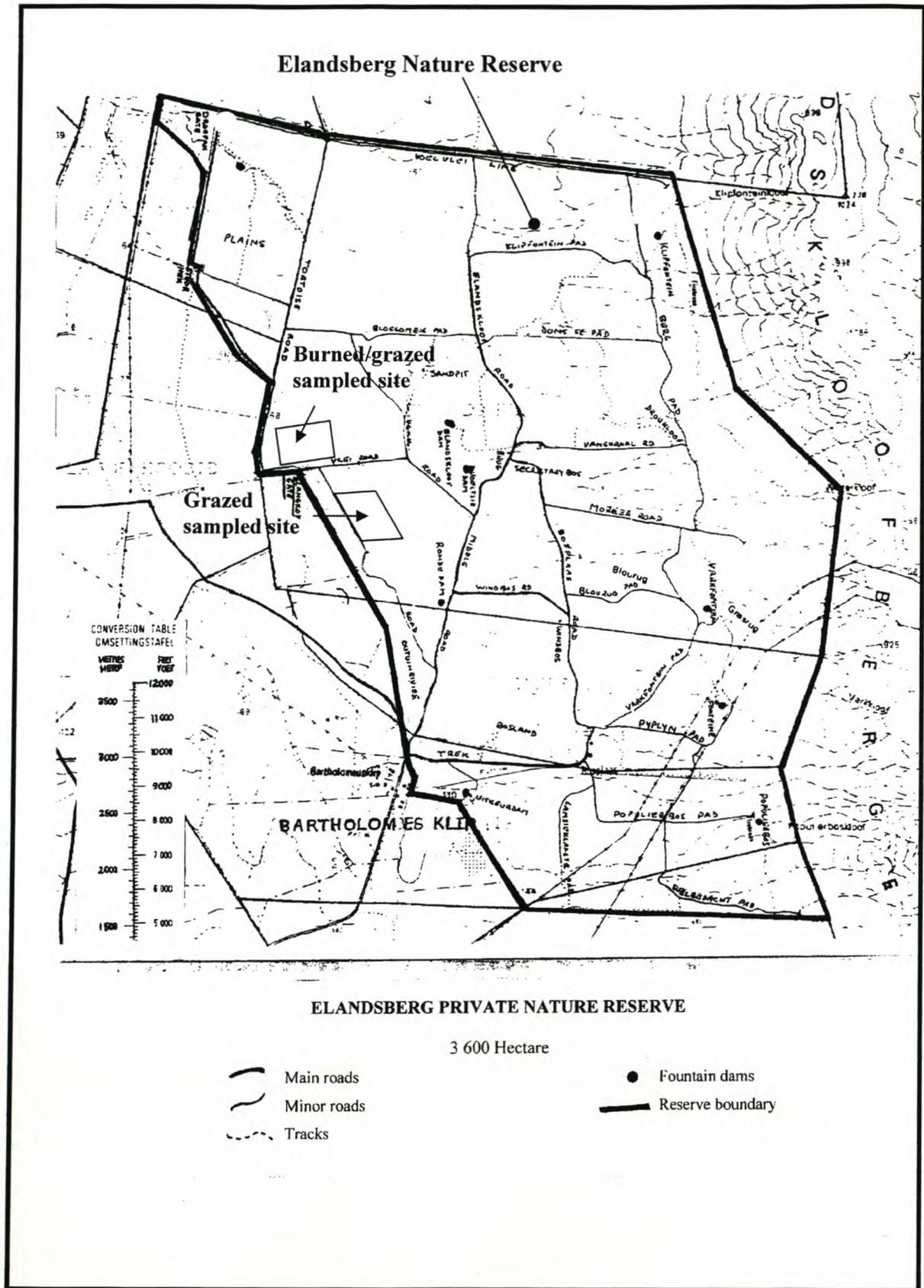


Figure 2.1: The sampled sites on Elandsberg Private Nature Reserve

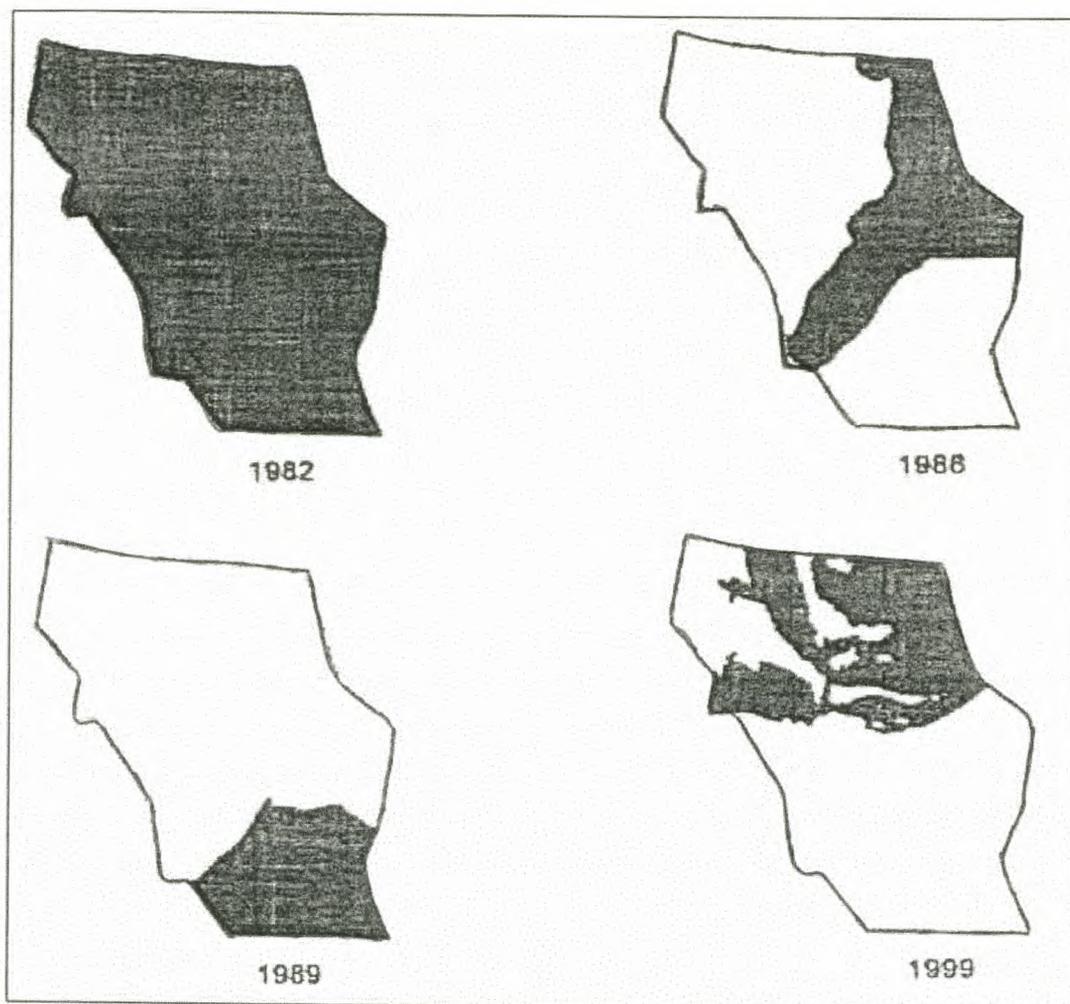


Figure 2.2: *The distribution and size of the four fires at Elandsberg Private Nature Reserve*

2.2 Jan Briers Louw Geometric Tortoise Reserve

The Jan Briers Louw Geometric Tortoise Reserve is situated at 33° 45' 45" S and 18° 50' 07" E (Low & Jones 1995), on the R312 Southwest of Paarl. It is a privately owned farm and specific authorization from the owner has been given for scientific research purposes. The Jan Briers Louw Nature Reserve was proclaimed in 1972 and is the property of the Briers-Louw family. The initial 8 ha reserve was expanded by an additional 20 ha extension area and encloses endangered Lowland Fynbos and renosterveld communities (containing at least seven threatened species, such as

Gladiolus citrinus). The protected area is surrounded on all sides by old lands and ploughed fields, which are heavily subjected to invasions of *Acacia saligna*. Due to the small area, species are present in small populations and are therefore more susceptible to extinction (Jones 1986). It also conserves a well-studied population of the geometric tortoise, *Psammobates geometricus* (Baard 1993, Baard 1995). Jan Briers Louw Nature Reserve, along the fence line to the west of the Klapmuts river, provided the ungrazed and unburned (control) area (Figure 2.3), due to the fact that grazing and burning activities have been excluded from this entire area for the past 10 – 15 years. The only animal activity that would cause disturbances would be the activities of termites (*Microhodotermes viator*), rodent species (porcupines, mole-rats) and small antelope such as *Sylvicapra grimmia* (Common duiker) and *Raphicerus campestris* (Steenbok) (Walker 1986).

These sampling areas and the data collected could thus provide comparative information as to the extent of alien grass invasion under each of these management regimes and shed some light on the possible factors influencing the invasion of alien grass species (small scale soil disturbances, competitive exclusion, safe recruitment sites, etc.).

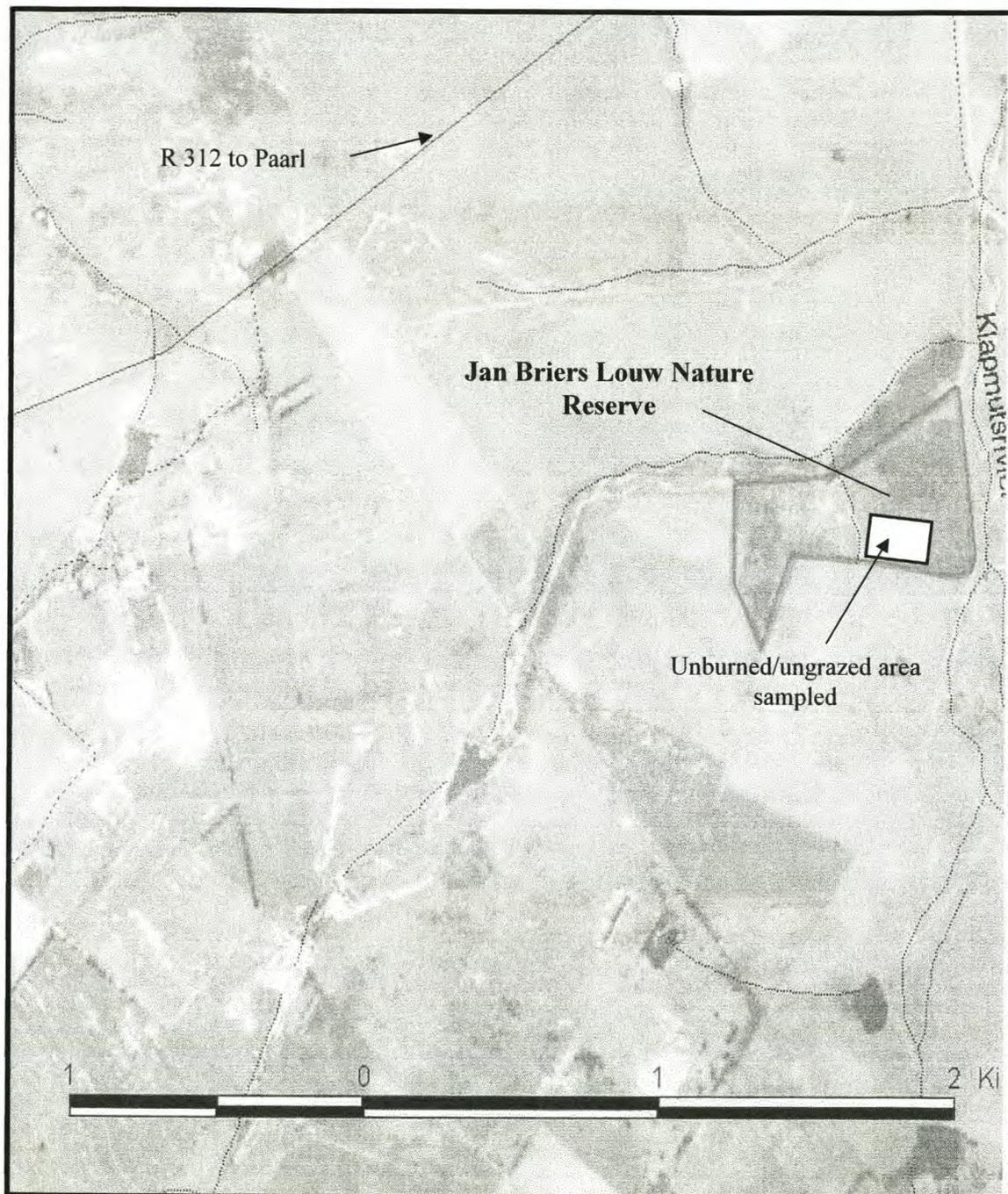


Figure 2.3: *The sampled site on Jan Briers Louw Nature Reserve*

2.3 References

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Chapter 3

Factors affecting alien grass invasion into West Coast Renosterveld fragments

3.1 Abstract

Remaining renosterveld fragments are subject to extensive edge effect including alien grass invasion. Competitive alien annuals decrease biodiversity and reduce resistance of natural communities to further invasion as well as recovery after invasion. Effective management regimes to inhibit the invasion of alien species into renosterveld are required. Three different management treatments (burned, grazed and a control area) were examined to determine what factors affect the extent of alien grass invasion into renosterveld patches. Alien grass cover, association with indigenous vegetation and correlation with small-scale soil disturbances were recorded. Briza spp., Bromus spp. and Avena fatua were the dominant alien grass species. A strong positive correlation between the occurrence of small-scale soil disturbances and alien grass establishment implicated animal activity as being the most important facilitator of invasion. Actively burned and grazed areas were more susceptible to alien grass invasion compared to a no management control area. It is hypothesized that management regime could control the extent of alien grass invasion, irrespective of the size of the remnant. It is possible that the most effective management regime would combine low-pressure grazing and sufficiently timed fire management to inhibit excessive alien invasion while maintaining maximum biodiversity.

Keywords: renosterveld, alien grass, burning, grazing, management regime, small-scale soil disturbances

3.2 Introduction

With the original extent of West Coast Renosterveld reduced to a mere 1.76% conserved (Hoffmann 1997, Holmes 2002, Low & Rebelo 1996), it is logical that the few remaining fragments have become a priority for conservation and research. Recent statistics stipulates only 0.7% West Coast Renosterveld protected and 92.3% exposed to degradation, transformation and road effects (Reyers *et al* 2001). Obtaining information about the dynamics of this vegetation type that currently faces extinction, has become crucial, especially since little information exists on how it can be effectively managed. In the past, the primary threat to renosterveld was agricultural expansion, and this continues to be a threat today (Cowling *et al* 1986, Low & Rebelo 1996, Parker 1982), however, mis-management of remaining small and often isolated patches has lead to increased alien invasion and a further loss of biodiversity (D'Antonio & Vitousek 1992, Dukes 2002, Parker 1982). Today the biggest threat to renosterveld is due to extensive fragmentation and the resulting extensive edge effects at the interface with surrounding cultivated lands (Harrison *et al* 2001, Kemper 1997, Parker 1982). Combined with altered disturbance regimes, fragmentation influences vegetation dynamics and composition of remaining natural vegetation (Hester & Hobbs 1992, Pyke & Knick 2003). Altered vegetation dynamics can thus create a 'plant invasion windows' for alien species to establish (Richardson *et al* 1992).

Alien invasion in any vegetation type has severe effects on biodiversity (D'Antonio & Vitousek 1992, Dukes 2002, Vlok 1988). The subsequent decline in biodiversity induced by alien invasion, reduces the community's resistance to invasion, as well as its ability to persist after invasion (Vlok 1988). Alien species infiltrate communities due to various habitat, biotic and demographic factors, giving non-native species the competitive advantage over the indigenous species of a given area (D'Antonio & Vitousek 1992, Kowarik 1995, Larson *et al* 2001, Reichard 2001, Rejmanek 1995).

Alien invasions are common in disturbed areas, while rare in pristine communities (Hester & Hobbs 1992, Williamson 1996). Disturbances include fire and grazing, which are also applied as management regimes (Boucher 1995, Tainton 1999). Like

fynbos, renosterveld is a fire-prone vegetation type with plant recruitment occurring predominantly after fire (Boucher 1995). Frequent burning of the vegetation at a cycle too short to allow regeneration of most plant species (Holmes 2002), promotes grass cover and is a management practice commonly used in renosterveld to provide extra grazing (Rebelo 1992, Tainton 1999). The problem is that alien grass species from the surrounding cultivated lands are well positioned to exploit a 'plant succession window' created in this community (Denslow 1985, Richardson *et al* 2000, Solecki 1997). Fires create and cause various effects and responses such as soil temperature increases, enhanced nutrient availability, alteration of physical and chemical soil properties, destruction of soil crusts, reduction in soil moisture and increased seed predation (Christensen 1985, D'Antonio & Vitousek 1992, Kruger 1987, Marais 2000, Rundel 1983). While all these effects can be positive under disturbance regimes of natural communities, the negative aspect is that they can facilitate the establishment of the more adaptable alien invaders.

Several studies indicate that alien invasions are more prevalent in fragments that have been grazed by livestock for long periods (Hobbs 2001). Different vegetation types display various degrees of susceptibility to alien infiltration, but stock grazing significantly increases the level of invasion (Holmgren *et al* 2000, Savory 1986). The reason for this is altered vegetation structure and composition (through physical damage to plants and harvesting of palatable species etc.), changes in physical and chemical soil properties (trampling, dung deposits, reduction in soil crust cover etc.) (Hobbs 2001, Stander 1988). Grazing animals also transport seeds – through their dung or stuck to their fur – which aids dispersal of alien species as well as indigenous species (Richardson *et al* 2000). Although the larger fauna has a marked impact in this respect, ants and termites are some of the important invertebrate contribution to the dispersal of seeds – especially short-distance dispersal (Milton & Dean 1993, Richardson *et al* 2000). Additionally, digging and burrowing activity of the fossorial animals may also move soil, create depressions and provide safe sites for alien seedlings to aggregate and germinate (Kotanen 1995, Kowarik 1995).

Although active management of an area holds definite positive results, mismanagement causes destruction and subsequent reduction in value, in this case the ultimate loss of biodiversity. It is thus crucial to establish what management regime

most effectively inhibits alien grass invasion. Early stages of alien colonization is a critical phase in the invasion process and could predict the success or failure of introduced species to invade, as well as to represent the stage at which invasions could be managed (Higgins 1998). In this chapter alien grass species posing the biggest threat to West Coast Renosterveld fragments are identified. The degree to which alien grasses invade under a range of management regimes is quantified. This study attempts to provide clarity on whether renosterveld should be burned, grazed or if all such activities should be excluded to best decrease alien grass invasion while at the same time managing for maximum biodiversity.

3.2 Materials and methods

3.3.1 Study site

Three remnant patches of West Coast Renosterveld were selected as study sites. Sites differed in management regimes and were all selected for their proximity to old lands [(1) a recently burned area, (2) a grazed area and (3) an unburned/ungrazed area providing a control sample]. The first two sampled areas were situated on the Elandsberg Private Nature Reserve, on the Elandsberg farm (at 33° 27' S and 19° 03' E, 3319AC Tulbagh), while the last mentioned sampled area was situated on the farm Eenzaamheid, the Jan Briers Louw Geometric Tortoise Reserve (33 45' 45" S and 18 50' 07" E on the R312 Southwest of Paarl).

Elandsberg farm (3 606 ha) consists of cultivated lands to the west, rehabilitating old lands (acting as a buffer zone separating the cultivated lands from the pristine vegetation of the reserve) and natural vegetation of the reserve to the north and east. The old lands are open grassy area, dominated by *Cynodon dactylon* in the summer and *Vulpia myuros*, *Briza spp.*, *Bromus spp.*, *Lolium perenne* and *Poa annua* in the winter. The transition zone to the natural vegetation is characterised by scattered *Elytrophapus rhinocerotis* shrubs encroaching into the field. The reserve area contains renosterveld and Mountain Fynbos and is subjected to sustained sheep and game grazing and the occasional wild fire. The entire reserve was burned in 1982,

followed by the burning of smaller patches in 1988, 1989, 1999 separately (Diemer 2000, Shiponeni 2002). Elandsberg thus provided the recently burned/grazed area (burned in 1999), at Slangkop gate along the side of the Vlei road, and a grazed area (not burned since 1982) along the Slangkop road – both adjacent to rehabilitating old lands.

Jan Briers Louw Geometric Tortoise Reserve was proclaimed in 1972. The 20 ha area enclose endangered Lowland Fynbos and renosterveld communities, excluding grazing and burning activities for the past 10 – 15 years (Jones 1986), surrounded on all sides by old lands and actively ploughed fields. The area sampled as a control site, was situated along the fence line to the west of the Klapmuts river.

3.3.2 Field sampling

The line-intercept method (Kent & Coker 1992) was used to sample vegetation (Figure 3.1). In addition, seedlings were counted within 50 cm X 50 cm quadrats every 5 m along each individual line. The 50 m intercept lines were measured from one meter inside an old land or pasture bordering the renosterveld fragment, towards the transition zone and continued into the natural renosterveld patch for 100 m. In the natural area, ten lines were measured at a one-meter interval, followed by an increased interval of 5 m for the next six lines measured. This was followed by another six lines at a 10 m interval. This particular spacing ensured the measurement of a total distance of 100 m into the renosterveld patch. The intercept lines were placed horizontal to the transition zone between the old land and the renosterveld patch. This was done to cover the most extensive area for measuring the frequency and gradients of occurrence of alien grass species. All indigenous and alien grass species, herbs, shrubs and restioceae species intercepting the line were recorded and their heights measured (Kent & Coker 1992).

Grasses were identified to species level where possible, using Van Wyk & Van Oudtshoorn (1999) and Wells *et al* (1986). The number of small-scale soil disturbances (pig diggings, porcupine, moles, termites, ants or rodents) intercepting the line transects were recorded as these could possibly contribute to factors affecting

the invasion of alien grass species into natural patches. All measurements were repeated in the three sampling areas. Data collection started in middle July 2002 and continued over August 2002 and the beginning of September 2002. The last measurements were completed during the last two weeks of October 2002.

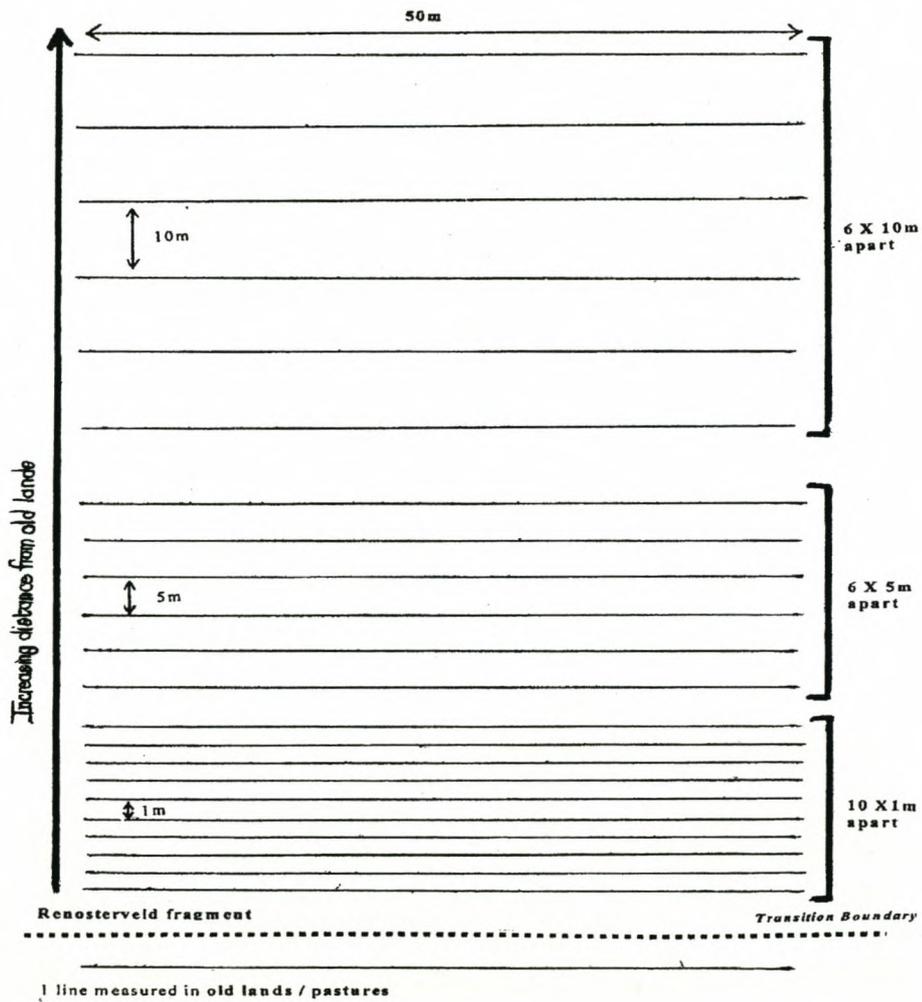


Figure 3.1: The line-intercept sampling design used for sampling

3.3.3 Data analysis

Data were processed in Microsoft Excel©. Firstly the relevant tests were done to establish whether the data showed a normal distribution (Kent & Coker 1992, Wheater & Cook 2000). STATISTICA (Statsoft Inc. 2003) was used to analyze the data collected and Brown (1968), Kleinbaum & Kupper (1978), Krebs (1989) and Mueller-Dombois & Ellenberg (1974) were consulted in interpreting and comparing the results.

Absolute alien grass cover data were calculated to show the percentage ground cover (total area measured in each treatment) by each alien grass species separately – thus a percentage of the total 1100 m measured in each treatment. The relative percentage cover of each alien grass was then calculated as the absolute cover (%) of each species expressed as a percentage of the total alien grass cover in each treatment. The same was done for percentage indigenous grass cover.

The variation of the mean percentage alien grass, indigenous grass and shrub cover between the first 10 m, the following 30 m and the last 60 m, of the 100 m measured into the remnant patch, were established for each of the treatments (burned, grazed and control). Univariate tests of significance, between the occurrence and abundance of the three groups of plants for each of the categories and the difference between and within explained and unexplained variation recorded for each, were calculated. This was followed by area-distance graphs showing the three compartments (0 – 10 m, 10 – 40 m, 40 – 100 m) to compare the distribution and impact of edge effects, including a second graph of the data subjected to the bootstrap confidence intervals (at 0.95). Normal probability plots were also drafted for each of the treatments and categories (percentage alien grass, indigenous grass and shrub cover) separately and finally the data were subjected to post hoc Bonferroni tests. This was done to statistically compare the different treatments and each distance zone within the treatments with each other.

The possible relationship between small-scale soil disturbances and the percentage alien grass, indigenous grass and shrub cover, were explored using 2D scatter-plots. The correlation coefficient and significance level were calculated for each comparison. Finally, the association between the percentage alien grass cover and the percentage indigenous grass and shrub cover were graphically and statistically examined, as well as the association between the percentage indigenous grass cover and percentage shrub cover. These statistical analyses provided the basis on which the importance of factors affecting or associated with the alien grass invasion could be determined (Kent & Coker 1992, Kershaw 1966, Li 1964, Steel & Torrie 1980).

3.4 Results

3.4.1 Alien grass species

Edge effects on alien grass distribution and the response of alien grass to land-use

Nine alien grass species were encountered at Elandsberg and ten at Eenzaamheid (Table 3.1). Most of these alien grass species originate from Europe and Asia and are annual pioneer species. The only exceptions are the two perennial species *Pennisetum clandestinum* (Kikuyu) which originated from tropical Africa and *Cynodon dactylon* (Couch grass) which has an uncertain origin and a world-wide distribution mostly associated with grazing disturbance.

Table 3.1: Alien grass (*Poaceae*) cover in renosterveld under three disturbance regimes. (1) Source of information on origin, life history and grazing value (Van Wyk & van Oudtshoorn 1999, Wells *et al* 1986) and (2) & (3) percentage alien grass cover recorded in each treatment

Species	Common name	Region of origin (1)	Life cycle (1)	Grazing value (1)	(2) % alien grass cover in each treatment (% of ground covered by each species)			(3) % alien grass cover in each treatment (% of total % alien grass cover in each treatment)		
					Control	Grazed	Burned & Grazed	Control	Grazed	Burned & Grazed
<i>Briza maxima</i>	Large quaking grass	Europe & Asia	Annual pioneer	Low	2.24	29.75	11.57	14	87	60
<i>Briza minor</i>	Small quaking grass	Europe & Asia	Annual	High						
<i>Avena fatua</i>	Common wild oats	Europe & Asia	Annual pioneer	High	5.44	1.71	0.77	34	5	4
<i>Lolium perenne</i>	Perennial rye grass	Europe & Asia	Perennial	High	0.79	0.21	0.77	5	0.6	4
<i>Bromus catharticus</i>	Rescue grass	Europe & Asia	Annual pioneer	High	1.41	0.21	0.31	8.8	0.6	1.6
<i>Bromus pectinatus</i>	Rippgut brome	Europe & Asia	Annual pioneer	Moderate	3.90	1.35	2.70	24.4	3.9	14
<i>Bromus diandrus</i>	Japanese brome	Europe & Asia	Annual pioneer	Low	1.05	0.15	0.85	6.6	0.5	4.4
<i>Cynodon dactylon</i>	Couch grass	Pan-Africa	Perennial pioneer	High	0.16	1.03	2.31	1	3	12
<i>Pennisetum clandestinum</i>	Kikuyu	Tropical Africa	Perennial	High	0	0.18	0.15	0	0.5	0.8
<i>Phalaris minor</i>	Small canary grass	Europe & Asia	Annual pioneer	Moderate	0.96	0.31	0.02	6	0.9	0.1
TOTAL COVER					15.99	34.19	19.28			

Table 3.1 shows the alien grass species percentage cover, in the control (unburned/ungrazed), grazed and burned areas respectively. *Briza* spp., *Bromus* spp. (the combined percentages of the *B. catharticus*, *B. pectinatus*, *B. diandrus*) and *Avena fatua* were the greatest invaders. These annual pioneer species showed a noticeable presence in all three treatments. The grazing value of these species was based on their production, palatability, nutritional value, growth vigour, digestibility

and habitat preference (Van Wyk & Van Oudtshoorn 1999). Species with a high grazing value, such as *Briza minor*, *Avena fatua*, *Lolium perenne*, *Bromus catharticus*, *Cynodon dactylon* and *Pennisetum clandestinum*, would thus show certain characteristics or a combination of some. Such characteristics are the production of a lot of leaf material, containing a high amount of nutrients, the capacity to re-grow rapidly after grazing, a low fibre content and the ability to grow in wet places, ensuring higher leaf production (Van Wyk & Van Oudtshoorn 1999).

Overall, the highest alien cover (Table 3.1, section (2)) was found in the grazed area (34.19%), with the control area showing the lowest levels of alien infestation (15.99%). The grazed and burned areas both showed dominance in alien grass invasion by *Briza spp.* – with the largest part of their total degree of invasion attributed to *Briza* (29.75% and 11.57% respectively). The control area showed a more uniform distribution in abundance of the alien grass species found throughout the whole area. The most abundant species was *Avena fatua* (5.44%) and *Bromus pectinatus* (3.90%) – closely followed by all the other species recorded there.

Table 3.1, section (3) shows the percentage of each alien grass species as a percentage of the percentage alien grass cover in each treatment (i.e. a percentage of the total found at the end of the first (2) section. *Avena fatua* (34%), *Bromus pectinatus* (24.4%) and *Briza spp.* (14%) primarily invaded the control area. *Cynodon dactylon*, as the one of the only two perennial alien grass species, did not show a high percentage cover in the control (unburned/ungrazed) area, in contrast to its substantial presence (12%) in the burned and intermediate occurrence (3%) in the grazed area. *Phalaris minor* made a substantial contribution (6%) to the alien grass cover in the unburned/ungrazed plot while it did not feature in the other two sampled areas. The invasion into the grazed area was dominated by *Briza spp.* (87%). The other abundant species, such as *Avena fatua* (5%), *Bromus pectinatus* (3.95%) and *Cynodon dactylon* (3%) followed at a much smaller percentage. *Lolium perenne* was recorded frequently in all treatments except the grazed area. More or less the same sequence of dominant alien grass species found in the grazed area, was seen in the burned and grazed area. The alien grass species in the burned area was overwhelmingly dominated by *Briza maxima* and *Briza minor* (60%) (keeping in mind that the sampling was done in mid-July, and the grass seedlings were still very young and it

was hard to distinguish between *Briza* and *Bromus* spp.). *Bromus pectinatus* (14%) and *Cynodon dactylon* (12%) also occurred frequently.

Table 3.2 Univariate tests of significance for percentage alien grass cover

Effect	SS	Degrees of freedom	MS	F	p
Intercept	32363.73	1	32363.73	190.6278	0.00
Area	5303.49	2	2654.75	15.6192	0.00
Distance category	797.77	2	398.89	2.3495	0.10
Area*distance	4059.64	4	1014.91	5.9780	0.00
Error	9677.14	57	169.77		

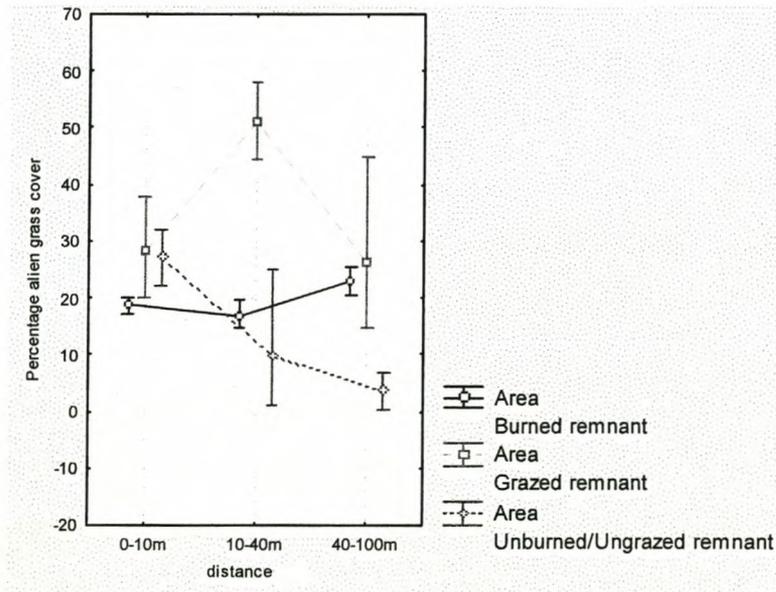


Figure 3.2: Bootstrap averages and 95% confidence intervals for percentage alien grass cover according to distance categories

Table 3.3: Post hoc Bonferroni tests: indication of significant differences ($p < 0.05$, bold) in % alien grass cover between each separate distance zone within and between each treatment

Cell no.	Bonferroni test: variable % alien grass species (Error: between MS = 65.463, df = 54.00)										
	Area	Distance zone	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
1	Burned remnant	0-10									
2	Burned remnant	10-40	1.0								
3	Burned remnant	40-100	1.0	1.0							
4	Grazed remnant	0-10	1.0	1.0	1.0						
5	Grazed remnant	10-40	0.0	0.0	0.0	0.0					
6	Grazed remnant	40-100	1.0	1.0	1.0	1.0	0.0				
7	Control remnant	0-10	0.88	0.69	1.0	1.0	0.0	0.80			
8	Control remnant	10-40	0.02	0.15	0.0	0.0	0.0	0.26	0.0		
9	Control remnant	40-100	0.03	0.22	0.0	0.0	0.0	0.38	0.0	1.0	

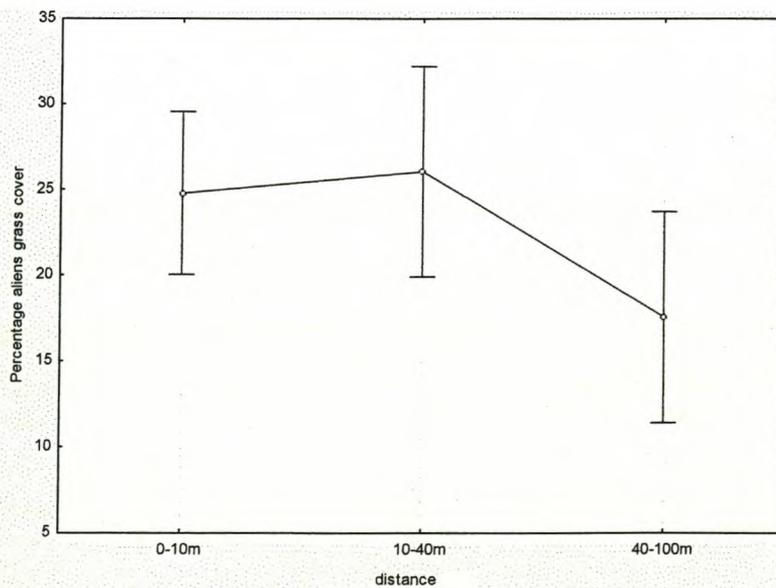


Figure 3.3: Means of alien grass cover according to distance categories (treatment areas pooled) – bars represent 95% confidence intervals for the means

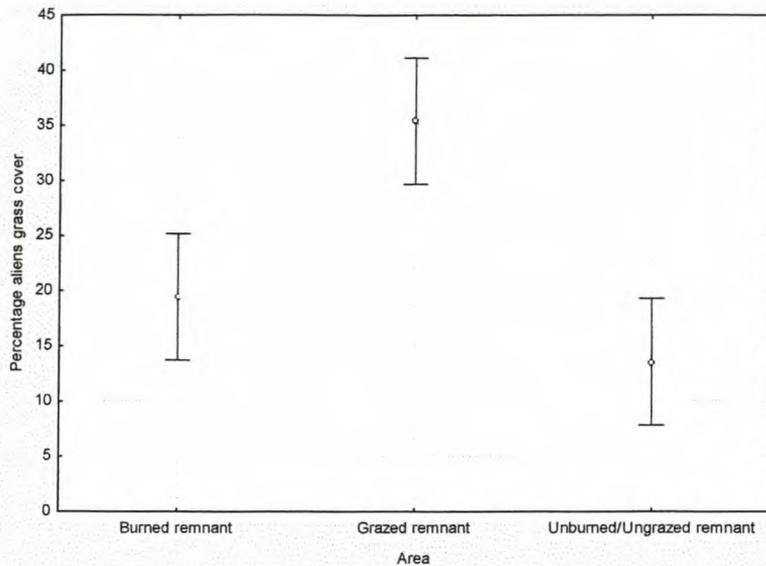


Figure 3.4: Means of percentage alien grass cover according to distance categories (distances pooled) – bars represent 95% confidence intervals for the means

The total percentage alien grass cover differed for each treatment. The grazed area showed the highest level of alien grass invasion (34.19%), followed by the burned area (19.28%) and the control area (15.99%) (Table 3.1). The univariate test of significance (Table 3.2) showed that there is a highly significant variation ($F_{4,57} = 5.9780$, $p < 0.01$) in the percentage alien grass cover (percentage of ground measured in intercept line covered by alien grass) between each of the three treatments. There is a significant interaction between the area and distances at which alien grass species were found and the unexplained variation is relatively uniform and at a low level. In examination of the raw residuals, a plot of expected normal values versus residuals indicated that data were skewed, hence the use of a bootstrap method to test for significant differences. The residual distance in the case of the alien grass cover recorded was generally consistent except for three points, which could be assigned to patchiness caused by ant activity. There is also a linear, distance-into-remnant-related effect present.

The difference in the percentage alien grass cover in and between the compartments (0 – 10 m, 10 – 40 m and 40 – 100 m) of each of the treatments before applying the

bootstrap method were examined ($F_{4,54} = 22.609$, $p < 0.01$). The control area showed the ideal and expected curve of distribution of the percentage alien grass cover, where the highest level of alien invasion occurred in the first 10 m of the remnant patch. The percentage cover of the alien grass drastically decreased from 15 m into the patch to stabilise at a noticeably lower level further away from the edge of the remnant.

The burned area showed the second lowest overall level of alien grass cover, which was not expected but could be due to early season sampling, making identification very hard. A relatively uniform distribution of alien grass throughout the whole area subjected to fire was found. There was a slight increase in alien grass cover from around 50 m into the remnant patch. The grazed area again showed a high level of percentage alien grass ground cover in the first 10 m into the patch, but the highest level was seen in the mid-section of the 100 m measured (from 15 –50 m). The amount of alien grass then decreased deeper into the remnant (from 60 m – 100 m). The grazed area, overall, had the highest level of alien grass invasion (Figure 3.4). The percentage alien grass cover decreased with distance from the edge of the remnant, in all cases except the burned area which only showed a slight increase (Figure 3.4). The control area showed the highest percentage alien grass cover initially at the edge of the remnant patch.

The Bootstrap 0.95 confidence intervals (Figure 3.2) ($F_{4,57} = 5.9780$, $p < 0.01$) showed low levels of unexplained variation in the data from the burned area, but illustrate the higher level of variation in the mean percentage alien grass cover found in the transect lines of the grazed area and the first two compartments of the control area.

The post hoc Bonferroni tests (Table 3.3) verify the results shown by the graphical analysis. All distance zones of each treatment were tested against all possible combinations of the other for significance differences. The 10 – 40 m distance zone of the grazed remnant was significantly ($p < 0.05$) more subject to alien grass than any of the other areas or compartments. In contrast, the last 60 m of the control (unburned/ungrazed area) showed significantly less alien grass invasion than most of the other distance zones. Thus the grazed area was subject to most of the alien grass invasion, especially in the mid-section of the measured patch. The control area, with

the exclusion of fire and animal activity, showed the minimum alien grass invasion. The impact of edge effects in this treatment could clearly be seen with the significant difference ($p < 0.05$) in percentage alien grass cover between the first 10 m of the remnant and the following extent of veld further away from the edge.

For an overview, the distributions of the alien grass were illustrated with the areas pooled ($F_{2,57} = 2.3495$, $p = 0.10$) (Figure 3.3). The vertical bars denote 0.95 confidence intervals. From this it is clear that there is a definite effect and that in all three treatments alien grass cover decreased with an increase in distance from the edge of the remnant. Unexpectedly, the highest alien grass cover was seen in the mid-section – within the 10-40 m zone of the patches. When pooling the distances (Figure 3.4), the grazed area showed the highest amount of alien invasion ($F_{2,57} = 15.619$, $p < 0.01$). The burned area showed the second highest percentage alien grass cover, with the control area containing the least.

3.4.2 Indigenous grass species

Edge effects on indigenous grass distribution and the response of indigenous grass to land-use

Seventeen indigenous grass species were encountered at Elandsberg and fifteen different species at Eenzaamheid (Table 3.4). The most frequently recorded indigenous species were perennial. Species most frequently recorded were similar in the burned and grazed areas.

Table 3.4: The distribution of percentage indigenous grass cover (as a percentage of total ground cover) in each of the sampled areas (common names from Van Wyk & Van Oudtshoorn 1999)

Species	Common names	% indigenous grass cover found in each treatment		
		Control	Grazed	Burned (& grazed)
<i>Aristida diffusa</i>	Iron grass	0.15	4.55	1.58
<i>Aristida junciformis</i>	Gongoni three-awn	1.05	12.94	3.95
<i>Digitaria sanguinalis</i>	Crab finger grass	-	-	1.04
<i>Ehrharta calycina</i>	Common calycina	5.73	10.48	11.71
<i>Ehrharta capensis</i>		-	-	11.46
<i>Festuca scrubra</i>	Munnik fescue	1.62	0.91	0.15
<i>Helictotrichon turgidulum</i>	Small oats grass	-	-	0.85
<i>Koeleria capensis</i>	Koeleria	0.71	0.18	0.15
<i>Pennisetum macrourum</i>	Riverbed grass	-	1.61	-
<i>Pentaschistis curvifolia</i>	Tasselgrass	7.47	0.91	0.14
<i>Pentaschistis pallida</i>	Dune grass	6.66	0.77	-
<i>Seteria verticillata</i>	Bur brittle grass	1.05	-	-
<i>Sporobolus africanus</i>	Ratstail dropseed	0.24	0.19	-
<i>Sporobolus fimbriatus</i>	Dropseed grass	-	2.84	2.05
<i>Themeda triandra</i>	Red grass	1.86	3.21	1.21
<i>Tribolium uniolae</i>	Hare grass	5.26	2.16	1.42
TOTAL COVER:		39.25	53.29	37.5

Aristida diffusa, *Aristida junciformis*, *Ehrharta calycina*, *Sporobolus fimbriatus* and *Eragrostis curvula* were the most frequently recorded species in the burned and grazed areas – all of these being palatable species, with the exception of *Aristida* spp. The grazed area showed the highest percentage indigenous grass ground cover (53.29% of the total ground cover measured throughout the whole area), while the lowest percentage cover was recorded in the burned area (37.5%). The control area showed an only slightly denser cover of indigenous grass (39.25%) being dominated by *Ehrharta calycina*, *Eragrostis curvula*, *Pentastichis curvifolia*, *Pentastichis pallida* and *Tribolium uniola*.

Table 3.5: Univariate tests of significance for the percentage indigenous grass cover

Effect	SS	Degrees of freedom	MS	F	p
Intercept	146224.1	1	146224.1	415.3805	0.00
Area	3906.2	2	1953.1	5.5482	0.01
Distance category	6932.2	2	3466.1	9.8462	0.00
Area*distance	2048.0	4	512.0	1.4545	0.23
Error	20065.4	57	352.0		

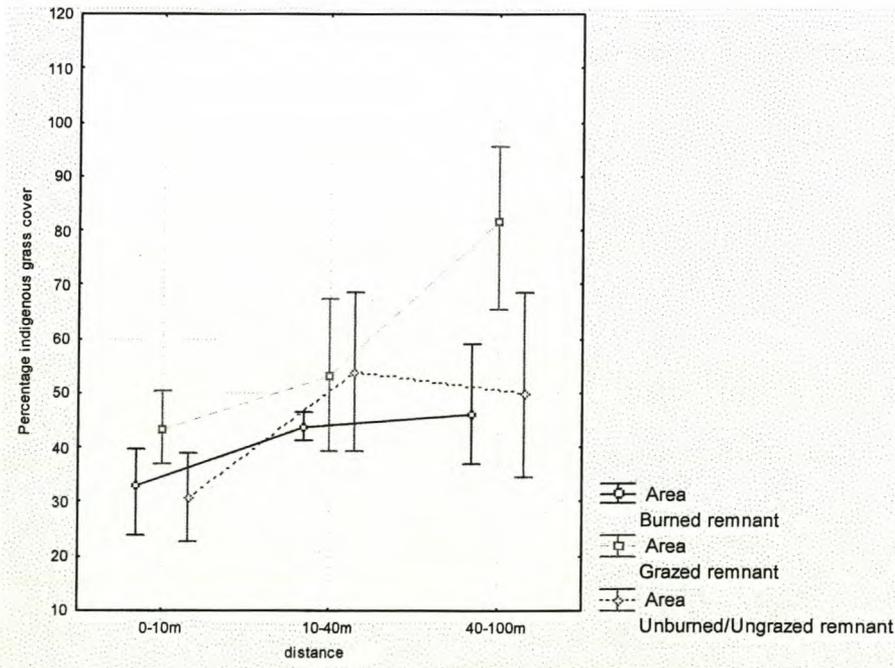


Figure 3.5: Bootstrap averages and 95% confidence intervals for percentage indigenous grass cover according to distance categories

Table 3.6: *Post hoc Bonferroni tests: indication of significant differences ($p < 0.05$, bold) in % indigenous grass cover between each separate distance zone within and between each treatment*

Cell		Bonferroni test: variable % indigenous grass species (Error: between MS = 352.02, df = 57.00)									
no.	Area	Distance zone	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
1	Burned remnant	0-10									
2	Burned remnant	10-40	1.00								
3	Burned remnant	40-100	1.00	1.00							
4	Grazed remnant	0-10	1.00	1.00	1.00						
5	Grazed remnant	10-40	1.00	1.00	1.00	1.00					
6	Grazed remnant	40-100	0.00	0.034	0.083	0.009	0.399				
7	Control remnant	0-10	1.00	1.00	1.00	1.00	0.901	0.00			
8	Control remnant	10-40	1.00	1.00	1.00	1.00	1.00	0.489	0.726		
9	Control remnant	40-100	1.00	1.00	1.00	1.00	1.00	0.201	1.00	1.00	

The distribution of indigenous grass within the sampled areas showed an interesting and contrasting pattern compared to the percentage alien grass cover recorded. The univariate tests of significance (Table 3.4) showed no significant difference ($p > 0.05$) in the overall pattern of distribution between the treatments and the compartments. The fact that there was no statistically significant difference between the explained and the unexplained variation is illustrated by the closely grouped pattern of indigenous grass occurrence (Figure 3.5). The control area showed an increase in indigenous grass away from the edge of the remnant patch, peaking at the mid-section of the patch measured. The burned area had the lowest general percentage cover of indigenous grass with the same increase away from the edge of the remnant patch. The highest percentage indigenous grass ground cover was recorded in the grazed area. The first 10 m contained the most indigenous grass of the three treatments examined and it is clearly seen that this treatment showed a definite and highest level of percentage indigenous grass increase further into the remnant patch. The 0.95 bootstrap confidence intervals ($F_{4,57} = 1.4545$, $p = 0.23$) only reduced the unexplained variation within each distance zone of the control and grazed areas (Figure 3.5), but

still maintained the same general distribution pattern witnessed in the previous graphical image.

The Bonferroni tests (Table 3.5) verified that the only significant difference ($p < 0.05$) in percentage indigenous grass cover was seen between the last 60 m of the grazed area and the first 10 m of the grazed and control area, as well as the first 40 m of the burned area. There was thus no significant difference ($p > 0.05$) in the amount or distribution of the indigenous grass in any of the treatments or sections of the sampled areas.

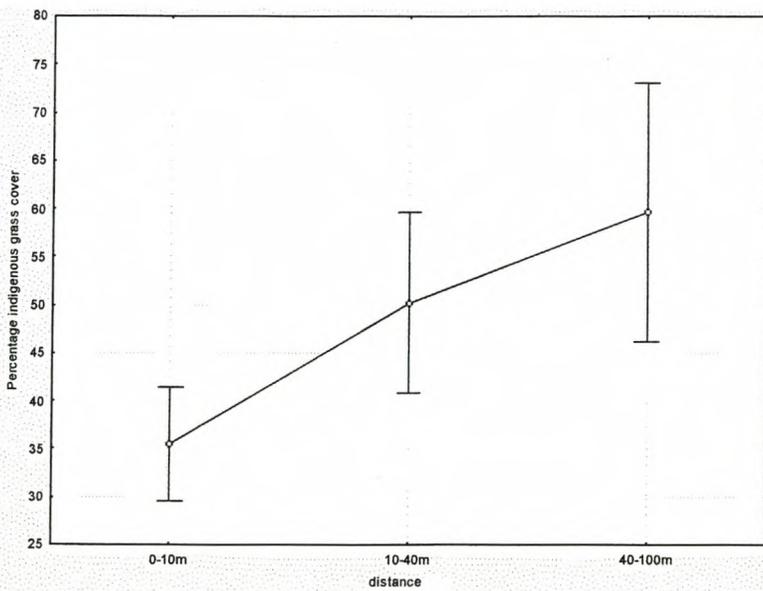


Figure 3.6: Means of the percentage indigenous grass cover according to distance categories (treatment areas pooled) – bars represent 95% confidence intervals for the means

Table 3.7: *The Post hoc Bonferroni tests for the percentage indigenous grass cover of the areas pooled*

Cell no.	Bonferroni test: variable % indigenous grass (Error: between MS = 352.02, df = 57.000)			
	Distance zone	(1)	(2)	(3)
1	0-10			
2	10-40	0.033		
3	40-100	0.00	0.42	

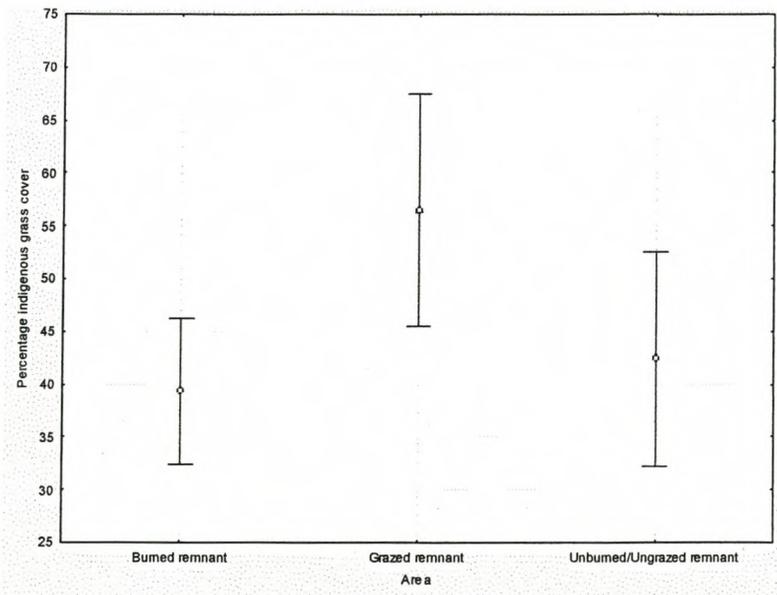


Figure 3.7: *Means of the percentage indigenous grass cover according to distance categories (distances pooled) – bars represent 95% confidence intervals for the means*

Table 3.8: *The post hoc Bonferroni tests for the percentage indigenous grass cover of the distances pooled*

Cell no.	Bonferroni test: variable % indigenous grass (Error: between MS = 352.02, df = 57.000)			
	Distance zone	(1)	(2)	(3)
1	0-10			
2	10-40	0.011		
3	40-100	1.00	0.047	

The distribution of the indigenous grass was illustrated with the areas pooled ($F_{2,57} = 9.8462$, $p < 0.01$) (Figure 3.6). The increase in percentage indigenous grass cover with increasing distance into the remnant patch can clearly be seen as a general occurrence in all three treatments. There is a significant difference ($p < 0.05$) between the amount of indigenous grass found in the first 10 m of these remnant patches and the last 60 m of each (Table 3.6).

The comparison of the three treatments ($F_{2,57} = 5.5482$, $p < 0.01$) (Figure 3.7) showed approximately the same pattern found in the distribution of percentage alien grass cover between the three treatments. The highest percentage of indigenous grass cover (percentage indigenous grass covering the ground surface measured in the intercept lines) was recorded in the grazed area, this being significantly higher ($p < 0.05$) than the percentage indigenous grass found in the other two treatments (Table 3.7). Of the two other treatments the control area proved to be slightly more beneficial for the establishment of indigenous grass compared to the burned area.

3.4.3. Shrub species

Edge effects on indigenous shrub distribution and the response of shrubs to land-use

Table 3.9: *The univariate tests of significance for the percentage shrub cover*

<i>Effect</i>	<i>SS</i>	<i>Degrees of freedom</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Intercept	189698.7	1	189698.7	606.7027	0.00
Area	51073.9	2	25537.0	81.6734	0.00
Distance cat	9940.1	2	4970.1	15.8955	0.00
Area*distance cat	3295.7	4	823.9	2.6351	0.04
Error	17822.3	57	312.7		

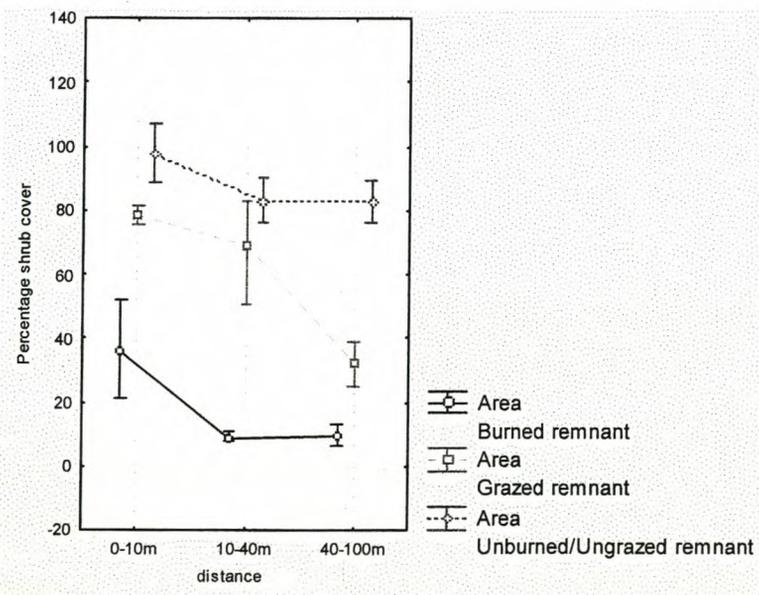


Figure 3.8: *Bootstrap averages and 95% confidence intervals for percentage shrub cover according to distance categories*

Table 3.10: Post hoc Bonferroni tests: indication of significant differences ($p < 0.05$, bold) in % shrub cover between each separate distance zone within and between each treatment

Cell no.	Bonferroni test: variable % indigenous grass species (Error: between MS = 352.02, df = 57.00)										
	Area	Distance zone	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
1	Burned remnant	0-10									
2	Burned remnant	10-40	0.18								
3	Burned remnant	40-100	0.21	1.00							
4	Grazed remnant	0-10	0.00	0.00	0.00						
5	Grazed remnant	10-40	0.03	0.00	0.00	1.00					
6	Grazed remnant	40-100	1.00	0.99	1.00	0.00	0.03				
7	Control remnant	0-10	0.00	0.00	0.00	0.77	0.09	0.00			
8	Control remnant	10-40	0.00	0.00	0.00	1.00	1.00	0.00	1.00		
9	Control remnant	40-100	0.00	0.00	0.00	1.00	1.00	0.00	1.00	1.00	

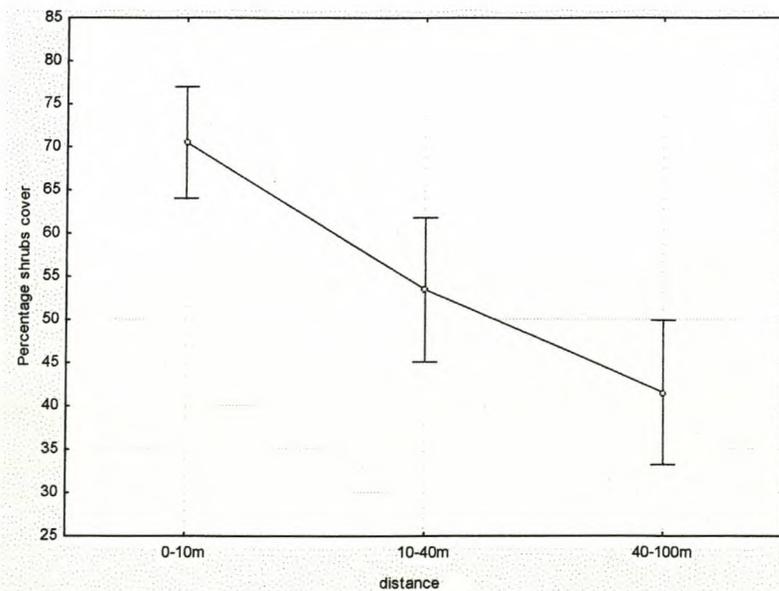


Figure 3.9: Means of the percentage shrub cover according to distance categories (treatment areas pooled) – bars represent 95% confidence intervals for the mean

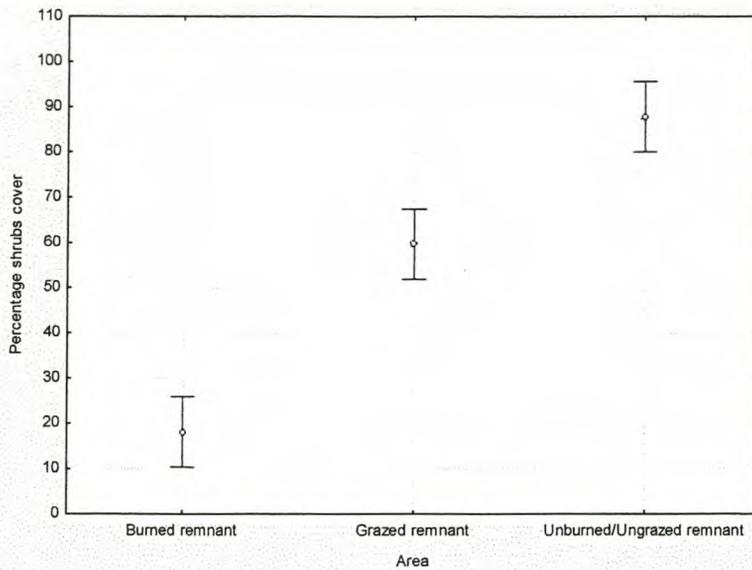


Figure 3.10: Means of the percentage shrub cover according to distance categories (distances pooled) – bars represent 95% confidence intervals for the means

The distribution of percentage shrub cover (Table 3.9) within and between the treatments examined showed a significant difference ($F_{4,57} = 2.6351$, $p < 0.05$). The examination of the raw residuals (expected normal values versus residuals) indicated some consistency in unexplained variation and the presence of a clear linear effect present, possibly related to distance from edge of remnant (as was also seen with the alien grass cover). The plot also showed the skewed distribution of the data, hence the use of a bootstrap method to test for significant differences. The difference in explained and unexplained variation is clearly seen with the low total percentage shrub cover in the burned area compared to the other two treatments (Figure 3.8). The control area showed the expected highest level of cover by shrubs, but with a slight reduction with increasing distance away from the edge of the remnant which then stabilized within 10 – 40 m from the edge to maintain this percentage shrub cover throughout the remnant. The low occurrence of shrubs in the burned area was also what would have been expected. The similar decrease in the percentage shrub cover with distance into the remnant patch was observed, but somewhat larger, followed by the uniform percentage shrub cover throughout the remnant.

Interestingly, the grazed area showed a similar picture in percentage shrub cover distribution for the first section of the remnant. The high percentage shrub cover decreased with increasing distance into the remnant, but instead of stabilizing in the mid-section, the percentage shrub cover dramatically decreased in the last 60 m of the patch as well.

The 0.95 bootstrap confidence intervals ($F_{4,57} = 2.6351$, $p = 0.04$) show the same pattern with a reduction in the unexplained variation – especially in the mid-section of the grazed area and the first 10 m of the burned area (Figure 3.8).

The Bonferroni tests (Table 3.10) showed that the control (unburned/ungrazed) area held significantly ($p < 0.05$) more shrub cover than the burned area or the last 60 m of the grazed area measured. The percentage shrub cover in the burned area was significantly lower ($p < 0.05$) than any other distance zone and treatment except the last 60 m of the grazed remnant.

As an overview, the distribution of the shrubs were illustrated with the areas pooled ($F_{2,57} = 15.895$, $p < 0.01$) (Figure 3.9). The percentage shrub cover decreased with increasing distance into the remnant. Where the distances were pooled (figure 3.10) ($F_{2,57} = 81.673$, $p < 0.01$), the percentage shrub cover was at its lowest in the burned area as would have been expected. The grazed remnant held the intermediate level of percentage shrub cover and the control area showed the highest level of shrub cover in the absence of fire and heavy grazing activity.

3.4.4 Correlation between alien and indigenous vegetation cover

Statistical analysis of the relationship between percentage alien grass cover and percentage indigenous grass cover using the Pearson's product moment correlation coefficient showed a weak positive association ($r = 0.1400$, $df = 57$, $p = 0.26$) where the variables have only 1.96% ($r^2 = 0.0196$) of their variation in common. The association between percentage alien grass cover and percentage shrub cover also showed a weak positive relationship ($r = 0.0960$, $df = 57$, $p = 0.44$) with the variables sharing only 0.92% ($r^2 = 0.0092$) of their variation. The weak negative relationship ($r = -0.1238$, $r^2 = 0.0153$, $df = 57$, $p = 0.32$) between percentage indigenous grass and percentage shrub cover were what was expected to some degree.

3.4.5 Association of vegetation with small-scale soil disturbances

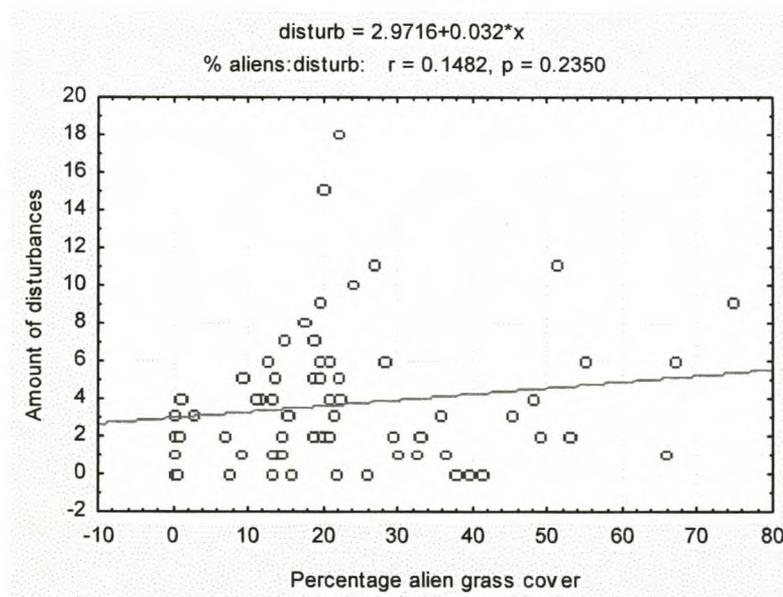


Figure 3.11: *The association of percentage alien grass cover with the amount of small-scale soil disturbances*

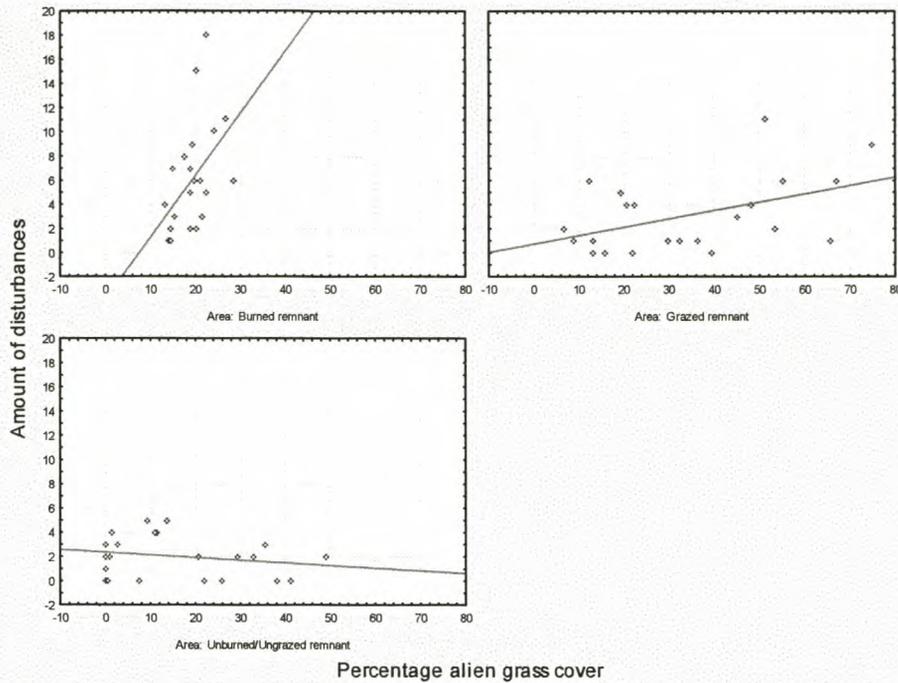


Figure 3.11.1: *The association of percentage alien grass cover with the amount of small-scale soil disturbances in the burned remnant, grazed remnant and the control remnant separately*

The Pearson's product moment correlation coefficient for percentage alien grass cover (Figure 3.11) showed a weak positive relationship ($r = 0.1482$, $df = 57$, $p = 0.24$) with small-scale soil disturbances in general. The percentage alien grass cover increased with the occurrence of small-scale soil disturbances in 2.2% ($r^2 = 0.02196$) of the cases. This was less than what was expected or what correlated with the visual observations. To analyze and depict the combined association, the correlation coefficient was calculated and illustrated for each treatment separately. The burned area (Figure 3.11.1) showed a significant positive correlation ($r = 0.4609$, $p = 0.03$) between the disturbances and the occurrence of alien grass recorded. Alien grass species occurrence increased with increased animal activity in 21.2% of the cases. The grazed area (Figure 3.11.1) showed the same significant positive correlation ($r = 0.4677$, $p = 0.03$) and a correlation in occurrence of 21.87%. The control area (Figure 3.11.1) showed an unexpected weak negative association ($r = -0.2016$, $p = 0.37$) which was not significant.

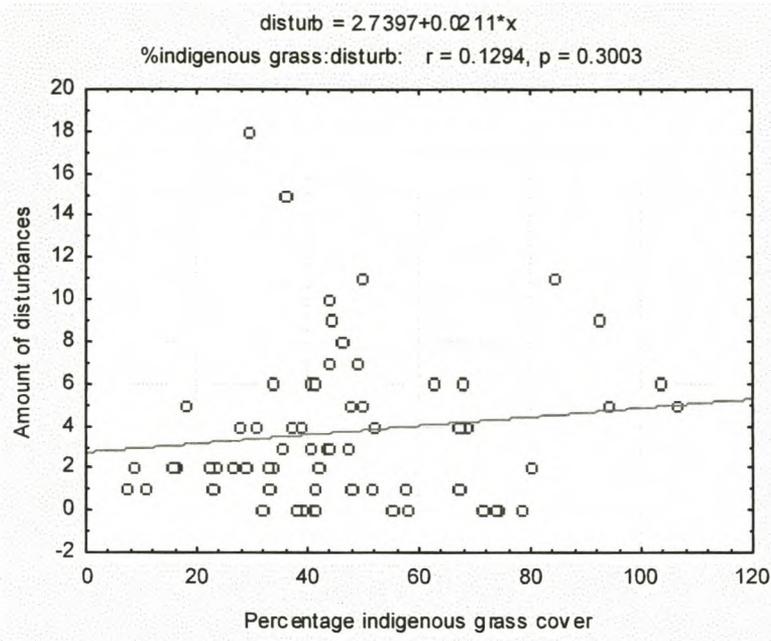


Figure 3.12: *The association of percentage indigenous grass cover with the amount of small-scale soil disturbance*

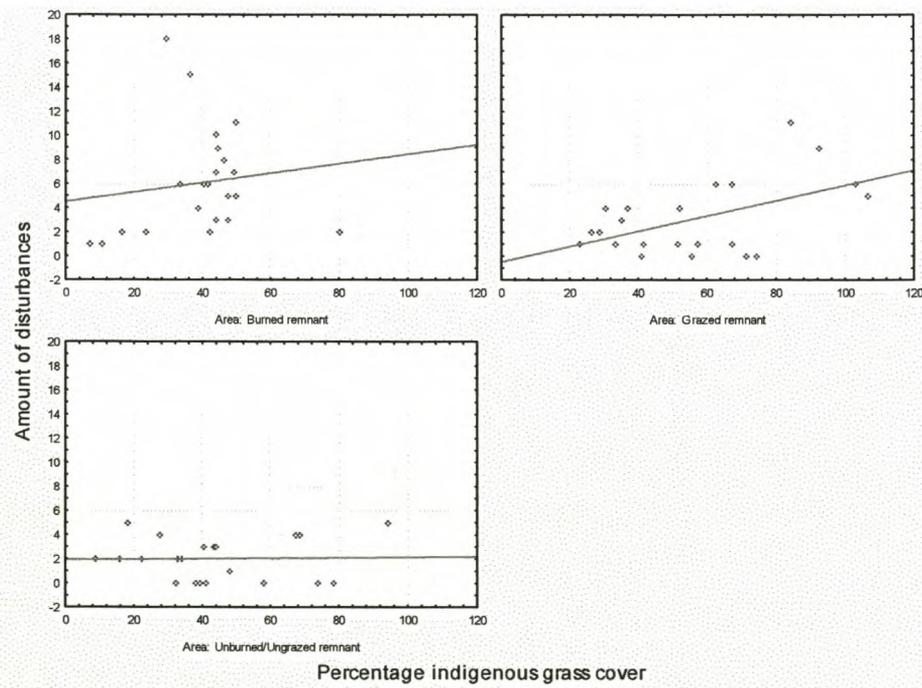


Figure 3.12.1: *The association of percentage indigenous grass cover with the amount of small-scale soil disturbances in the burned remnant, grazed remnant and the control remnant separately*

The percentage indigenous grass cover (Figure 3.12) also showed a weak positive correlation ($r = 0.1294$, $df = 57$, $p = 0.30$) with small-scale soil disturbances. The indigenous grass only associated with the disturbances 1.67% ($r^2 = 0.0167$) of the time, but a stronger positive relationship would have been expected in this case as well. Separately analyzed, the percentage indigenous grass and small-scale soil disturbances on the burned area (Figure 3.12.1) showed a weak positive correlation which was not significant ($r = 0.1367$, $p = 0.54$). The expected significant positive relationship was seen in the grazed area ($r = 0.5149$, $p = 0.01$) where indigenous grass was associated with soil disturbances in 26.51% of the cases (Figure 3.12.1). The percentage indigenous grass and small-scale soil disturbances on the control area (Figure 3.12.1) showed a weak, non-significant positive correlation ($r = 0.0265$, $p = 0.90$).

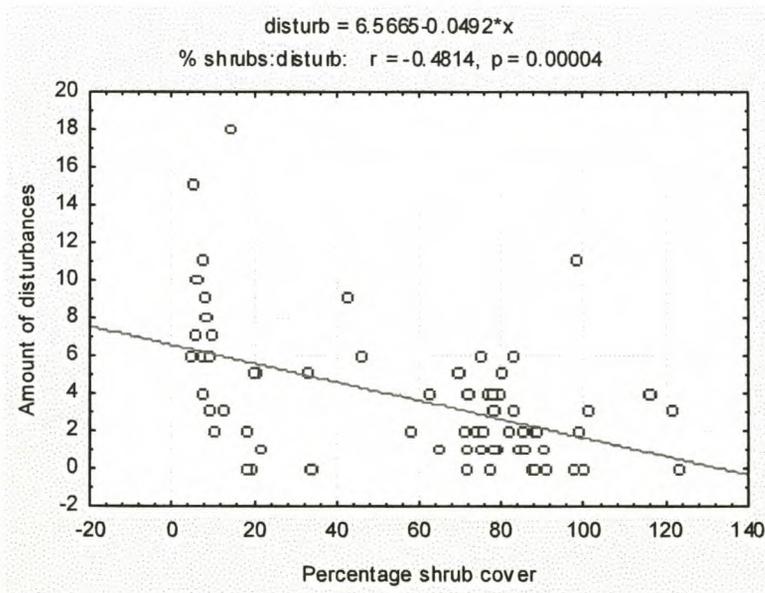


Figure 3.13: *The association of percentage shrub cover with the amount of small-scale soil disturbances*

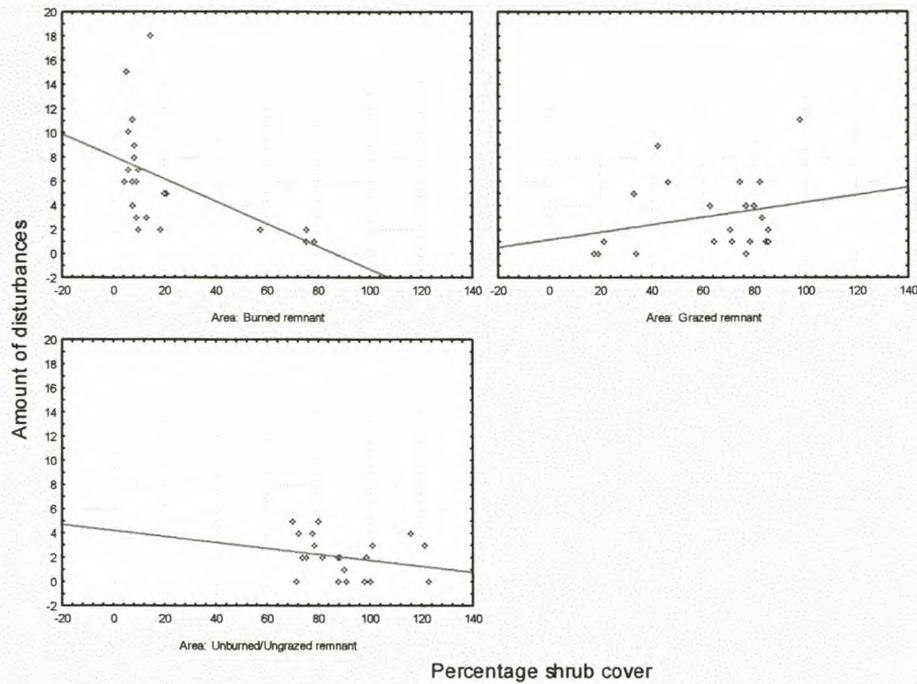


Figure 3.13.1: *The association of percentage shrub cover with the amount of small-scale soil disturbances in the burned remnant, grazed remnant and the control remnant separately*

The percentage shrub cover (Figure 3.13) showed a stronger negative relationship with the small-scale soil disturbances recorded ($r = -0.4814$, $df = 57$, $p < 0.01$). The 23.17% ($r^2 = 0.2317$) cases of inverse association between these two variables were a better reflection of what would be expected. When analyzing the treatments separately, it was clear that the resulting negative association was largely due to the significant strong, negative correlation ($r = -0.5214$, $p = 0.01$) between the occurrence of shrub species with soil disturbances (Figure 3.13.1). The grazed area showed (Figure 3.13.1) a weak, non-significant positive correlation ($r = 0.2509$, $p = 0.26$) with $r^2 = 0.06295$. Within the control area (Figure 3.13.1) there was also a weak negative association between the percentage shrub cover and the occurrence of small-scale soil disturbances, but this was not significant ($r = -0.2244$, $p = 0.32$) with only 5% of the cases showing the inverse association.

3.5 Discussion

3.5.1 Alien grass species

The effects of alien grasses on ecosystem function (in relation to fire regime, nutrient loss, altered local microclimate, and prevention of succession) are significant on the local scale and are becoming increasingly important on regional and global scales (D'Antonio and Vitousek 1992). Alien invasion, primarily by pasture grasses, is one of the most important threats facing renosterveld fragments and results obtained in this study help to determine, or give some insight into, which factors increase the risk of alien invasion. It was originally assumed that active grazing or burning of renosterveld patches would ultimately secure the highest level of biodiversity and the lowest degree of alien invasion into these remnant fragments. The objectives of this study included the examination of which management activity achieved the favored results (reduction in alien grass invasion), the evaluation of the impact of edge effects and the identification other factors facilitating alien grass invasion (such as small-scale soil disturbances and indigenous vegetation growth and establishment).

All the annual alien grass species are undesirable as a result of their ability to replace indigenous species through their competitiveness for space, light, water and nutrients or by altering disturbance regimes such as fire frequency (D'Antonio & Vitousek 1992) or soil processes (Mack *et al* 2001). The results of this study show *Briza spp.*, *Bromus spp.* and *Avena fatua* were the most significant invading alien grass species, supporting findings by Duvenhage (1993), Helme (pers. comm. 2002) and Vlok (1988). The most dominant species, *Briza maxima*, is assumed to pose the biggest threat. It is important to consider the timing of the data collection. Because of limited opportunity for sampling, the July sampling of the burned area did not provide enough time for the grass seedling development to facilitate identification. Therefore most seedlings resembled *Briza* and were noted as such. The abundance of *Briza spp.* (especially *Briza maxima*) correlates with results found in a study done by Shiponeni (2002) on Elandsberg. Sixty percent of the seeds collected in her study were grass seeds (dominated by alien pasture grass, *Briza maxima*, *Vulpia myuros* and *Cynodon dactylon*). All the alien grass species appear to have the same detrimental effect, namely the replacement of indigenous species through maintaining the competitive

advantage for space, light, water and nutrients (Van Wyk & Oudtshoorn 1999, Wells *et al* 1986) and alteration of soil processes and disturbance regimes (D'Antonio & Vitousek 1992).

It is assumed that grazing activity favors the establishment of alien grass with high grazing value, due to the distribution of seeds through dung (Malo & Suarez 1995, Milton & Dean 2001, Shiponeni 2002), transport in fur (Richardson *et al* 2000, Schmida & Ellner 1983, Sorensen 1986, Willerding & Poschlod 2002), stimulation of growth by grazing itself (Tainton 1999) etc. This would thus explain the presence of *Avena fatua*, *Lolium perenne*, *Bromus pectinatus* and *Cynodon dactylon* in the grazed and burned areas and support the findings of D'Antonio & Vitousek (1992) that animal activity facilitates the spread and establishment of *Bromus*. Growth of animal dispersed *Bromus* is increased by nutrient enrichment, while wind dispersed *Briza* preferred establishment after the first pioneer species following a disturbance event (Simons 1998). This would confirm the theory that fertilizers from the surrounding crops could favor the establishment of *Bromus* in the unburned/ungrazed area, while the disturbances and 'plant succession windows' in the areas subjected to fire and animal activities facilitated the establishment of *Briza*. Also, all of the alien species recorded were annual pioneers, providing another explanation for their presence in the burned area and wherever small-scale soil disturbances created a 'plant invasion window' (Richardson *et al* 1992) through grazing or any animal activities (Solecki 1997, Boucher 1983).

3.5.1.1 The influence of management regimes on the alien grass species

It would have been expected that burning would prove to be the most effective management tool for renosterveld due to the fact that it is a fire-prone vegetation type with plant recruitment occurring predominantly after fire (Boucher 1995). In contrast to this, fire and grazing seemed to facilitate the highest degree of alien grass invasion. Further examination of the soil property changes with the occurrence of fire and its precise influence on the alien and indigenous vegetation is needed.

The control area showed the lowest invasion by alien grass species, followed by the burned area, whereas, the grazed area in the unfavorable position facilitated the

highest establishment of alien grass species. Results of other studies confirm that fire and animal activity increased the risk of alien grass invasion into remnant patches (D'Antonio & Vitousek 1992, Denslow 1985, Loucks *et al* 1985, Savory 1986). The grazed area thus contained the combination of factors most beneficial to alien grass invasion. Further research to investigate factors facilitating establishment of alien grass species is needed. Here, I only evaluate small-scale soil disturbances, the presence of indigenous plant species (shrubs and grass) and the nutrient additions from the surrounding areas (as contributors to edge effects).

The abundance of alien grass in the grazed area fluctuated in response to the distribution of small-scale soil disturbances recorded. As expected, this could also be ascribed to the animal activity and formation of termite nests (Holmgren *et al* 2001, Vieillefosse 2001). The high level of alien invasion in the first 5 m would be the result of edge effects and animal activity due to the easy accessibility and high grazing value of the alien grasses present (Hobbs 2001, Holmgren *et al* 2001, Savory 1986, Van Wyk & Oudtshoorn 1999, Wells *et al* 1986). The increase in percentage alien cover at 15 – 55 m could again possibly be due to cautious animals keeping away from the more exposed areas closer to the transition zone. Additionally the presence of a small stream increased water availability at the mid-section of the grazed area and could have enhanced conditions favorable for the establishment of alien grass species. Compared to the control area, the higher grass cover and lower shrub cover recorded in the grazed area supported the conclusion of Savory (1986), that overgrazing does not appear to affect the survival of annuals.

The low percentage cover of alien grass species recorded in the burned/grazed area must be ascribed to the problems concerning the sampling done at that stage (insufficient growth of the grass to be identified beyond a reasonable doubt). Theoretically it should have shown the highest level of alien grass invasion, especially due to the combined effects of animal activity and the initial dominance of alien grass species after a fire due to nutrient additions (Christensen 1985, D'Antonio & Vitousek 1992, Kruger 1987, Richardson *et al* 1992, Solecki 1997). Insufficient hydration for germination and all other factors creates a harsh and unfavorable habitat for indigenous species after a fire, while alien species could be more adapted for survival in unfavorable conditions (Holmes 2002). Data did show the expected relatively

uniform distribution of alien grass throughout the whole area subjected to fire, except for a slight increase after 50 m into the remnant. Possible explanations would include edaphic factors (Christensen 1985), water availability (Christensen 1985) (due to the unpredictability of natural conditions) or the association of seedling establishment with animal activity (Karr & Freemark 1985) - increasing further away from the edge of the fragment (which is a road used for daily game drives). The highest level of animal activity was seen further into this area due to the easy access to the geophytes for herbivores, after most shrubs were removed by the fire (Karr & Freemark 1985). These small-scale soil disturbances would have contributed to the percentage alien cover by creating safe sites for the recruitment of alien grass seedlings. The initial reduction in alien grass cover could also be due to the fact that the first 5 m were burned at an earlier stage and that particular area would have had more time for the indigenous species to re-establish and decrease the level of alien grass cover. An additional study of burned areas at various stages after the fire should allow sufficient time to ensure sufficient growth to identify grasses to species level.

3.5.1.2 Edge effects and alien grass species

It was anticipated that the proximity of fertilized crops would enhance the impact of edge effects, with disturbance increasing alien grass invasion deeper into the remnant patches (Harrison *et al* 2001, Hester & Hobbs 1992). The burned and grazed areas in this study were surrounded by rehabilitating old lands, while the control area was adjacent to cultivated lands and thus subject to an increased influx of seeds from cultivated, palatable alien grass species such as *Avena fatua*, *Bromus* spp. and *Lolium perenne*. Even with this increased inflow of alien seeds, the control area showed the greatest resilience to the establishment of alien grass species. This could be attributed to the possible higher level of biodiversity in the less disturbed renosterveld remnant (Dukes 2002, Richardson *et al* 2000).

Examination of the percentage alien grass cover as a whole and the distribution of alien grass through each of the sampled areas indicated that edge effects were easier to observe in the unburned/ungrazed area. The first 15 m contained the highest level of alien invasion, possibly due to nutrient enrichment from the fertilizers of the adjacent cultivated lands. Indigenous shrubs also showed an increase in percentage

cover in the first section of the control area fragment. This supports the theory that fertilizers enhance the establishment and growth of the adjacent vegetation (the first 10 – 15 m at least) through run-off or filtration etc. (Bond *et al* 1988, McDowell & Moll 1992, Richardson *et al* 1992). In contrast, the lack of the same pattern in indigenous species could indicate that the edge of fragments are subject to conditions, irrespective of fertilizer or water additions, which could be unfavorable to indigenous species but beneficial to alien grass establishment. The more likely explanation would be that the alien grass species are highly competitive and so tend to inhibit the successful establishment of the indigenous grass species. The competitive characteristics of alien grasses then deprive the indigenous grass of any increased availability of nutrients and water – alien species being better adapted to take up nitrogen and phosphates and convert them to biomass (Van Wyk & Oudtshoorn 1999, Wells *et al* 1986). There seemed to be less ant and termite activity in the control area, which could also have contributed to the ideal pattern of edge effects recorded, while the grazed and burned areas were subject to a more irregular pattern of alien grass distribution.

3.5.2 Indigenous grass species

The reason for examining the indigenous vegetation is to test the hypothesis that the alien grass species could favor the same conditions for establishment and even be facilitated by the established indigenous vegetation.

The distribution of indigenous grass within the sampled areas showed a contrasting pattern to the percentage alien grass cover recorded. Again, the species most frequently recorded coincided in the burned and grazed areas and were mostly perennial. The grazed area showed the highest percentage cover by indigenous grass, followed by the control area. The high level of indigenous grass ground cover in the grazed area showed that animal activity could therefore be favorable for indigenous as well as alien grass species. These favorable conditions are created or include animal diggings creating safe sites for recruitment, animals acting as dispersers (Richardson *et al* 2000) and even physically stimulating growth by regular grazing (Tainton 1999).

The low percentage cover of indigenous grass found in the burned area would also be expected. This would be due to the competitive effect of the dominant alien grass directly after the fire (Helme pers. comm. 2002), combined with various factors and changes brought about by the fire itself (in terms of soil chemistry, water availability or destruction of seeds) (Christensen 1985). Thirdly, the control area showed the same increase of indigenous grass cover away from the edge of the remnant, also recorded by Tyser and Worley (1992) and seen in the burned area. This could thus correlate with the decrease in alien grass abundance and subsequent competition (D'Antonio & Vitousek 1992, Holmes 2002, Richardson *et al* 1992).

3.5.3 Shrub species

In the absence of fire and animal activity (especially grazing and trampling) the highest shrub cover was, as would be expected, recorded in the control area. The slight reduction seen after the first distance category could possibly be ascribed to the reduction in effect of the fertilizers and irrigation used for the adjacent cultivated lands. The percentage shrub cover stabilized after this reduction and was maintained throughout the rest of the remnant patch. The abundant burned bush 'skeletons' left by the fire seemed to provide safe germination sites for grass and other shrub seedlings. Due to the absence of the obstruction large shrubs posed, animal activity was also more prominent and abundant – digging up of geophytes a constant occurrence. The area burned slightly earlier than the rest of the fragment, showed a higher percentage shrub cover and subsequent lower level of alien grass cover. This strip, closest to the rehabilitating land and the other pieces of unburned remnant fragments could have benefit from a larger seed influx (Bond *et al* 1988) and thus had a quicker recovery and consequent higher percentage shrub cover. In general, the pattern of shrub cover in all three treatments were similar, except where the presence of a stream curving through the grazed area (Diemer 2000) could be outlined and correlated with the increased abundance of *Pennisetum macrourum* (Riverbed grass) and reduction in shrub cover. The consequential increase in soil moisture could have decreased the likeliness of shrub establishment.

3.5.4 Correlation between alien and indigenous vegetation cover

The association between the indigenous vegetation and the alien grass species is definitely more complex than simply comparing occurrence and needs a separate in-depth study. The association between indigenous and alien grass establishment could indicate that alien species prefer the same conditions and the germination could possibly be facilitated by the presence of adult indigenous individuals in much the same way they would facilitate the establishment of their own kind (Richardson et al 2000). After initial establishment it is clear that the alien grass species dominate the indigenous species through their competitive advantage in terms of space, water, nutrients, ability to survive and growth rate (Van Wyk & Oudtshoorn 1999, Wells et al 1986). Grasses have long been recognized as good competitors against herbaceous and woody species. In numerous studies, the establishment of large seeded and woody perennials has been found to be limited in the presence of dense grass cover (D'Antonio & Vitousek 1992).

The positive association found between alien and indigenous grass, supports the fact that most of these grass species prefer the same habitat and physical conditions to establish in (such as the small-scale soil disturbances, which provide safe-recruitment sites and increased accessibility to water and nutrients). Through the dispersal of seeds by wind or animals, the alien and indigenous seeds would also be transported to generally the same places. Consequently it is clear that competition will be inevitable and considering that the alien species are adapted to be more effective competitors and withstand harsh conditions (Solecki 1997), the establishment of indigenous grass would be inhibited (Holmes 2002).

The same positive association was found between the occurrence of indigenous shrubs and the alien grass. In this case it would be more likely that the shrubs provide safe recruitment sites, protection from grazing (as most of the alien species are palatable) and trampling, as well as some cover from the elements to the alien grass seedlings. There could even be some exchange of nutrients or some other symbiotic relationship. This result contradicts the statement made in previous studies that herbivory of small mammals under closed shrub stands reduces the abundance of

alien annuals (Vlok 1988). This, however, could possibly be applicable to the indigenous grass.

There was a weak negative association between the indigenous grass and shrub cover. Clearly the indigenous vegetation utilize different physical or temporal germination conditions and the indigenous grass do not rely or prefer the same protection from the shrubs, as was possibly seen in the alien grass species. Indigenous grass could prefer more direct sunlight or less competition for water and nutrient resources. The alien grass species, on the other hand, are hardier in terms of surviving in various conditions (Solecki 1997). Their survival depends on their ability to find open areas where their seedlings could germinate – so these grass species will survive and establish wherever they find some space (Richardson *et al* 2000), irrespective of the somewhat less than optimal conditions they would have to face (Solecki 1997).

3.5.5 Association of vegetation with small-scale soil disturbances

The amount of game (density and diversity), and related digging activity and grazing, were substantially more in the burned and grazed areas. The reserve kept to the calculated carrying capacity of the natural veld, but this is compared to the absence of most of these antelope and other animals in the control area (except for very few small antelope –the small possible impact of which is omissible). Termite and ant activity is a possible contributor to the overall alien invasion (Milton & Dean 1993, Richardson *et al* 2000, Vieillefosse 2001), assuming that these nests in all three sampled areas be subject to the same probability of occurrence.

The small-scale soil disturbances, as mentioned before, include animal diggings and all other activity such as trampling, browsing, etc. as well as termite nests. There is a definite correlation or association between these small-scale soil disturbances and alien grass establishment. Observations indicated a definite connection between the two factors. Patches of alien grass seedlings surrounded all termite nests and filled the hollows created by animals.

3.5.5.1 Alien grass species & small-scale soil disturbances

Statistical analysis proved the existence of a significant positive association between alien grass and small-scale soil disturbances in the burned and grazed areas – especially after fire. This is what would be expected and the even stronger correlation found in the burned area prove that the clearing of the shrubs increased animal activity (higher accessibility to geophytes etc.). As stipulated before, these animals carry seed in their fur and dung, which aids dispersal (Richardson *et al* 2000). They further dig and burrow which creates safe recruitment sites, release nutrients and water, create hollows in which wind-blown seeds are collected and trample established vegetation to create clearings in which grass or other seedlings could germinate (Kotanen 1995). The alien grass species are mostly highly palatable and eagerly eaten by animals (Van Wyk & Oudtshoorn 1999, Wells *et al* 1986). These seeds are also adapted to disperse more effectively than some of the indigenous species (Rouget *et al* 2001).

The weak negative relationship (although not significant) between alien grass establishment and small-scale soil disturbances seen in the absence of fire or grazing attributes the facilitation of alien grass invasion to some other factor. The animal activity seen in this area seemed to be more abundant closer to the transition zone – the animals will forage more in the nutrient enriched areas adjacent to the cultivated lands. This combined with edge effects created the increased alien invasion in the area closest to the edge of the remnant.

3.5.5.2 Indigenous grass species & small-scale soil disturbances

The establishment of indigenous grass seedlings is definitely being favored by the occurrence of small-scale soil disturbances. The percentage indigenous grass associated with the disturbances increased deeper into the remnants – replacing the alien grass seedlings as they decreased. The effect of fertilizers close to the edge of the control area would also have decreased deeper into the fragment and so the alien grass species could have declined due to the reduction in favorable conditions. The burned area with its concentration of animal activity showed an accompanying high level of indigenous grass cover. At this particular point, direct competition between

the two groups of grass species would determine which one is more abundant. The grazed area showed the expected positive effect animal activity has on the recruitment and establishment of the indigenous grass species as well as alien grass species (Holmgren *et al* 2000, Savory 1986). This particular treatment would be important in the conclusion about the relationship between grass seedling establishment and animal activity – due to the fact that this area is subject only to grazing (no burning or any other form of management). The state of this particular piece is thus a true rendition of the effect animal activity would have on renosterveld and whether it should be an integral management tool.

3.5.5.3 Indigenous shrub species & small-scale soil disturbances

Most of the shrub cover consisted of *Elytropappus rhinocerotis* (Renosterbos) which is not very eagerly eaten by any of the herbivores. Animal activity focused around these and all the other shrubs would mostly be due to the seedlings growing in the shade of these shrubs or the buried geophytes throughout the whole area. Small rodents sometimes favor the protection offered by these shrubs to hide the entrances to their burrows. In some cases seeds of shrubs have been carried into termite or ant nests, germinated and grow on or around these nests (Milton & Dean 1993, Richardson *et al* 2000). For these reasons shrubs could be associated with animal activities.

The burned ‘skeletons’ of the shrubs did not provide any protection or appeal for the fauna and animal activity was focused in clearings to easily access geophytes and insects. The shrubs in the grazed area showed the only positive association, although weak. This could be explained by the fact that there was a positive association between the (palatable) alien grass species and the occurrence of shrubs. Animals would thus be attracted to the food provided by alien grass and thus show an increased activity close to shrubs. The control area again showed that animals would prefer clearings in which to forage and dig. The small antelope species found in this area, cannot break or damage the tough shrubs found in renosterveld and the shrub species found here were apparently not favored as forage plants given that animal activity was not associated with the presence of shrubs.

3.6 Conclusion

The **dominant alien species** were found to be: *Briza* spp., *Bromus pectinatus* and *Cynodon dactylon* in the burned/grazed area, *Briza* spp., *Avena fatua*, *Bromus pectinatus* and *Cynodon dactylon* in the grazed area and *Avena fatua*, *Bromus pectinatus* and *Bromus* spp. in the control area. The **most effective management regime controlling alien grass invasion** was the exclusion of high intensity grazing and short cycle burning (control area) and there was a **reduction in the edge effect** after 20 m into the high biodiversity/low disturbance maintained pristine fragment. The data showed a positive **association of alien grass species with indigenous grass**, but alien grass out-compete indigenous species in the long term. In contrast there was a weak negative **association of alien grass species with shrub species**. There was also a definite visual and statistical **association of alien grass species with small-scale soil disturbances**.

3.7 References

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Chapter 4

Synthesis and conclusions

4.1 Synthesis of major findings

The results of this particular study imply that the grazed and burned areas were more susceptible to alien grass invasion than the unburned/ungrazed area. The grazed and burned area disclosed a vulnerability to the increased possibility of alien grass establishment associated with small-scale soil disturbances combined with the edge effects from the adjacent rehabilitating old lands. The unburned/ungrazed area showed a lower degree of alien grass invasion, irrespective of the fact that the edge effects of the adjacent fertilized crops favor alien grass species. This could be due to the stability and complexity of the more matured renosterveld found here. This agrees with the findings of Scott (1986) supporting the intermediate disturbance hypothesis in that high species diversity was obtained at an intermediate disturbance level (the control area subject to significantly lower levels of grazing as mentioned before – but there still is some grazing by wild game). Above the optimum, severe grazing decreases diversity by limiting the number of species capable of surviving to only the few most competitive plants (Savory 1986). Although disturbance by grazing in this case should have a more positive effect on the species richness of the burned and especially the grazed area (Stander 1988), the focus of this study was on the effect it has on the invasion by alien grass species. The results indicate that although the extent of grazing and animal activities on Elandsberg should maintain diversity in renosterveld patches, the small-scale soil disturbances, dispersal of seeds and growth stimulation caused by herbivory and facilitated the invasion of alien grass species.

The extent of the edge effects could clearly be seen in the control area and indicate these negative effects decreased at 20m into the renosterveld fragment. This implies that road reserves are a non-viable conservation option for pristine renosterveld fragments, due to the fact that they are aggressively exposed to edge effects from both sides (McDowell & Moll 1992). The burned and grazed areas were subject to animal activity, small-scale soil disturbances and especially grazing which influences the

species composition, biodiversity and thus the resilience to disturbances and alien invasion (Hobbs 2001, Holmgren *et al* 2000, Kowarik 1995, Savory 1986, Scott 1986, Stander 1988). The edge effects made an impact deeper into the remnant fragments because of this and consequently it has to be deduced that fire and grazing, with all their interlinked contributing factors (Christensen 1985, Denslow 1985, Hobbs 2001, Karr & Freemark 1985, Kotanen 1995, Kowarik 1995, Kruger 1987, Marais 2000, Richardson *et al* 2000, Solecki 1997), facilitate the establishment and spread of these alien grass species. The less invaded unburned/ungrazed area also showed less small-scale soil disturbances. There is a possibility that the presence of more indigenous grass species in this area could inhibit the establishment of alien grass species (Dukes 2002, Loucke *et al* 1985), while the presence of shrubs, on the other hand, seemed to facilitate alien grass establishment.

It is concluded that the correct management regime could effectively control the excessive invasion of alien grass species into the remnant renosterveld patches. Kemper (1997) reported that large fragments appear more stable than small or medium fragments and subject to a smaller degree of alien invasion. This study showed that, irrespective of the size (the grazed and burned areas were part of a much larger fragment than the control area measured), the management regime could control the extent of alien grass invasion into these remnant renosterveld patches. Grazing (including all animal activity and small-scale soil disturbances) was the main facilitating alien grass establishment - even over-riding edge effects by facilitating alien grass establishment much deeper into the remnant patches. It is therefore suggested that combined low-pressure grazing and fire management might contribute to the effective control of alien grass species while maintaining optimum biodiversity.

4.2 Conclusion

There is little known about how this vegetation type should be managed, due to a lack of knowledge about the historical composition and structure of renosterveld. Human impacts are changing the remaining remnants, the effects of alien invasions only being one example. The problem remains that the control of invasive alien plants is by far the most expensive and time-consuming task for nature conservation authorities and landowners. Finding more effective and cheaper solutions to this escalating problem is probably one of the most urgent challenges. Through establishing how far alien grass species protrude into the remnant patches, the parameters of an effective, pristine fragment could be calculated. This could contribute to the improved management of vegetation corridors, green belts and road reserves for conservation. For example, it is possible that the planting of competitive indigenous species in such areas might buffer adjacent natural vegetation against certain edge effects such as invasion by alien annual grasses. The evaluation of existing renosterveld patches on the basis of edge to area ratio and disturbance management, would also determine the effectiveness of conservation to date and contribute to better management plans for these threatened areas.

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