

**Dispersal of seeds as a constraint in revegetation of old fields in
Renosterveld vegetation in the Western Cape, South Africa**

By

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**Thesis presented in partial fulfilment of the requirements for the degree of
Master of Science at the University of Stellenbosch**



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March 2003

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.

Dedicated to the Renosterveld Restoration Project

Acknowledgements

My sincere acknowledgements go to WWF/Life-project in Namibia and the Africa-America Institute, for financially supporting my stay in South Africa. The same sincere gratitude is extended to WWF-South Africa/ Table Mountain Fund who have funded this project. Special thanks go to Mike Gregor and the entire staff at Elandsberg Private Nature Reserve for the wonderful working environment they provided and for allowing the study to be carried out in their Reserve, particularly Bernard Wooding and Nicola Farley for organising my stay and transportation around the reserve. I would like to thank my supervisors, professor Sue Milton and Rainer Krug for their support and the same special gratitude of appreciation goes to Connie Krug for all the effort, support and directions. Thanks to all my colleagues in the Conservation Ecology Department for their support and friendship, to my dear friend Theopo for her moral support and to my cousin Ndina for just being there.

Abstract

Species-rich Renosterveld vegetation does not return to old agricultural fields even after many years (10-20) of abandonment. In most cases the fields are slowly taken over by non-indigenous species, particularly alien pasture grasses and African lawn grass. While poor survival of indigenous seedlings due to competition, grazing or any other establishment constraints, might explain the failure of natural vegetation to colonise old fields, here I am testing the hypothesis that recolonisation by indigenous plant species is limited by seed dispersal. I have quantified changes in seed density with distance from the natural vegetation into old fields using seed traps and soil seed bank assessment. I have also looked at seed dispersal in the dung of large herbivores. Shrubs (with the exception of *Eytropappus rhinocerotis*) were poorly represented in the seed rain indicating that they might be seed limited. *Dicerotheramnus rhinocerotis* (a dominant shrub in Renosterveld) and certain geophytes (that were recovered in the soil bank) have proven that seed dispersal is not the primary constraint to their return to ploughed fields. *Dicerotheramnus rhinocerotis* produces a large number of seeds that are dispersed long distances into the old field and a number of geophytes were well represented in the soil bank. Large herbivores are dispersing a lot of herbaceous forbs in their dung but make very little contribution to the dispersal of indigenous tussock grass and shrubs. Seeds of indigenous Renosterveld tussock grasses (e.g. *Tribolium hispidum*) were restricted to the edge of the natural vegetation. My research has shown that some indigenous seeds, particularly those dispersed in wind and through large mammals, do reach the old ploughed field. I therefore conclude that seed dispersal is not the primary constraint to the natural recovery of populations of some indigenous plant species on old fields, but may limit recovery of certain indigenous geophytes, grasses and shrubs.

Opsomming

Spesie-ryke Renosterveld plantegroei hervestig nie op ou landerye nie, selfs ná baie jare (10-20) van verlating. Oor die algemeen word hierdie grond stadig oorgeneem deur uitheemse spesies, veral uitheemse weidingsgrasse en kweekgras. Terwyl swak oorlewing van inheemse saailinge as gevolg van kompetisie, weiding of enige ander vestigingsbeperkings, die mislukte vestiging van natuurlike plantegroei op ou benutte grond kan verduidelik, toets ek hier die hipotese dat hervestiging deur inheemse plantspesies deur saadverspreiding beperk word. Ek het veranderinge in saadigheid oor afstand vanaf die natuurlike plantegroei na ou landerye gekwantifiseer, deur gebruik te maak van saadopvangsvalle en sand saadbank beramings. Ek het ook gekyk na saadverspreiding in die mis van groot herbivore. Struik (behalwe *Eytropappus rhinocerotis*) was swak verteenwoordig in die “saadreën”, wat mag toon dat struik saadbeperk is. *Eytropappus rhinocerotis* (‘n dominante struik in Renosterveld) en sekere geofiete (wat in die saadbank gevind is) het bewys dat saadverspreiding nie die hoofbeperking is vir hulle terugkeer na geploegde lande nie. *Eytropappus rhinocerotis* produseer ‘n groot hoeveelheid saad wat oor groot afstande oor die ou landerye versprei word en ‘n aantal geofiete was goed verteenwoordig in die saadbank. Groot herbivore versprei ‘n groot hoeveelheid kruidagtige forbe in hulle mis, maar maak ‘n baie klein bydrae tot die verspreiding van inheemse polgras en struik. Saad van inheemse Renosterveld polgrasse (bv. *Tribolium hispidum*) was beperk tot die some van die natuurlike plantegroei. My navorsing het getoon dat sommige inheemse saad, veral dié wat deur die wind en deur groot herbivore versprei word, wel die ou geploegde landerye bereik. Ek maak dus die gevolgtrekking dat saadverspreiding nie die hoofbeperking is vir die natuurlike herstel van populasies van sommige inheemse plantspesies op ou landerye nie, maar mag die herstel van sekere inheemse geofiete, grasse en struik beperk.

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CHAPTER 1

Introduction

1.1 Renosterveld and the Cape Floristic Region

Renosterveld is a vegetation type of the Fynbos biome, a major component of the larger Cape Floral Kingdom in the South Western part of South Africa. Renosterveld resembles Fynbos shrubland in that like Fynbos it is dominated by low microphyllous evergreen shrubs. However the three plant families that characterise Fynbos, namely Ericaceae, Restionaceae and Proteaceae are either rare or absent in Renosterveld which is characterised by Asteraceae and Poaceae (Cowling and Richardson 1995; Rebelo 1996a ; Holmes and Richardson 1999). The major crucial difference between the two vegetation types however lies in the soil structure and nutrient richness. While Fynbos is confined to nutrient poor and sandy soils, Renosterveld on the other hand grows in nutrient-rich, fine-grained shaley soils (Cowling and Richardson 1995). This characteristic of Renosterveld has made it suitable for agricultural crop production, leading to its major transformation observed today.

The relatively higher nutrient soil of Renosterveld is responsible for the major differences that separates Renosterveld and Fynbos today in terms of land use, research conducted and conservation status. While the neighbouring Fynbos vegetation attracted research in different biological arenas, Renosterveld's fertile soils have proved attractive for production of agricultural crops (especially wheat, wine, fruit, olives and canola). This has lead to the major agricultural transformation of Renosterveld up to currently remaining less than 3% of the original West Coast Renosterveld vegetation (Low and Rebelo 1996). It is this major transformation that has now awakened a concern in conservation bodies of what should be done to save the remaining patches of Renosterveld and to investigate ways to restore this natural vegetation.

The current conservation status of Renosterveld is described as poor, with less than 1% of West Coast Renosterveld conserved (Rebelo 1996b) whereas the IUCN requires that 10% of each vegetation type should be conserved. The current Renosterveld landscape constitutes of islands or fragments (patches) of natural

vegetation and a number of old abandoned agricultural fields (fields abandoned when they are no longer suitable for crop production or due to changes in land use), in a sea of active agricultural fields. Figure 1.1 shows the distribution of the remaining patches in a sea of a transformed West coast Renosterveld landscape. The conservation potential of Renosterveld lies in the remaining natural fragments (Kemper, Cowling and Richardson 1999) as the source to restore abandoned fields. While Conservation laws and policy are trying to ban further transformation of the remaining natural patches, on the other hand conservation bodies are looking into possible ways to restore the veld.

As part of a strategy to enhance the conservation status of Renosterveld, a number of these abandoned past agricultural fields are incorporated into nature reserves in the hope of returning to their more or less natural state. However even in the fields that have been abandoned for a long time (more than 20 years), there has been poor or no progression to the natural recovery of these sites. In many cases the lands have been slowly taken over by alien plant species especially pasture grasses, or become covered in one or more of the African lawn grass species (mainly *Cynodon dactylon*), the condition that is hypothesised to reduce the indigenous shrubs and tussock grass establishment due to competition imposed by these grasses. Competition by grass as a limiting factor in the regeneration of natural vegetation on old pastures after abandonment is well reported in other systems (Chapman and Chapman 1999; Holl 1999; Holl, Loik, Lin and Samuels 2000; Posada, Aide and Cavellier 2000; Zimmerman, Pascarella and Aide 2000). This among other hypotheses to explain the poor recovery in Renosterveld's old transformed lands is yet under investigation. Another hypothesis based on observations is that the return of species-rich renosterveld is seed limited due to poor seed dispersal.

Renosterveld is currently regarded as a shrubland but whether it was originally a shrubland or grassland is still under debate (Cowling, Pierce and Moll 1986; Rebelo 1996a). In terms of vegetation, it is characterized by the dominance of Renosterbos shrub -*Dicerotheramnus rinocerotis* (Asteraceae), but other shrubs including species of the genera *Eriocephalus*, *Felicia*, *Helichrysum*, *Pteronia*, *Relhania* (all Asteraceae); *Aspalathus* (Fabaceae); *Anthospermum* (Rubiaceae); *Hermannia* (Sterculiaceae) and *Passerina* (Thymelaeaceae) are also prominent (Rebelo 1996a). Renosterveld is also

renowned for its high species richness of geophytic plants of the families Iridaceae, Liliaceae and Orchidaceae and winter-growing grasses (*Ehrharta*, *Pentaschistis*, and *Tribolium*). Renosterveld vegetation type is categorised into Lowland and Inland types. Within the Lowland type there are four geographical subtypes (Cowling and Heijnis 2001). From West to East these are the Swartland, Boland, Overberg and Riversdale subtypes. Swartland and Boland fall under West Coast Renosterveld, Overberg and Riversdale are characterised as South Coast Renosterveld. West Coast and South Coast Renosterveld differs in vegetation composition and structure, the South Coast being more grassy than the West Coast (Acocks 1953). This study focuses on the Boland region of the Coastal Renosterveld which is part of the West Coast Renosterveld (*sensu* Low and Rebelo 1996). The Boland Renosterveld is one of the most species rich and one of the most transformed and therefore highly threatened Renosterveld types.

1.2 Dispersal syndromes and South Africa's Biomes

Dispersal syndrome, a trait that relates dispersal attributes of plant diaspores to particular categories of dispersal agents (van der Pijl 1972 in: Castley 1992), is one of the important ecological phenomena in plant ecology. The knowledge of dispersal syndromes present in different vegetation types is essential for conservation, management and restoration of indigenous vegetation communities (Manders 1986; Chambers 2000). Natural communities have been highly transformed up to a point that now their further persistence lies in the transformed landscapes being restored towards their original state. This is where the importance of the knowledge of dispersal syndromes comes in (see review by Bonn, Poschlod and Tackenberg 2000), so that dispersal driving forces could be conserved together with their remaining fragments. Often this trait is ignored until large transformations are made when there will not be enough natural vegetation left to carry out ecological investigations.

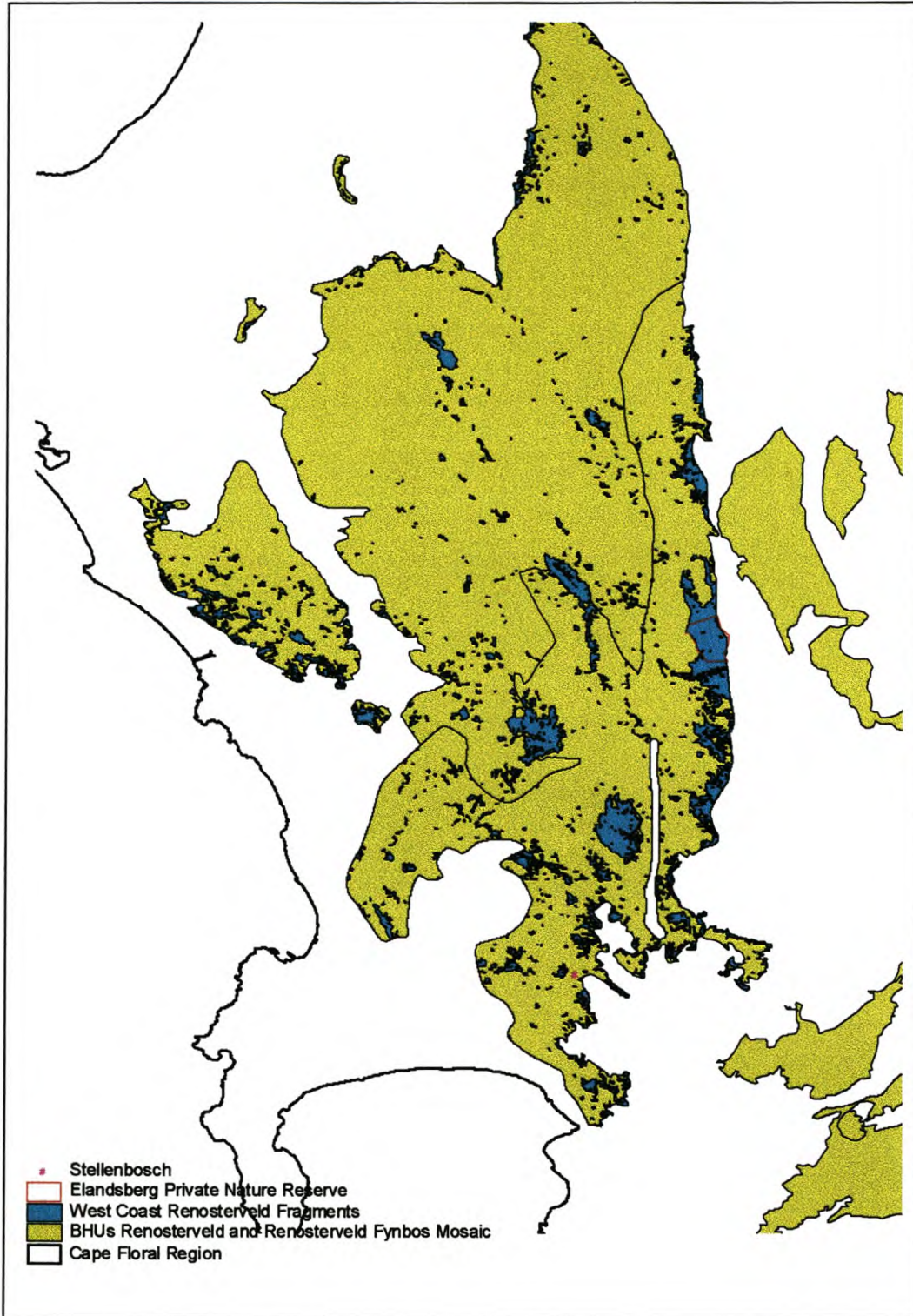


Figure 1.1 The Current fragmented landscape of West coast Renosterveld. Data source: Cowling and Heijins (2001); Ian Newton, UWC (unpublished data)

Ecological processes and adaptations typical of each ecosystem are related to the natural conditions under which the system evolved. This also applies to seed dispersal syndromes. For example, elaiosomes (food appendages attached to certain seeds that are adapted for ant dispersal) are very common in ant rich ecosystems (Hughes *et al* 1982 in: Jurado, Estrada, and Moles 2001); epizoochorous diaspore traits are more common where chances of mammals moving the seeds are high, e.g. in grasslands (Jurado, Westoby, and Nelson 1991); fleshy fruits are common where birds and arboreal mammals are numerous such as in rainforests (Foster and Janson 1985 in: Jurado *et al* 2001), and wind-adapted diaspores are expected to be more frequent in environments where wind is an important factor such as arid open environments.

South Africa carries a substantial amount of the world's plant diversity, ranging from deserts through savannas, grasslands to forests (see Huntley 1997; Low and Rebelo 1998). Esler and Pierce (1990) have demonstrated dispersal spectra for South African vegetation types which are summarised in Table 1.1. The grasslands where grazing is high are characterised by high abundance of epizoochoric plant species. In savannas, the grass layer contains grass species and other herbaceous forbs whose seeds are dispersed in herbivore dung as they feed (Janzen 1984). The tree layer is made up of species producing hard coated seeds that are dispersed in herbivore dung (e.g. African Acacias). In forests with high nutrients and relatively high rainfall, frugivory is important whereby plants produce fleshy fruits and berries that are consumed and dispersed by large frugivorous mammals and birds. In the Karoo, where the major threat is drought, seeds usually ripen towards the end of the growing period, but are retained in capsules that remain closed until they are soaked by rain (Esler and Cowling 1995). The Fynbos biome is composed of fire prone vegetation communities with several adaptations to fire. The majority of reseeders in Fynbos have soil stored seeds, but canopy seed storage (serotiny) is also common among over-storey dominants (Holmes and Richardson 1999). These (canopy-stored) seeds are stored in persistent seed capsules and only released after the fire has killed the parent plant (Holmes and Richardson 1999) and dispersed by wind on the open burnt area, after being released (Bond 1988). Myrmecochory, a major dispersal syndrome in Fynbos (Slingsby and Bond 1981) is also thought to provide protection of seeds from hot fire on the surface, as the seeds are being buried underground by ants. Resprouting is

another adaptational characteristic for fire in Fynbos, with more than half the species reported to resprout after fire from epicormic buds, lignotubers or geophytic bulbs, corms and rhizome (van Wilgen and Forsyth 1992 in: Holmes and Richardson 1999).

Table 1.1 is a summary showing the five biomes in South Africa and their predominant dispersal syndromes. The information in the table is not exclusive of other dispersal syndromes. For example in the Karoo shrublands, which are generally considered to have wind and water dispersed seeds (Milton, Yeaton, Dean and Vlok 1997), zoochory has also been shown as an important dispersal strategy for many of the Karoo plants (Milton and Dean 2001) and it is common among species occurring on nutrient rich *heuweltjies* (little hills or heaps of fertile soil over termite mounds) or mesic patches where mammals, birds and insects are common (Dean, Milton and Siegfried 1990; Milton *et al* 1997).

Table 1.1 Major vegetation Biomes and their dispersal syndromes (Key references: Esler and Pierce (1990); Cowling, Richardson and Pierce (1997a))

Biome	Main natural forces	Predominant Dispersal syndromes
Succulent and Nama Karoo	Droughts	Wind and Water
Fynbos	Fires	Myrmecochory
Forests	High rainfall, geographical isolation	Frugivory
Grasslands	Grazing	Epizoochory
Savannas	Herbivory	Endozoochory

1.3 Dispersal Syndromes in Renosterveld

Surrounded by Fynbos and Succulent Karoo, the two well researched vegetation types, Renosterveld lacks important information on ecological processes. Dispersal syndromes have been intensely researched in Fynbos (le Maitre and Midgley 1992; Cowling, Richardson and Mustart 1997b) and in Karoo vegetation types (Esler 1999; van Rooyen 1999; Milton and Dean 2001), but this is not the case for the

neighbouring Renosterveld. Until now in its highly endangered stage, the vegetation remained almost unexplored in terms of its ecological processes. Cowling *et al* (1986) requested an urgent need of studies that includes biological attributes of key species in the restoration of Renosterveld. This is the vital information required for the current restoration projects in the area. Renosterveld seems to have taken different evolutionary pathways in terms of its dispersal syndromes, from the adjacent Nama and Succulent Karoo biomes and even from the more closely related Fynbos vegetation.

The nutrient poor Fynbos vegetation type is characterised by a high incidence of myrmecochory (ant dispersal) (Slingsby and Bond 1981) and serotiny (plants with canopy seed bank, dispersing their seeds only after fire). Both these strategies are well explained and related to the Fynbos natural disturbance regime, fires. Ant dispersal is associated with regions of poor nutrient soils particularly in sclerophyll vegetation (Milewski and Bond 1982 in: Andersen and Morrison 1998; Bond and Slingsby 1984; Westoby, Rice and Howell 1990) where they disperse seeds to their nutrient rich nests, but it is also known to provide for protection of the seeds from hot fire at the soil surface. Serotiny serves as a banking strategy of seeds for recruitment after the parent plants are killed by fire (Bond, le Roux and Erntzen 1990; le Maitre and Midgley 1992). Renosterveld which is also classified as a fire prone vegetation lacks both canopy seed banks and myrmecochory (Slingsby and Bond 1981; Cowling *et al* 1997b). However, whether myrmecochory has evolved in nutrient-poor environments for the advantage of directed dispersal to nutrient-rich ant nests is not yet fully agreed (Westoby *et al* 1990; le Maitre and Midgley 1992).

Most plant species of Renosterveld are observed to resprout after fire (Kemper *et al* 1999) or to be dispersed by wind (Cowling *et al* 1994 in: Kemper, Cowling, Richardson, Forsyth and Mckelly 2000). The seeds of *Dicerotheramnus rinocerotis*, a dominant shrub in Renosterveld, and a few other species in this vegetation type, are light and feathery with plumes (Cowling *et al* 1986), well suited for wind dispersal. However, there has not been a specific study done on potential dispersal of these seeds. This type of information required for planning and managing the persistence of indigenous plants, and for restoration purposes.

Due to high soil fertility it is thought that Renosterveld was perhaps responsible for the herds of large game in the Fynbos Biome few hundred years ago (Rebelo 1996a). The effect herbivory might have had on the evolution of dispersal syndromes is not known nor has the role that the antelope that currently inhabit the region (introduced or reintroduced) play in dispersing seeds ever been addressed. The Cape mountain zebra (*Equus zebra zebra*), Quagga (*E. quagga*), Blue antelope (*Hippotragus leucophaeus*), Red hartebeest (*Alcelaphus buselaphus*), Eland (*Taurotragus oryx*), Bontebok (*Damaliscus dorcas dorcas*), African elephant (*Doxodonita africana*), Black rhino (*Diceros bicornis*) and African buffalo (*Syncerus caffer*) were common large herbivores, suggesting that grazing by large herbivores was important (Rebelo 1996a). A substantial quantity and range of seeds recorded as germinating from dung of large herbivores in Africa (Milton and Dean 2001) and elsewhere (Janzen 1984; Welch 1985; Malo and Suarez 1995; Pakeman, Digneffe and Small 2002) indicates how these herbivores could have a significant effect on the dynamics and species richness of these systems (Pakeman *et al* 2002). Animals are also known to influence and even help maintain plant species richness in terrestrial systems (Hewitt and Miyanishi 1997) not only by direct feeding on the plants but also by disseminating their seeds.

Bird-dispersed species are prominent in Renosterveld, with about 26-46% of Renosterveld shrub species reportedly dispersed by birds (le Maitre and Midgley 1992). Plants like wild olives (*Olea europea africana*) that are found on nutrient-rich *heuweltjies* have berries that could be eaten by birds that would disperse them as they fly from *heuweltjie* to *heuweltjie*. *Eriocephalus ericoides* was reportedly used as bird nesting material in the Karoo (Dean *et al* 1990) and related species are also common in Renosterveld. However, for the restoration of open old fields, bird-dispersed species are not likely to colonise in the absence of suitable perches or nest sites. Renosterveld is known for the high diversity of geophytes. Many geophytes have relatively large and passively dispersed seeds that only disperse over short distances (Kemper *et al* 1999) and therefore the successful return of these to restored areas without aid by seeding is questionable.

Members of myrmecochorous genera in Fynbos are also found to be wind dispersed, with winged fruits in Renosterveld (Bond and Slingsby 1983 in: le Maitre and

Midgley 1992). The still unknown explanation behind this difference in evolutionary pathways is unclear. The absence of myrmecochory from relatively high fertile Renosterveld soils could be that the costs of ant-dispersal outweigh the benefits by fertile soils.

1.4 Seed dispersal as a constraint

Degraded or disturbed areas suffer many factors that delay or stop their regeneration, a number of which are summarised in Chapman and Chapman (1999). The relative importance of these factors varies at different temporal and spatial scales as well as between studies and depends on the intensity of the disturbance (Holl 1999; Holl *et al* 2000). Seed limitation and competition of seedlings with pasture grass are the most important factors impeding recovery of disturbed areas (Holl *et al* 2000; Zimmerman *et al* 2000). Availability of seeds is an important onset to recovery. Holl *et al* (2000) indicated that the first step in studying the recovery of any ecosystem is to see whether propagules are present in the disturbed areas. Seed limitation is widely reported to constrain vegetation recovery or regeneration (Dzwonko and Loster 1992; Primack and Miao 1992; van Dorp, van den Hoek, and Daleboudt 1996; Duncan and Chapman 1999; Holl 1999; Wijdeven and Kuzee 2000; Bischoff 2002). The same process has been studied at the landscape scale in terms of the colonization of new sites (Lee 1993, Scherff, Galen and Stanton 1994; in: Coulson, Bullock, Stevenson and Pywell 2001), and these studies have generally found that dispersal is the limiting factor. Agricultural activities especially for extended periods deplete the soil seed bank and the success of restoration therefore largely depends on the accessibility of the seeds of desirable plant species to these sites (Berendse *et al* 1992 in: van Dorp *et al* 1996). Recommendations towards successful restoration of disturbed patches are highlighted by Wali (1999) who pointed out the importance of the size of disturbed area, the size and proximity of seed sources and dispersal mechanisms. Seed dispersal is not always a limiting factor: for example in the Kibale forest, sufficient seeds were found to arrive in the old pasture (Uhl and Jordan 1984 in: Chapman and Chapman 1999) but seedlings were unable to grow due to competition from herbaceous and dominant shrub and tree species. Fort and Richards (1998) in their study of seed dispersal limitation in desert playas have also found that seeds were

dispersed up to more than 700 m from the adjacent vegetation and thus dispersal could not be the factor limiting plant colonization.

It is in the light of all this that I am carrying out a study to determine whether seed dispersal is limiting the return of species-rich Renosterveld back to old ploughed fields that span the landscape.

1.5 Objectives of the study

The current poor conservation status and management of Renosterveld have prompted an urgent need to restore this vegetation. The main objective of this study is to provide information on the knowledge of seed dispersal rates of indigenous vegetation into old agricultural fields. Through this objective, the question of seed dispersal as a limit to the revegetation of old fields is addressed. To reach the set objective, the study **aims** at:

1. Revealing the various dispersal syndromes in Renosterveld.
2. Testing the hypothesis that regeneration of some plant species present in adjacent Renosterveld is seed limited in old fields.

By addressing the following **specific questions**:

1. How far and by what means do seeds move from natural Renosterveld into old lands?
2. How is the dispersal distance related to seed morphology?
3. Does the soil seed population change along a gradient from natural Renosterveld into old fields?
4. Is there a trade-off between dispersal in space and in time?

1.6 Study structure

The study considered both spatial and temporal scales. To address the question of seed limitation, I trapped seeds at various distances from the natural vegetation into an old field and have investigated soil seed bank composition at different distances from the natural vegetation as well as seeds that are dispersed in animal dung. On a temporal scale, I compared seed dispersal patterns over 12 months and sampled the composition of fresh and accumulated soil seed banks.

1.7 Thesis structure

Chapter 1 is an introduction and includes a literature review on seed dispersal syndromes. Chapter 2 describes the study area, as well as a short review of methods used in seed dispersal studies as related to the goal of this research. Chapter 3, 4 and 5 cover the three aspects of the study: seed traps, dispersal in the dung of large herbivores and soil seed banks assessment respectively. Each of these three chapters consists of a short introduction to the chapter, materials and methods used, and results with discussion. Chapter 6 combines and compares as well as discusses overall seed patterns in old seed bank and fresh seed rain and Chapter 7 concludes the study with a synthesis and points out applications of the study to management.

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CHAPTER 2

Study site and review of methods

2.1 Study area

The Elandsberg Private Nature Reserve (EPNR) (19°03' E, 33°27' S) lies in the western foothills of the Elandskloof Mountains south of the Voelvlei Dam, approximately 25 km north of Wellington in the Western Cape province of South Africa. Covering 3 606 ha in extent, it is one of the largest lowland conservation areas in the Cape Floristic Region and reportedly, conserves the biggest patch of the remaining West-Coast Renosterveld (Rebello 1996).

Climate: The climatic description is based on data from Wellington, the nearest town approximately 25 km south of the Reserve. The area is typically Mediterranean with most of its mean annual rain falling in winter (Figure 2.1). Precipitation occurs all year round but there are dry periods late in summer. The rainfall peaks in June with an average of 114 mm whereas the average minimum precipitation (10 mm) is in December. The coldest month, in winter (July), has an average of 6°C whereas the hottest month in summer (February) has an average of 31.3°C. Wind predominantly blows from the south for most of the year, and become northerly in the winter (Diemer 2000).

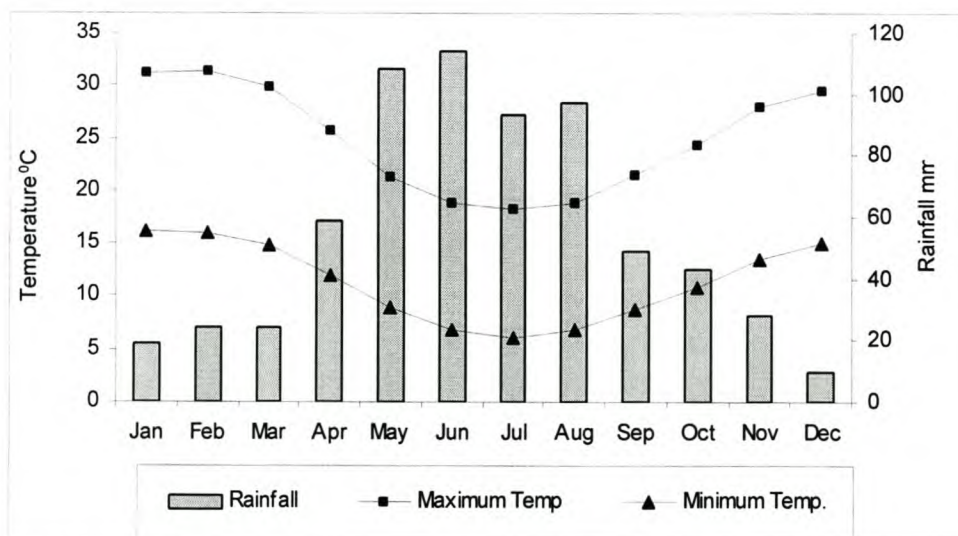


Figure 2.1 Average monthly temperatures over a period of 59 years (1879-1902, 1951-1984) and rainfall over a period of 35 years (1951-1984) at Wellington. (Data obtained from the South African Weather Bureau Climate Statistics up to 1984, Department of Environmental Affairs)

Geology, topography, soils and drainage -The Elandskloof mountains mark the eastern border of the reserve. The reserve ranges from 68 to 400 m a.s.l. with a west-facing aspect such that the slope gets steeper towards the eastern border. (Diemer 2000) (Figure 2.2). This topography makes the area well drained by runoff water from the mountains and in winter when rainfall is high, 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 small dams and one large dam (Figure 2.2).

Geologically the reserve forms part of the Cape Granite suite, which overlies the Malmesbury geology group, consisting mainly of sedimentary rocks, which were deposited in a geosynclines (Visser 1984 in: Diemer 2000). The soil was derived upon weathering of these predominantly clay substrates (Deacon *et al* 1992 in: Diemer 2000) forming the clay nutrient rich soil that is less sandy on the lower slope and which is occupied by Renosterveld in the reserve (Figure 2.3). The soil on the lower slope is also deeper due to the weathering of soil material from the mountains (Cowling and Richardson 1995). On the eastern portion of the reserve where the slope is steep, the soil is nutrient poor, shallow and weakly developed and thus is dominated by the mountain Fynbos (Figure 2.3).

Vegetation –Renosterveld at Elandsberg Private Nature Reserve is classified as Coastal Renosterveld according to Acocks (1988) and occurs in the Boland area according to Cowling and Heijnis (2001)'s Broad Habitat Units of classification. It covers the largest area of the reserve whereas mountain Fynbos mainly occurs on the mountain slope on the eastern border (Figure 2.3). Fields marking past ploughing activities are incorporated into the reserve and are referred to as old lands in Figure (2.3) but hereafter in this thesis, these will be referred to as old fields. These fields were cultivated for wheat from the late 1960s up until 1987 when they were left abandoned from any agricultural activity (ploughing or livestock grazing) and became incorporated into the reserve. The fields are bounded by active agricultural cultivation to the west, and thus act as a buffer zone between the farming area and the natural vegetation to the north and east. The general description of these old fields in terms of vegetation is an open grassy area, with the dominance by one of the perennial African lawn grasses, *Cynodon dactylon*, in summer, and annual alien pasture grasses

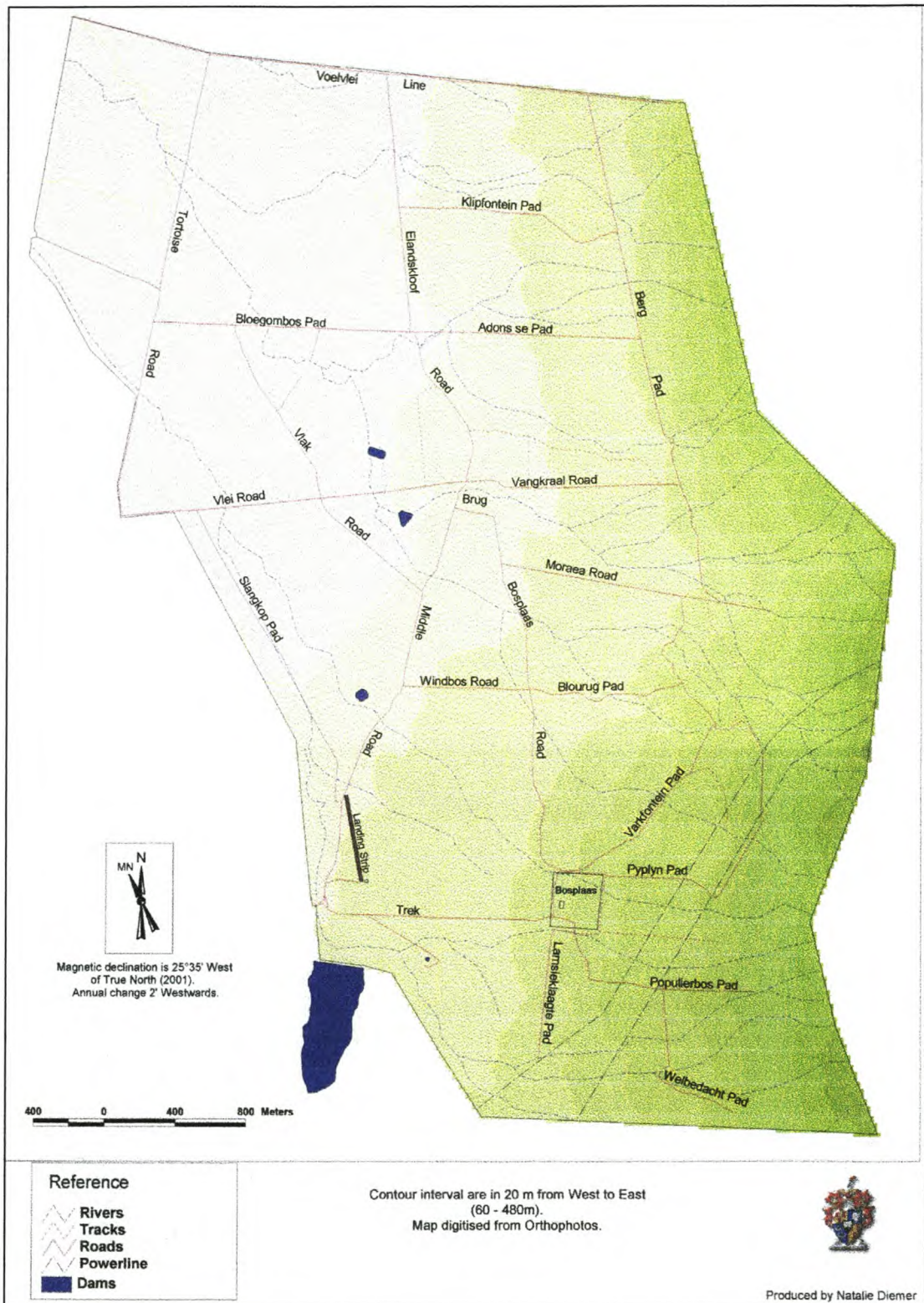


Figure 2.2 The Elandsberg Private Nature Reserve (Diemer 2000)

Vulpia myuros, *Briza maxima*, *B. minor*, *Bromus diandrus*, *B. pectinatus*, *Lolium* spp., *Poa annua*) that dominate the fields after winter rainfall. This particular study was conducted on the marked field in Figure 2.3, and there is an ecotone between the natural vegetation and old field. In this transition zone, there is some returning Renosterveld vegetation and waves of *Dicrothamnus rinocerotis* (a dominant shrub in Renosterveld) could be seen encroaching into the field mainly along the ploughed furrows that span the field and run parallel with the ecotone. Sparsely scattered Renosterveld vegetation could also be seen in the field including the shrub species of the genera *Helichrysum*, *Hermannia* and *Thesium*, and an indigenous perennial forb *Leysera gnaphaloides*. The natural vegetation is dominated by *D. rinocerotis* which is also the height dominant, but other prominent shrubs include *Eriocephalus africana*, *Relhania fruticosa* and *Athanasia trifurcata*. An indigenous annual grass *Tribolium hispidum* dominated the grassy layer of the natural vegetation up into the transition zone where grasses of the old field took over.

Past and present disturbance regimes affecting the vegetation

Historically, the area was used for livestock grazing until 1973 when it was stocked with re-introduced populations of antelopes (Table 2.1) and partly cultivated for wheat and grain (Mike Gregor pers.com). Cultivation in what is now the reserve area ceased in 1987 when the reserve was proclaimed and registered as a private nature reserve in 1988. These mammalian grazers, browsers and other small herbivores (Table 2.2) roam freely in the reserve, using both the natural vegetation and the old ploughed fields. The reintroduced antelope now appear to be important in controlling the structure and composition of the vegetation and allegedly converted the old fields into *Cynodon dactylon* covered fields. Introduced feral pig, *Sus scrofa* digs up geophytes and open significantly large patches especially in the closed cover of lawn grass in the old field which might provide niches for the establishment of seedlings. Dug holes were also evident in the natural vegetation, an activity by porcupines as they dig and feed on geophytes. In addition to herbivory and past agricultural activities, patchy fires influence vegetation patterns in Elandsberg Nature Reserve (Figure 2.4). The entire reserve was burned in 1982 and then smaller fire patches occurred in 1988, 1989 and 1999 (Figure 2.4).

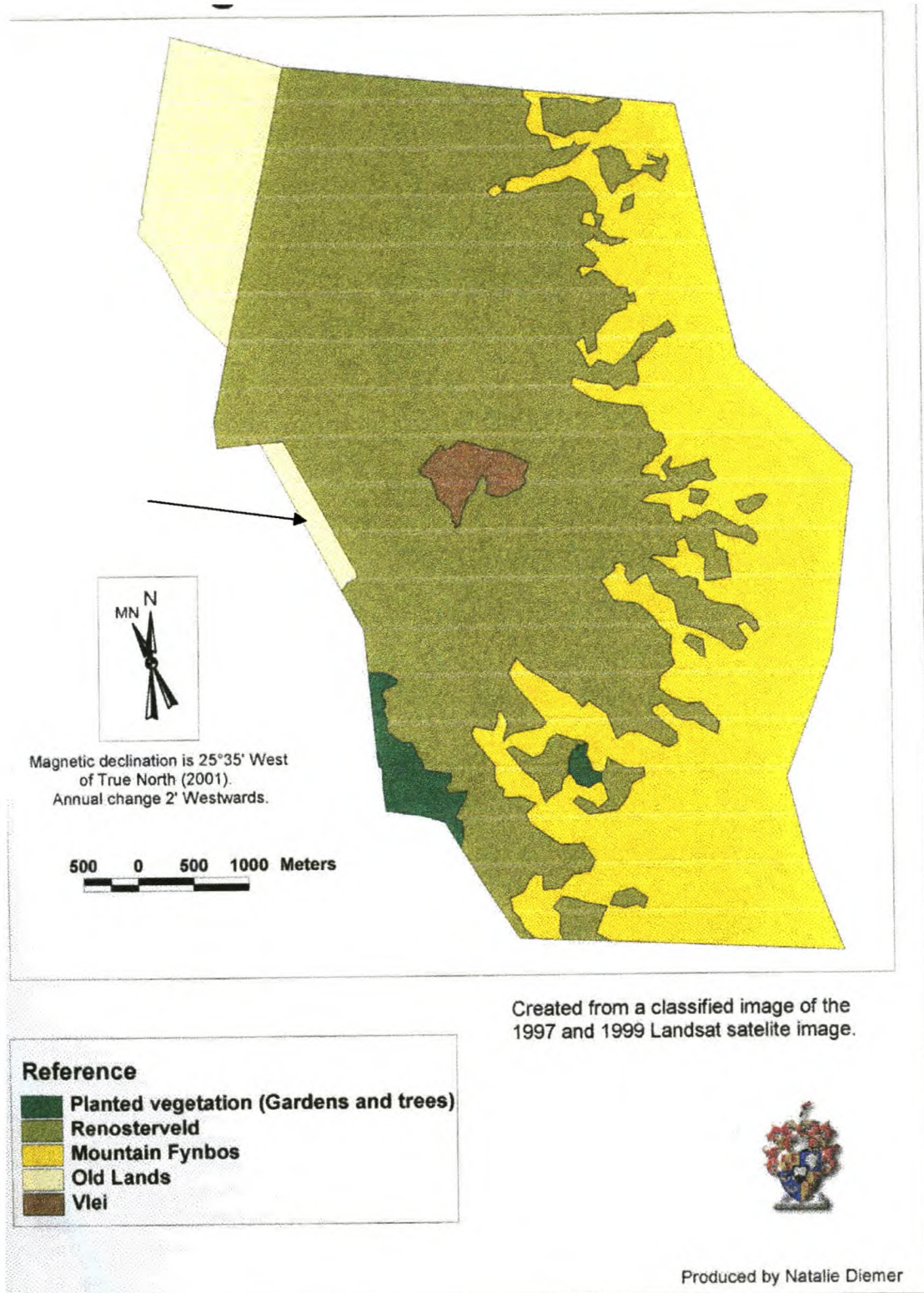


Figure 2.3 Vegetation communities at Elandsberg Private Nature Reserve (Diemer 2000).

The arrow marks the old field that was investigated for this study

Table 2.1 Large mammals found in Elandsberg Private Nature Reserve. Species list is obtained from the Reserve's office. (Data on feeding category are extracted from Grossman, Holden and Collinson 1999; Bothma, van Rooyen and du Toit 2002)

Animal	Major feeding category
Black wildebeest (<i>Connochaetes gnou</i>)	Short grass grazer
Blue wildebeest (<i>Connochaetes taurinus</i>)	Grazer
Bontebok (<i>Damaliscus dorcas dorcas</i>)	Short grass grazer
Burchell's zebra (<i>Equus burchelli</i>)	Mixed feeder
Cape mountain zebra (<i>Equus zebra</i>)	Long-medium grass grazer
Eland (<i>Taurotragus oryx</i>)	Mixed feeder
Gemsbok (<i>Oryx gazella</i>)	Long grass grazer
Grey rhebok (<i>Pelea capreolus</i>)	Mixed feeder
Red hartebeest (<i>Alcelaphus buselaphus</i>)	Short grass grazer
Springbok (<i>Antidorcas marsupialis</i>)	Mixed feeder

Table 2.2 Other animals that occupy the Elandsberg Nature Reserve. Species list is obtained from the Reserve's office. (Source of information are: 1 (Brown, Urban and Newman 1982), 2 (Skinner and Smithers 1990), 3 (Rall and Fairall 1993)

Animal	General sources of food
Aardvark (<i>Orycteropus afer</i>)	Ants and termites (2)
Feral pig (<i>Sus scrofa</i>)	Bulbs, corms, rhizomes, insects (2)
Mole rat (<i>Georychus capensis</i>)	Bulbs, corms, rhizomes (2)
Other rodents	Seed eaters, leaves, insects (2)
Ostrich (<i>Struthio camelus</i>)	Soft annual plants, flowers and seeds (1)
Porcupine (<i>Hystrix africae australis</i>)	Bulbs, corms, rhizomes (2)
Tortoises (<i>Psammobates geometricus</i> ; <i>Chersine angulata</i>)	Soft annual plants and flowers (3)

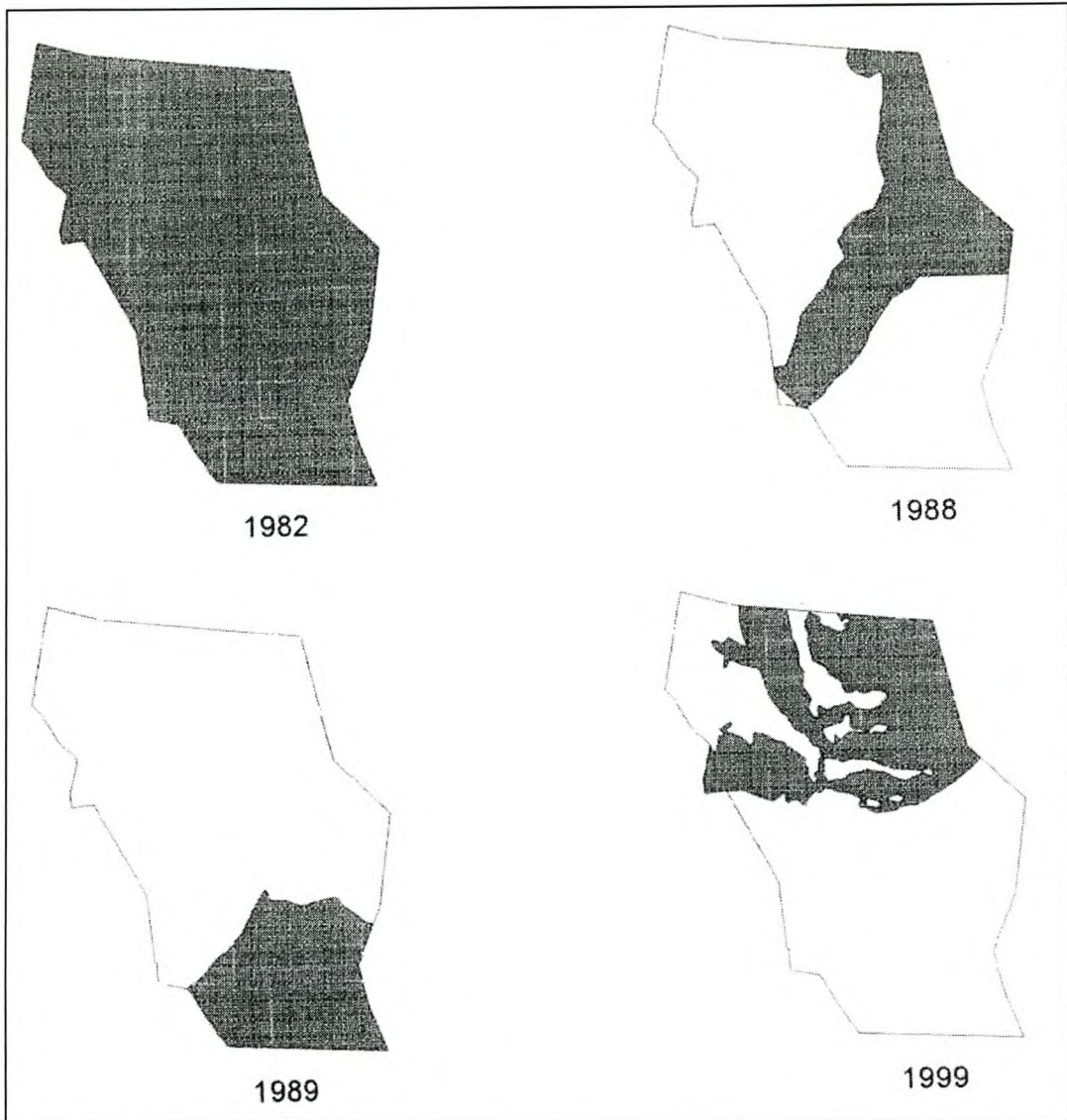


Figure 2.4 Distribution and sizes of the four fires at Elandsberg Private Nature Reserve. (Map obtained from the Reserve office)

The field studied covers an area of 1 068 m by 190 m (20.29 ha) from which a sampling sub-area of 2.5 ha (250 m by 100 m) was used to collect data (Figure 2.5). On the northern border of the field there is an area that burned in 1999, three years ago. The vegetation here does not comprise the dominance of any species because the vegetation is still young and comprises a mixture of herbaceous plants and shrub seedlings. Further 190 m to the west border, is an active wheat field. Further 190 m to the west border, is an active wheat field.

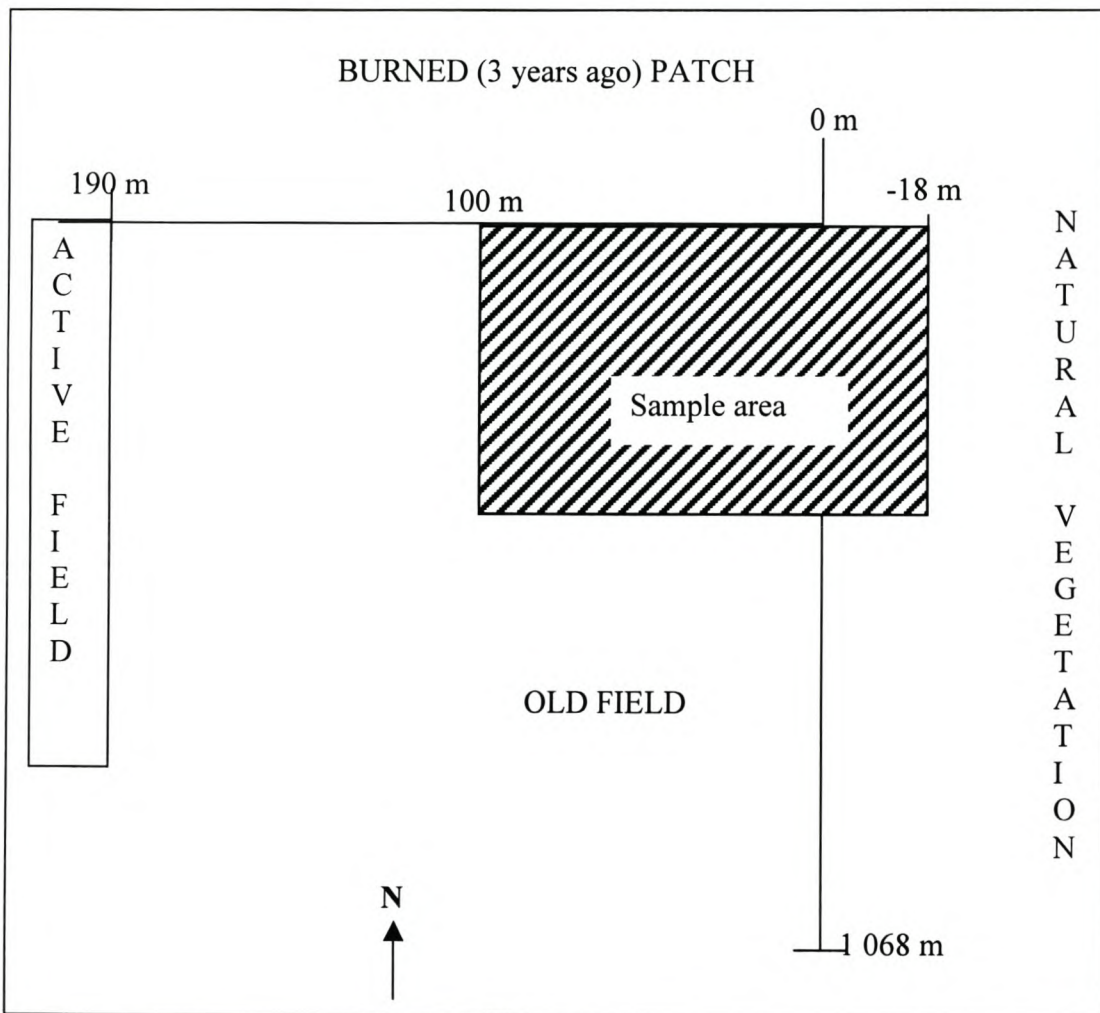


Figure 2.5 The study field and sampling area (NOT TO SCALE)

2.2 Review of methods for studying seed dispersal

The process of seed dispersal is described as one of the most difficult to measure among factors that govern plant distribution and abundance (Bullock and Clarke 2000; Jongejans and Telenius 2001). Yet, an understanding of dispersal behaviour is needed to understand the fate of plant communities during climatic change (Primack 1992; Pakeman 2001), the invasion of natural habitats by invasive species (van Wilgen and Siegfried 1986; Holmes 1990; Knight and Macdonald 1991; Lonsdale 1993) and the regeneration of disturbed areas (Manders 1986; Bond 1988; Musil and de Witt 1990; Chapman and Chapman 1999; Duncan and Chapman 1999; Martínez-Garza and González-Montagut 1999; Holl, Loik, Lin, and Samuels 2000; Bischoff 2002). In seed limitation studies, the aim is to obtain spatial and temporal dispersal patterns and density distribution from the source (seed shadow).

Sowing experiments are the most straightforward way to assess seed limitation, done by adding seeds and comparing the resulting seedling numbers with control plots in which seed availability is not augmented (Eriksson and Ehrlen 1992; Tilman 1997; Nathan and Muller-Landau 2000; Rand 2000; Turnbull, Crawley and Rees 2000; Foster 2001). These experiments, however, say little about the absolute degree of seed limitation, or of the relative importance of seed supply compared with other factors in natural communities (Nathan and Muller-Landau 2000). Seeds disperse both in space and in time. The spatial density distributions are obtained via studies of seed rain whereas temporal dispersal patterns are those of seed bank and seasonal variation in dispersal. As a requirement for these studies, there should be a source of seeds of known distance in proximity to the restored site. The exact method to quantify seed rain depends on the vegetation structure and dispersal syndromes of the area. For example in forests where dispersal by frugivorous birds is common (Foster and Janson 1985 in: Jurado, Estrada and Moles 2001), their behavioural patterns are mapped. Wind dispersed seeds from tall trees are trapped using elevated or suspended seed traps above ground (Lonsdale 1993; Holl 1999), and in grazed ecosystems, dispersal via animal dung is also considered.

Renosterveld is a shrubland with a high proportion of wind-dispersed plants (Cowling *et al* 1994 in: Kemper, Cowling, Richardson, Forsyth and Mckelly 2000) and some plants with seeds that could potentially be dispersed in herbivore dung. Frugivory is

restricted to shrubs found on *heuweltjies* (termitaria). Data on dispersal distances of wind-dispersed or tumbling seeds are primarily obtained by seed trapping (Aguiar and Sala 1997; Rand 2000). Two types of commonly used seed traps are pit falls (seed counts) and seed free medium trays (seedling counts). Pit fall traps may be constructed in a wide range of sizes and shapes, but the main idea is that seeds are able to be trapped in and not bounced back, seed predation is minimal (Hoppes 1988) and water is drained out of the trap (Verkaar, Schenkeveld and van de Klashorst 1983; Aguilar and Sala 1997). Pit fall traps are set so that the mouth of the trap is level with the ground surface so as to trap tumbling seeds as well as flying seeds. The trap entrance should not be buried below the surface because the trap would soon be filled with litter or soil. The second type of seed trapping is done by putting trays filled with seed-free medium on the ground, in the study area, and recording any germinants (Morris, Marks, Mohler, Rappaport, Wesley and Moran 1986; Wijdeven and Kuzee 2000). In addition to providing spatial distribution, seed free trays also give information on the germinability of the dispersed seeds.

A general understanding from the literature is that the majority of seeds at dispersal fall close to the source (Sinha and Davidar 1992; Holmes and Richardson 1999; Cain, Milligan and Strand 2000) and therefore trapping layouts are designed so as to increase trapping effort close to the potential seed source. Trapping effort may also be increased further away from the seed source in order to increase the possibility of catching the few seeds that disperse long distances, because the probability of a seed falling into a single seed trap decreases with distance from the seed source (Hoppes 1988; Sinha and Davidar 1992).

Animals play a major role in influencing the systems they live in, not only by feeding on plants but also by circulating their seeds either as potential dispersers or accidentally as they take in the foliage (Janzen 1984; Hewitt and Miyanishi 1997). For endozoochory, the rate at which dung is deposited in the study area, patterns of distribution and density is important, as this will determine the patterns of seed distribution. Dung is therefore collected at intervals and their dry weights determined before transferring samples to the glasshouse for germination trials (see studies by Welch 1985; Malo and Suarez 1995; Milton and Dean 2001; Pakeman, Digneffe and Small 2002; Slater and du Toit 2002). Depending on seed sizes in the area, other

studies have also attempted physical dissection and direct counts of intact seeds in dung pellets (Milton 1992; Milton and Dean 2001). Both methods (seedling germination method and direct seed count) have advantages and disadvantages over one another. Direct count reveals both germinable and dormant species (Milton and Dean 2001), but it is limited because even unviable seeds might be counted. Seedling counts on the other hand might underestimate seeds with special requirements with regard to germination conditions that are not met in the glasshouse (Milton and Dean 2001; Pakeman *et al* 2002) or by a too short seasonal period under which these studies are carried out.

Temporal dispersal information is provided by soil seed bank assessment as well as by looking at the seasonal variation of dispersal patterns. Studies of soil seed banks are important in plant population ecology, conservation, restoration and management of plant communities (Araki and Washitani 2000). The soil seed bank is composed of all viable seeds lying on the surface or buried in the soil (Ferrandis, Herranz and Martinez-Sanchez 2001). The methodology for collecting soil samples and determining seed density varies and depends on the goal of the project and on the time available for the study. Some important considerations in soil seed bank studies are outlined by Simpson, Leck and Parker (1998) and also by Guo, Rundel and Goodall (1999). Soil samples should be taken preferably at least twice a year, to cover seasonal variation in the seed bank (Guo *et al* 1999). In the field, soil samples are collected using soil sampling core augers of known dimensions. Many studies have concentrated on the top 5 cm soil because this top layer is where most seeds are stored (Ferrandis *et al* 2001), and below the depth of 5 cm, seed density in the soil profile generally declines greatly (Roberts 1981 in: Pierce and Cowling 1991). Seedlings from seeds buried any deeper generally do not establish successfully (Pierce and Cowling 1991).

Once samples are collected, extracting seeds from the soil is not easy and results are often influenced by sampling techniques, the time of sampling and methods used to determine seed numbers as reviewed by de Villiers, van Rooyen and Theron (1994). Estimating the size of the seed bank is done either by placing the soil samples under conditions suitable for seed germination (seedling emergence) or by direct physical seed counts (Joubert 1983; Simpson *et al* 1989; Russi, Cocks and Roberts 1992; de

Villiers *et al* 1994; Garcia-Fayos and Verdu 1998; Guo *et al* 1999; Ferrandis *et al* 2001). In the emergence method, soil samples are spread into seed trays that are then exposed under optimal germination conditions (watering in the glasshouse). The depth in the seed tray is important as this could affect seeds that cannot germinate at certain depths due to insufficient light (Dalling, Swaine and Garwood 1998), but depths up to 15 cm have been used (Augusto, Dupouey, Picard and Ranger 2001). In such a deep soil layer, only a subsample of the total seed bank is likely to germinate and thus results will not be an absolute estimation of the seed densities in soils (Augusto *et al* 2001). As in the seedling emergence studies of dung samples, the germination trials for the soil samples may underestimate the seed bank population because the number of seeds that germinate depends critically upon the temporal patterns of seed dormancy and the availability of suitable condition to meet specific germination requirements for all species (Simpson *et al* 1989; Carey and Watkinson 1993; de Villiers *et al* 1994; Guo *et al* 1999). Physical counting of seeds in soil samples on the other hand might overestimate the seed bank unless they are adjusted for viability (Gross 1990 in: de Villiers *et al* 1994), which is not always possible for many species (Roberts 1981 in: de Villiers *et al* 1994). Physical counts also tend to detect mostly larger seeds rather than smaller seeds that are detected more efficiently in emergence methods (Pierce and Cowling 1991; de Villiers *et al* 1994).

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CHAPTER 3

Wind dispersal

3.1 Introduction

The success of restoring endangered plant communities especially where soil seed banks have become depleted, largely depends on the sufficient deposition of seeds of the desired plants (van Dorp, van den Hoek, and Daleboudt 1996). Long-term ploughing of the soil alters the soil seed bank composition and the recovery of these lands mainly depend on fresh seed rain (van Dorp *et al* 1996). Seed dispersal is a key factor in the regeneration process that facilitates the arrival of seeds to the restored sites. The knowledge of dispersal patterns present in different vegetation types is important for restoration projects as it gives information on the rate of natural recovery of the field, should recruitment depends on seed availability. Seed trapping is widely used to assess seed dispersal patterns (Dalling, Swaine and Garwood 1998; Holl 1999). This chapter aims to present the results of seed rain and their spatial patterns as obtained from seed traps. Three types of seed trapping were used as described on the method section below. The last section of the chapter presents the results obtained followed by discussion.

3.2 Methods

Data were collected over the period of one year (August, 2001 to August, 2002) along three transect lines extending from 18 meters within the natural Renosterveld vegetation, to 81 meters into the old field, from the edge of the natural vegetation and the old field (Figure 3.1). Transects were set up at an angle (29°) to avoid traps affecting each other. Three types of traps (pitfalls, vermiculite trays and sticky traps) were used in order to obtain information about seed movement over the ground and through the air. A short description of the traps and their arrangement is outlined below. To assess the influence of the aboveground vegetation on seed trap results, a vegetation surveys were carried out during trapping sessions between January 2002 and July 2002. This was done by placing a ring, 1 m diameter, around each pit trap estimating the percent cover for species found within the ring (Figure 3.4).

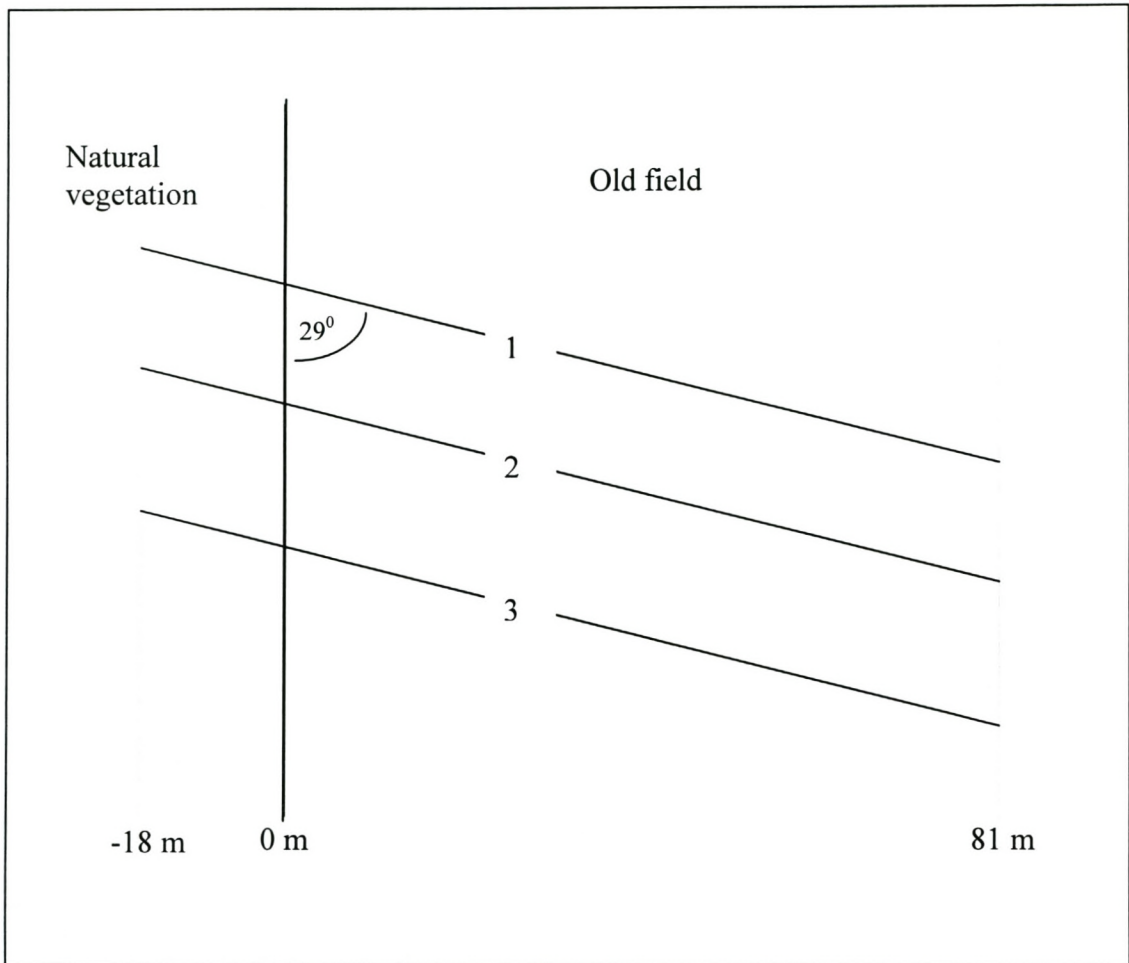


Figure 3.1 The three transect lines run from -18 m within the natural vegetation up to 81 m in the old field

1. **Pit traps** were constructed from metal cans (9 cm diameter by 20 cm long, covering a surface area of 63.6 cm²) with lids. The cans were sunk in the soil so that the lid was flush with the soil surface. This allows both tumbling seeds and flying seeds to land in or get trapped. Twenty traps were set out along each of the transect lines at interval points marked in Figure 3.2. For each trapping session, each can was lined with a new plastic bag held open by a coiled strip of firm plastic and left open (lid removed) for four days. Bags are then taken out and cans were closed to prevent rain damage while not trapping. The seeds in the plastic bags were identified and counted with the aid of a dissecting microscope. This was repeated monthly over the period of one year with the exception of December 2001 and February 2002, starting in September 2001.

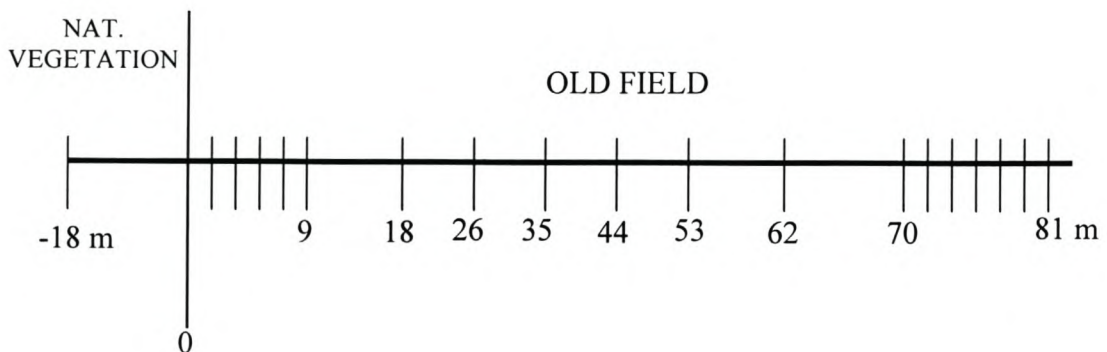


Figure 3.2 One transect layout showing data point distances, measured from the edge of the natural vegetation.

2. **Sticky traps** were used to assess the heights dispersing seeds were travelling at. They were made of 4 by 20 cm pieces of plastic film (transparencies) covered with a thin layer of a sticky ant barrier (Tangle Foot©) on one side and fixed on vertical wooden poles at four different heights between 10 cm up to 135 cm from the ground (Figure 3.3). Four poles were set up per transect at -18, 0, 35 and 81 m from the natural vegetation. Once a month, the transparencies were replaced, and seeds on the transparencies were identified and counted with the aid of a dissecting microscope.

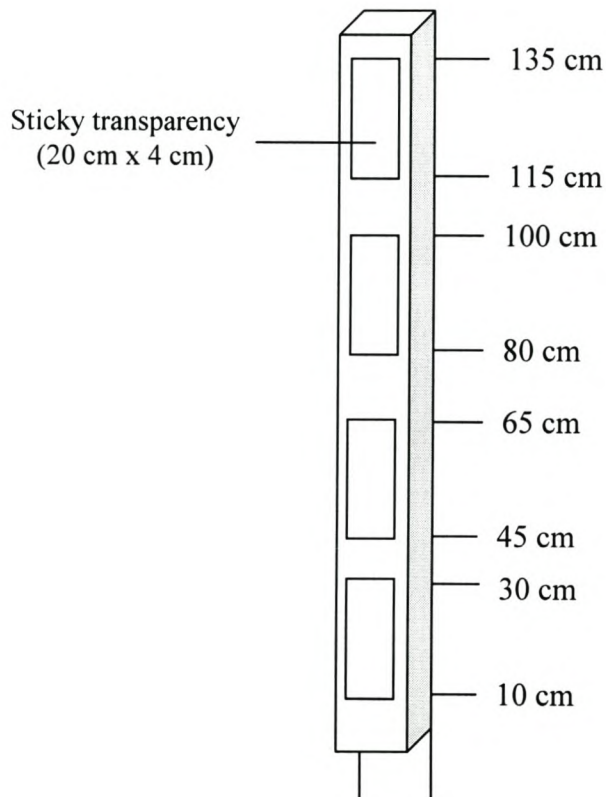


Figure 3.3 A vertical wooden pole with pieces of sticky transparency for trapping seeds at different heights above the ground

3. **Vermiculite traps:** at the same locations as the sticky traps, four nursery seed trays filled with vermiculite (and a layer of gravel on top to prevent the vermiculite from being blown away by the wind) (Figure 3.4) were set up along each transect line. The vermiculite trays were left to continuously trap seeds for an extended period for seedling counts. The first set of trays was left in the field for seven months (August 2001 to March 2002) when they were transferred to the nursery for watering and were replaced with the second set of vermiculite trays. The second set of trays stayed in the field trapping for four months (i.e. until July 2002) when they were transferred to the nursery for germination. The period August to March marks the dry season and no seedlings emerged while in the field but germination started in the nursery upon watering. In the nursery, seedling counts were done almost every month while the trays were kept moist by a spray watering system that was adjusted seasonally to suit the seedlings. During dry and hot summer months, watering was increased to maintain optimal conditions. Seedlings were identified and removed to allow further germination and if they were not immediately identified they were transplanted to individual pots until identified or pressed after flowering, for identification. Vermiculite trays were kept in the nursery until the experiment was terminated at the end of September 2002. As the first set of trays was kept in the nursery for a longer period and stayed in the nursery over winter (the natural growing season for Renosterveld species in the field), it yielded more germinants than the second set of vermiculite traps that stayed in the nursery only for three months, the hotter and dry summer months.

Data analysis

Seeds and seedlings were classified into four plant growth forms: shrubs, forbs (all non-woody species excluding grasses), grasses (including sedges) and geophytes; and the distribution patterns were determined. Grasses and forbs also included some alien species and these were noted. Densities of seeds from the field and seedlings in the nursery for each species were determined and expressed as seeds per m². For the pit traps, peak dispersal seasons were also determined. Seed densities were correlated with the vegetation plant cover around the seed traps. A two-way ANOVA was used to test the effect of distance from the natural vegetation and height above the ground on seed density for the sticky trap data, and a significant level of $p < 0.05$ was used. Data were not normally distributed and so were log-transformed. This changes the

distribution to normality, before the parametric statistical tests were performed. Statistical tests were performed in STATISTICA 6.0.

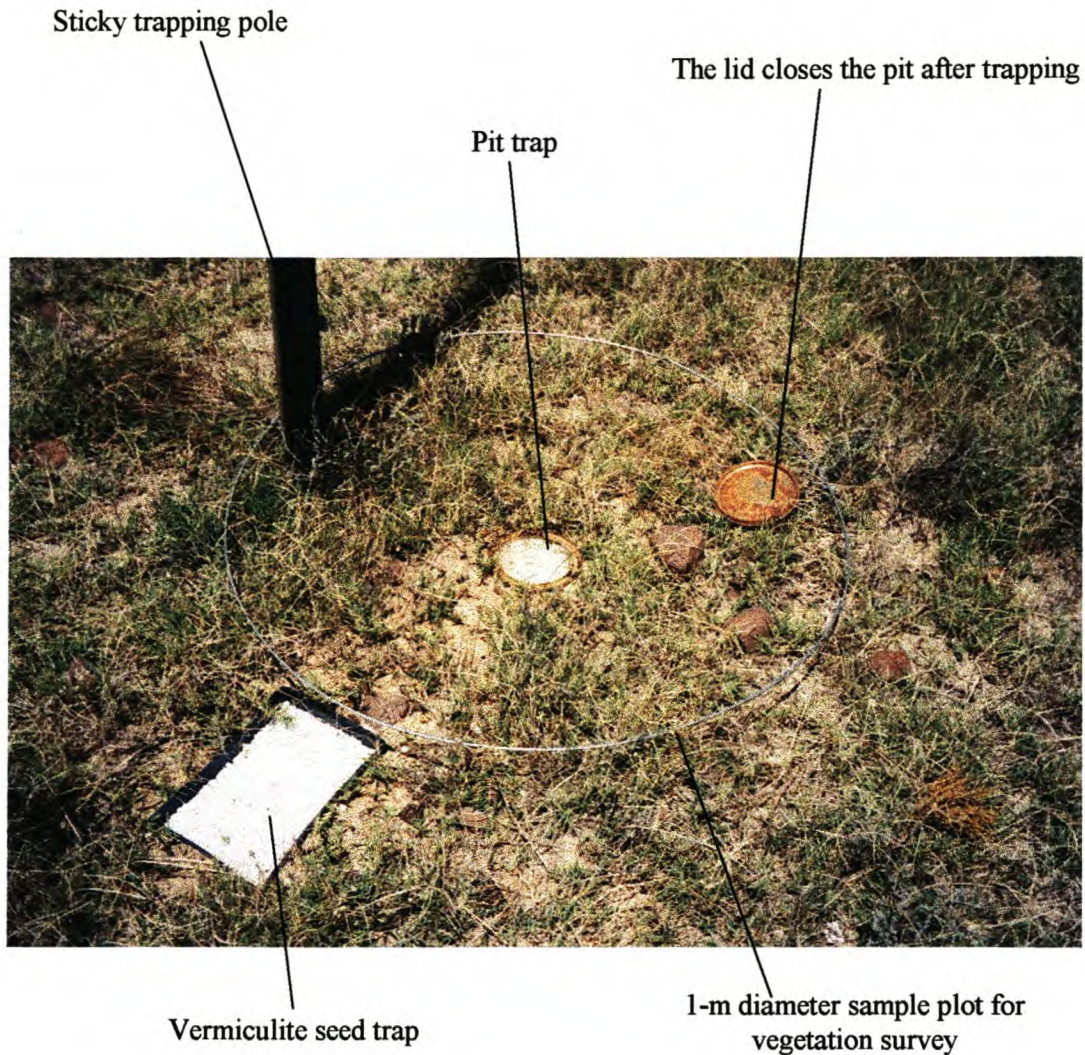


Figure 3.4 The picture showing pit trap, vermiculite trap, half of the vertical pole for sticky traps and the *C. dactylon* dominated cover around the traps

3.3 Results and Discussion

3.3.1 Describing the vegetation around seed traps

3.3.1.1 Results and Discussion

25 species were recorded from the vegetation surveys that were carried out around the pit traps including 9 species of shrubs, 12 species of grasses, 1 forb and 3 species of geophytes. Of the 9 shrubs recorded around seed traps, *Athanasia trifurcata*, *Lobostermum argenteus*, *Muraltia heisteria* and *Relhania fruticosa* were restricted to the natural and transition zone and did not go beyond 9 m into the old field (Table 3.1). Furthermore, *Aspalathus* spp., *Hermannia* sp., *Thesium* sp. and *Dicerotheramnus rinocerotis* were recorded around seed traps throughout the trapping area. The first three of these shrubs have seeds adapted for dispersal in animal dung where as *D. rinocerotis* have seeds with plumes, adapted for wind dispersal and these long distance dispersal syndromes have helped these species reach the old field. *Helichrysum* is another shrub with seeds that are adapted for long distance dispersal via wind. It was recorded around the traps in the old field but not in the natural vegetation and this indicates that *Helichrysum* is one of the pioneers. From this distribution, we can say that the first set of species (*A. trifurcata*, *L. argenteus*, *M. heisteria* and *R. fruticosa*) is seed limited in the old field due to poor seed dispersal, although other untested factors could also be playing a role.

Only one species of forb was recorded around the traps, *Leysera gnaphaloides*, a perennial indigenous forb. This is because other forbs are mainly annuals and the vegetation survey only ran from January to July, thus missing the growing season to record annuals. Therefore during the vegetation survey, most of the annuals were then seedlings and could not be identified. *Leysera gnaphaloides* has seeds that are adapted for wind dispersal and it was recorded around seed traps at all distances in the old field but not in the natural vegetation. Most geophytes appear above ground only in winter and spring and the few that were recorded occurred only in the natural and the transition zone, and thus showed signs of dispersal limitation (the hypothesis of this study) in the field.

Species richness around the pits (Figure 3.5) follows the predictions of the intermediate disturbance that states that the highest diversity is maintained at the intermediate levels of disturbance (Connell 1978). Figure 3.5 shows that species richness was greatest on the ecotone than both in the least disturbed natural vegetation and in the highly disturbed old field vegetation. This also supports the ecotonal edge effect, whereby ecotone communities support a mixture of both natural and disturbed vegetation and thus have increased diversity of species. In the least disturbed natural vegetation, diversity is reduced due to competitive exclusion of dominant species, *Dicerotheramnus rinocerotis* in this case. Studies of seed dispersal have shown that at dispersal, most seeds disperse nearer to the seed source and only few seeds disperse further away (Howe and Westley 1997). This makes more propagules available for colonisation and establishment at the transition zone than in the old field. Species from the natural vegetation with short distance dispersal will also only be able to colonise the transition zone.

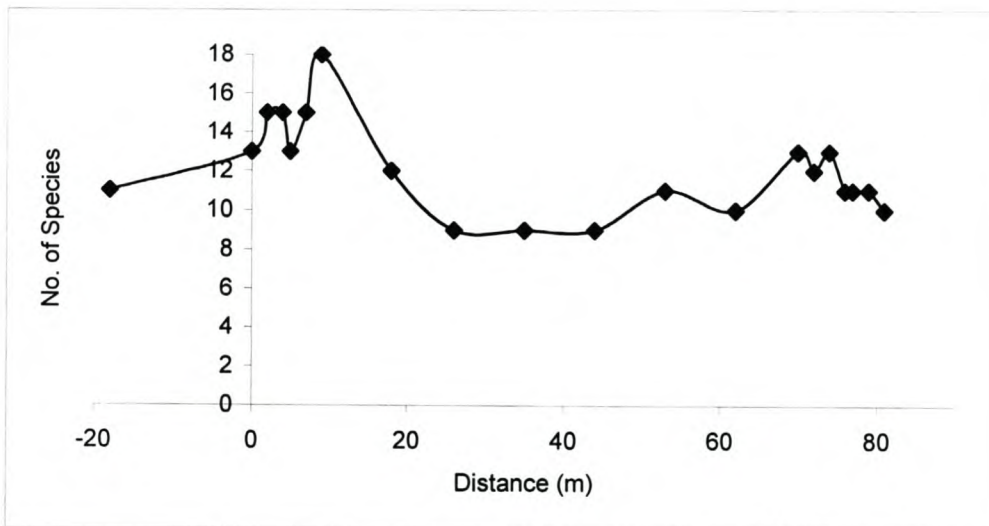


Figure 3.5 Change in species richness around the pits, with distance from the natural vegetation

Table 3.1 Species recorded around seed traps and their average percentage covers. (*) Indicates alien species, values are average percent covers calculated from the 5 months of sampling and over three transects at each distance.

Species	Growth form	Distance (m) from the natural vegetation																			
		-18	0	2	4	5	7	9	18	26	35	44	53	62	70	72	74	76	77	79	81
<i>Dicerthamnus rinocerotis</i>	Shrub	86.33	76.33	56	7.33	12.33	38	5.67	28	2	10.4	0	11.47	0	1.67	7.33	4.27	0	1	5.33	0
<i>Aspalathus</i> sp.	Shrub	4	16.67	11	1.67	0	0	4.67	7.66	0	4.67	2	2.33	2.33	2	1.67	6	2	2.67	3.6	8
<i>Hermannia</i> sp.	Shrub	0	7.67	0	0	0	1.33	0.53	1	0.67	0	0	3.33	0.67	4.33	1.33	0	1.47	4	0.47	7.33
<i>Thesium</i> sp.	Shrub	2.67	2	5.33	4	0.87	4.53	0.67	0.67	0	0	1.33	6.33	0.53	1.2	1.67	1.13	0	0	0	0
<i>Lobosteruon argenteus</i>	Shrub	2.33	0	0	0	0	0	1.13	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Muraltia heisteria</i>	Shrub	0	8.33	5	2	1.8	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Relhania fruticosa</i>	Shrub	9	6	27.67	23	5.53	3	1.67	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Athanasia trifurcata</i>	Shrub	0	4.33	13.67	17.8	1.33	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Helichrysum</i> sp.	Shrub	0	0	0	0	7.33	13	13.33	3	1	20.33	6.67	9	13.33	14.67	12	12	6.67	9.67	8.33	8
<i>Leysera gnaphaloides</i>	Forb	0	0.67	11.3	26.3	42.7	35	38.7	35.4	5	24.7	7.67	12.7	16.9	11.8	7.67	4.33	3	7.87	8	7.53
<i>Avena</i> sp.*	Grass	0	0	0	1.33	0	0	0	0	0	0	0	0	1.53	0	0	0.33	0.33	0.87	0	0
<i>Briza maxima</i> *	Grass	22.13	10	3.47	6.4	4.87	4.07	7.47	4.13	7.4	4.6	6.67	4.33	6.13	6.87	5.87	7.33	9.47	10.9	8.73	6.73
<i>Cynodon dactylon</i>	Grass	0	0	7.87	64.3	65.8	75.1	101	105	144	107	132	107	110	110	120	114	122	109	111	114
<i>Briza minor</i> *	Grass	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0
<i>Bromus diandrus</i> *	Grass	0	0	1	0	0	0	0	0	0	0.33	0	0	0	1	0.67	1.33	0.33	0	2	0.67
Unidentified species (G3)	Grass	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified species (G4)	Grass	0	0	1.53	6.53	0	0.13	0.13	0.47	0	0	0	0	0	0.33	0	0	0	0	0	0
Unidentified species (G5)	Grass	6	0.53	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tribolium hispidum</i>	Grass	8.73	15.7	22.5	13	7.53	8.87	10.1	5.2	1.67	2.47	5	2.47	5.33	2	1.5	4.47	1.33	3.73	0.67	0.7
<i>Tribolium uniola</i> e	Grass	0	6	1.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vulpia myuros</i> *	Grass	0	0	0	0	0	0.2	1.33	0.73	3	0	3.33	4.33	2.67	2.6	3.33	3	3.33	3.67	3.67	2
<i>Pentaschistis airoides</i>	Grass	4	0	0.4	2.33	0.33	2	0.53	3.53	0.47	0.53	0.33	2.2	1.67	1.47	2.67	5.53	4.53	5.27	2.13	3.33
<i>Babiana</i> sp.	Geophyte	0	2	0	2.67	0.13	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hexaglottis lewisial</i>	Geophyte	0.33	0.27	0	1.93	0.13	0.47	0.47	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Romulea geizoryza</i>	Geophyte	2	0	0.2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Number of species		11	14	15	15	13	15	18	12	9	9	9	11	11	13	12	13	11	11	11	10

3.3.2 Pit traps

3.3.2.1 Results

Represented flora

A total of 8 636 seeds belonging to 20 different species were collectively trapped during a period of one year, sampled for four days each month (except December and February) between September 2001 and August 2002. Seventeen of all taxa were identified to the genus or species level with more than 50% of the species identified as grass (4 alien and 5 indigenous), two shrubs, four (one indigenous and three alien) classified as forbs- a group including all non woody species (Table 3.2). Grass seed density also made up 60% (dominated by alien pasture grass *Vulpia myuros* and *Briza maxima*) of all seeds whereas shrubs dominated by *Dicerothamnus rinocerotis* made up 36% of the seed rain. Indigenous species were dominated by *Cynodon dactylon* (41%) and *D. rinocerotis* (52%) followed by *Tribolium hispidum* (6%), all other indigenous species occurred in less than 1% of the total indigenous species.

Seasonal or temporal dispersal of seeds Table 3.2 shows that there was variation in seasonal dispersal of different species with the largest number of species dispersing their seeds during October through to April (summer months) while few species disperse their seeds in winter, May to September. *Dicerothamnus rinocerotis* does not overlap with other trapped species in its dispersal season. The alien seeds are shed earlier in summer than the seeds of indigenous plants. For example, seed dispersal in *C. dactylon*, *Tribolium hispidum*, *T. uniolae* and *Helichrysum*, peak in March (late summer), while all alien pasture species have their dispersal peaks as early as October (Table 3.2).

Table 3.2. Represented taxa of seeds found in pit traps and their temporal variation of dispersal (* indicates alien species; values are seeds per m²; peak dispersal season for individual species, most species disperse their seeds in summer).

Growth form	Species	Sep	Oct	Nov	Jan	Mar	Apr	May	Jun	Jul	Aug	Tot
Forb	<i>Erodium moschatum</i> *	938	3770	938	573	39	0	0	0	0	0	6257
Forb	<i>Hypochoeris radicata</i> *	156	1953	156	104	39	0	0	0	0	0	2409
Grass	<i>Vulpia myuros</i> *	208	17422	8438	8229	1055	352	0	0	0	0	35703
Grass	<i>Avena</i> *	0	59	52	0	0	0	0	0	0	0	111
Grass	<i>Briza maxima</i> *	0	11152	1979	5052	2031	352	391	0	0	0	20957
Grass	Unidentified species (G1)	0	918	104	0	0	0	0	0	0	0	1022
Grass	<i>Briza minor</i> *	0	879	260	0	0	0	0	0	0	0	1139
Grass	<i>Bromus diandrus</i> *	0	2695	469	313	234	195	0	0	0	0	3906
Grass	<i>Bromus pectinatus</i> *	0	2520	469	0	0	39	0	0	0	0	3027
Forb	<i>Leysera gnaphaloides</i>	0	273	52	0	0	78	0	0	0	0	404
Grass	<i>Lolium</i> *	0	176	0	0	0	0	0	0	0	0	176
Grass	Unidentified species (G2)	0	20	52	0	0	0	0	0	0	0	72
Grass	Unidentified species (G3)	0	0	104	0	0	0	0	0	0	0	104
Grass	<i>Pentaschistis airoides</i>	0	0	208	573	0	0	0	0	0	0	781
Forb	<i>Trifolium angustifolium</i> *	0	0	0	260	0	0	0	0	0	0	260
Grass	<i>Tribolium uniolae</i>	0	0	0	0	898	39	0	0	0	0	938
Shrub	<i>Helichrysum</i>	0	0	0	0	742	117	0	0	0	0	859
Grass	<i>Cynodon dactylon</i>	0	2539	4427	32500	41758	10117	5859	0	0	0	97201
Grass	<i>Tribolium hispidum</i>	0	273	52	3750	5781	2383	1445	0	0	0	13685
Shrub	<i>Dicrothamnus rinocerotis</i>	0	0	0	0	0	0	2188	32305	85039	3281	122813
	TOTAL SPECIES	3	14	15	9	9	9	4	1	1	1	20
	ALIEN SPECIES	3	9	8	6	4	4	1	0	0	0	
	TOTAL SEEDS (seeds/m ²)	1302	44648	17760	51719	52578	13672	9883	32305	85039	3281	311823

Spatial density distribution

Both overall seed density and the number of alien species were higher in the old field than in the natural vegetation (Figure 3.6). There was however a decline in seed density of the Renosterveld (indigenous) species at the edge and transition zone into the old field as well as into the natural Renosterveld (Figure 3.6 C). The high seed density at the edge and transition zone is due to *D. rinocerotis*, a shrub that accounted for more than 35% of all seeds trapped at each of the edge-transition distances (-18 to 7 m from the edge of the natural vegetation) as well as *C. dactylon* that also accounted for more than 35% of the seeds trapped as from distance 5 m away from the edge. *Cynodon dactylon* is also responsible for the relatively high seed number recorded in the entire field (Table 3.2). High variability in seed and species density occurs both among the indigenous species and the alien pasture species (Figure 3.6). The maximum number of indigenous species was also recorded at the edge.

An indigenous tuft grass, *T. hispidum* occurred at high densities at distances -18 up to 2 m. This species dropped from 6 263 seeds per m² at the edge to less than 200 seeds per m² after 7 m from the natural vegetation (Table 3.3; Figure 3.7) while seeds of alien pasture grasses like *B. maxima*, *V. myuros* and an African lawn grass (*C. dactylon*) were found throughout the entire old field at higher density (Figure 3.7).

The forbs were dominated by the two alien species, *Erodium moschatum* accounting for 64% and *Hypochoeris radicata* 30% (Table 3.3) of forbs. *E. moschatum* was more densely distributed in the middle of the field, decreasing in density towards the end of trapping distance. *Leysera gnaphaloides* was recorded in the old field, at low density and shows a gentle decline into the old field (Table 3.3). Also observable from the seed distribution of *D. rinocerotis* and *T. hispidum* is a low seed density inside the natural vegetation compared to the transition zone. In other words, individuals in the natural stand are seemingly producing fewer seeds than individuals in the more open edge (Figure 3.7).

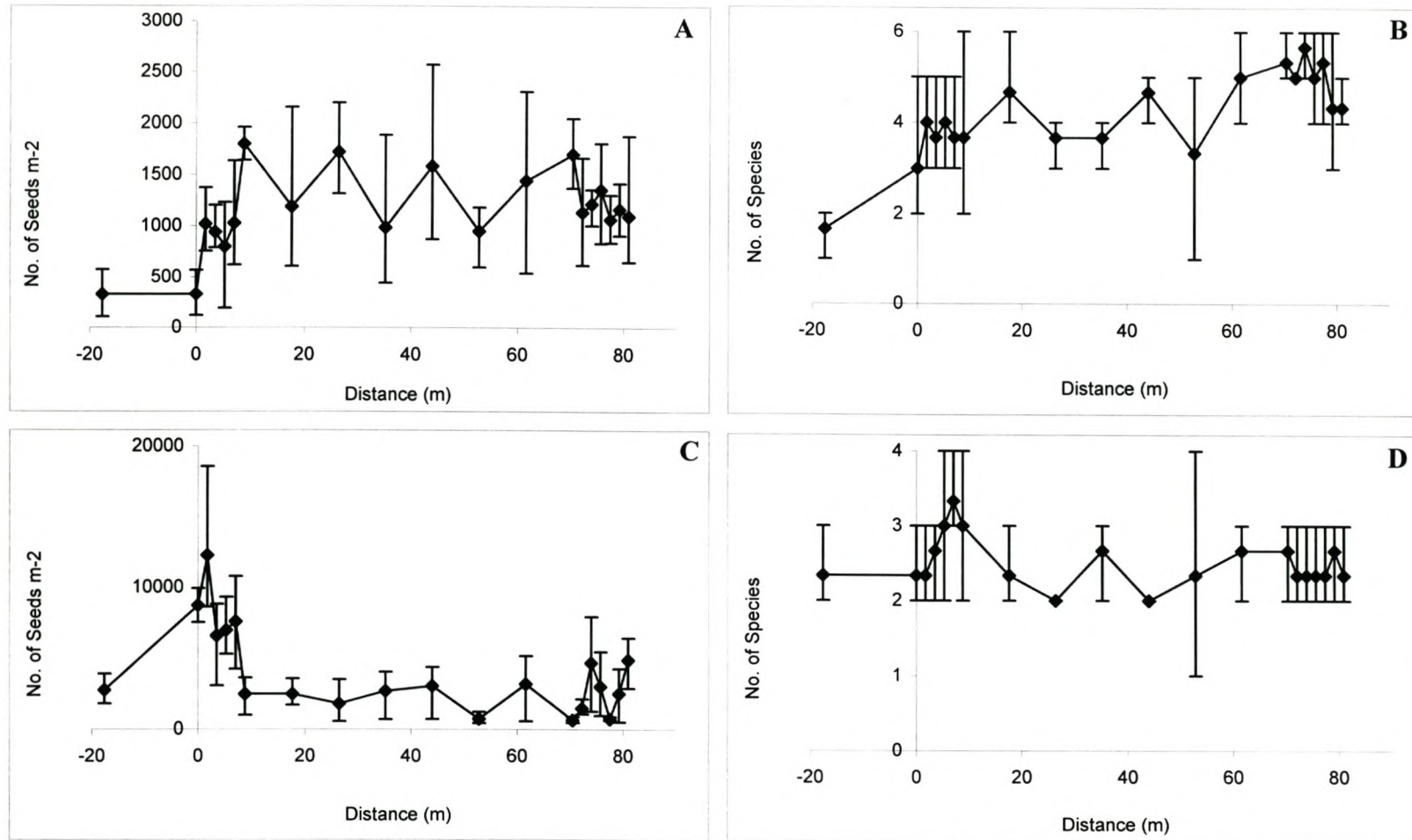


Figure 3.6 Changes in the density of seeds and in the number of species between alien species (A; B) and indigenous species (C; D) along the three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

Table 3.3 Represented taxa of seeds found in pit traps and their spatial variation of dispersal. (*) Indicates alien species. Values are seeds per m². The table is arranged by life-form in the following order: grasses, forbs and shrubs.

Species	Distance (m) from natural vegetation																			
	-18	0	2	4	5	7	9	18	26	35	44	53	62	70	72	74	76	77	79	81
<i>Avena</i> sp.*	0	0	0	0	20	0	52	0	20	0	0	0	0	0	20	0	0	0	0	0
<i>Briza maxima</i> *	573	5475	1094	488	358	807	1602	879	1556	853	1569	339	508	827	495	586	723	768	697	762
<i>Briza minor</i> *	0	0	0	293	0	39	52	59	0	0	0	0	0	0	215	221	143	59	59	0
<i>Bromus diandrus</i> *	0	0	104	0	59	137	0	482	0	0	0	0	469	98	169	618	632	156	371	612
<i>Bromus pectinatus</i> *	0	0	52	156	215	215	228	20	78	98	59	156	20	475	384	195	371	169	98	39
<i>Lolium</i> sp.*	0	0	0	0	176	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cynodon dactylon</i>	39	0	78	2656	9323	12057	664	2617	3053	6615	7578	143	8073	833	2773	13138	7480	781	5859	13438
<i>Vulpia myuros</i> *	299	833	1074	1367	1654	1810	3275	1908	2676	1380	1855	1660	1979	3223	1849	1719	2012	1699	2103	1328
<i>Tribolium uniola</i>	938	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pentaschistis airoides</i>	0	104	0	0	0	0	0	156	0	156	0	104	52	0	0	0	0	0	208	0
<i>Tribolium hispidum</i>	1367	4023	6263	853	267	234	78	0	0	39	0	143	39	78	156	0	52	0	52	39
Unidentified species (G3)	0	0	104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified species (G2)	0	0	0	0	0	52	0	0	20	0	0	0	0	0	0	0	0	0	0	0
Unidentified species (G1)	0	104	0	0	20	39	20	0	0	0	0	78	20	0	137	0	98	449	39	20
<i>Trifolium angustifolium</i> *	0	0	0	156	52	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypochoeris radicata</i> *	104	72	39	0	0	0	0	39	0	0	443	59	404	169	0	20	20	215	156	560
<i>Erodium moschatum</i> *	0	98	697	0	39	78	137	182	833	521	833	645	957	319	286	299	169	143	20	0
<i>Leysera gnaphaloides</i>	0	0	0	137	20	78	0	59	0	0	0	0	0	52	0	39	0	20	0	0
<i>Helichrysum</i> Sp.	0	0	0	0	0	156	703	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dicerotheramnus rinocerotis</i>	5898	21914	30391	16055	11289	10156	5977	4609	2305	1289	1563	1758	1406	1016	1367	898	1406	977	1367	1172
Total seeds per m ²	9219	32624	39896	22161	23490	25859	12839	11009	10540	11061	13900	5085	13926	7090	7852	17734	13105	5436	11029	17969
Total species	7	8	10	9	13	13	12	11	8	8	7	10	11	10	11	10	11	11	12	9

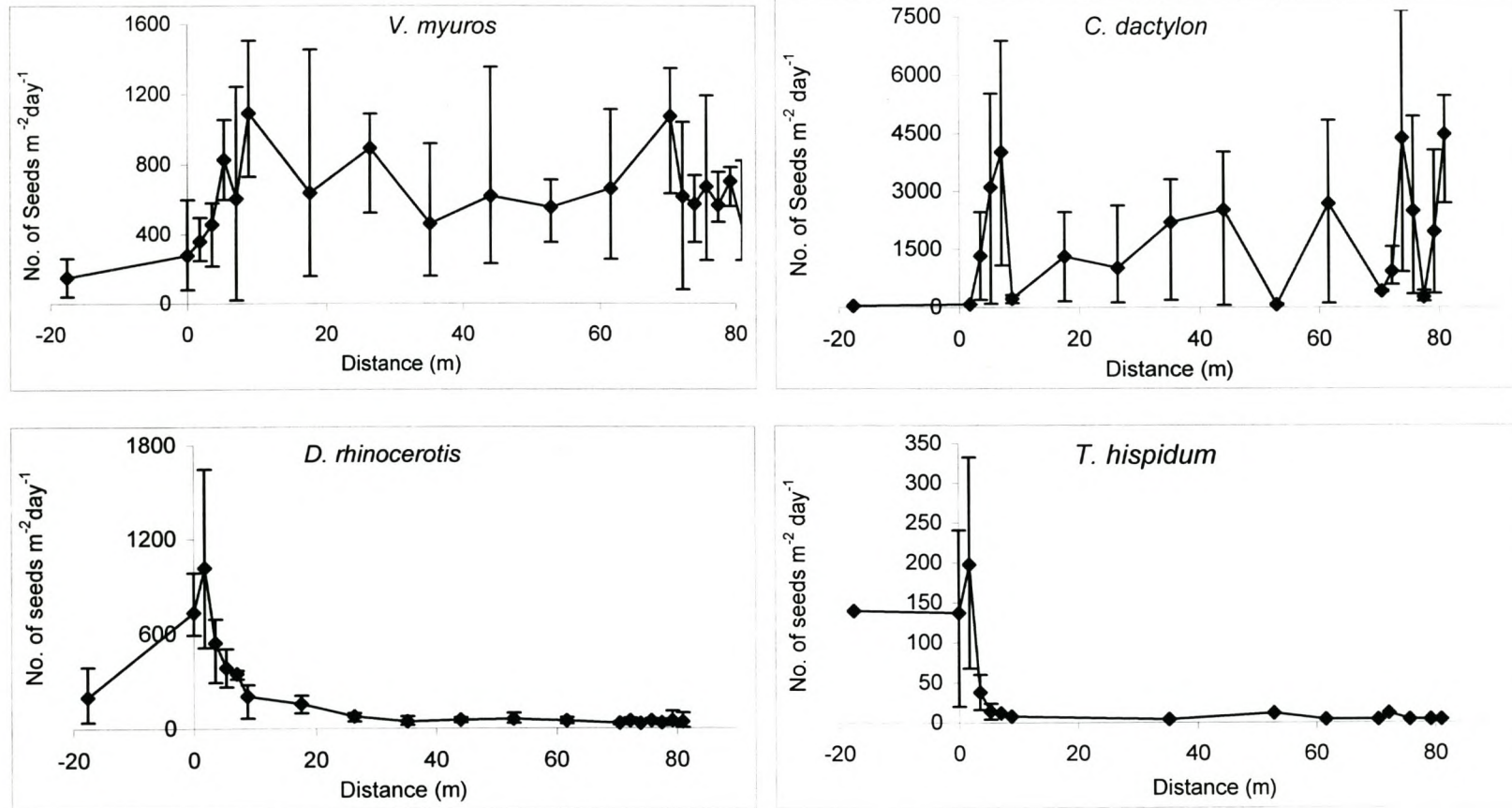


Figure 3.7 Dispersal curves for selected common species. Means; maxima and minima were calculated from the three transects

3.3.2.2 Discussion

That alien species disperse seeds before the indigenous species might explain why they are often such successful invaders. In addition, they also produce large number of seeds. The dispersal season of *Dicerotheramnus rinocerotis* matches that reported by Levyns (1927). The observation that many species dispersed their seeds during the dry season is supported by Holl (1999).

The shape of the dispersal curve for *D. rinocerotis* follows that predicted for wind dispersed seeds; leptokurtic and right skewed (Rabinowitz and Rapp 1981; Greene and Johnson 1989; Thiede and Auspurger 1996). For *T. hispidum* and *D. rinocerotis*, the natural vegetation acts as a seed source. Seeds of both species declined in density at the transition zone, indicating that seeds are moving into the old field. *D. rinocerotis* with light wind blown seed disperses further into the old field than *T. hispidum*, the later showing a sharp decline at 5 m while *D. rinocerotis* goes as far as 36 m before levelling off. Therefore, while most of *T. hispidum* seeds are dispersed within 5 m, most of the seeds of *D. rinocerotis* are dispersed within 36 m from the natural vegetation. Bischoff (2002) considered species as strongly seed limited due to poor seed dispersal when most seeds were dispersed within 1.5 m. *D. rinocerotis* can be considered as not being seed limited as relatively more seeds still disperse through the entire field at a constant density. Individuals inside the natural vegetation (*D. rinocerotis* and *T. hispidum*) yielded seeds at low density in the seed rain compared to the more open natural vegetation. This could be ascribed to ecological or biological factors like competition between individuals in the natural vegetation, which might lead to lower seed production. Site quality is reported to have a direct effect on resources available for reproduction; for example, light availability was positively correlated with seed production in the woodland herb primrose (*Primula vulgaris*) (Valverde and Silvertown 1995; in: Nathan and Muller-Landau 2000).

There was a strong correlation between seed density and plant cover in both *D. rinocerotis* ($R^2 = 0.62$) and *T. hispidum* ($R^2 = 0.69$) (Figure 3.8). *Cynodon dactylon* and alien pasture grasses occurred at high densities throughout the field as did the plants themselves. The relationship between cover and seed density for *C. dactylon* and *V.*

myros was weaker. A possible reason for this is the consumption of flowering heads of both species by grazing animals and their redistribution in the dung.

High variability in *C. dactylon* spatial density distribution is because seeds are dispersed either as individual seeds or as the entire seed head which contains hundreds of seeds. Patterns of seed dispersal and deposition depend on the spatial pattern of reproductive adult and their seed output (Nathan and Muller-Landau 2000) and this could contribute to high variability in seed shadow observed both in alien species and in Renosterveld species. Reviews by Hoppes (1988) and Holl (1999) have also shown that seed rain varies greatly over small distances and this high variability in seed dispersal is one of the causes of the patchy recovery commonly observed in most successional ecosystems.

Forbs were poorly represented in the seed rain from pit traps perhaps because of the difficulty in detection of the tiny seeds these forbs/ annuals often possess. This information is supplemented by vermiculite traps (discussed in section 3.3.3) that look at the seedlings germinating in traps than directly counting seeds. The seeds of *L. gnaphaloides* (the only indigenous forb recovered from pit traps) are light with feathery plumes adapted for wind dispersal that allow for flying long distances when carried by wind. This forb was recorded at low density in the seed rain and is sparsely distributed in the old field, avoiding the natural vegetation, and at distances further away from the natural Renosterveld. *L. gnaphaloides* is perhaps one of the pioneer species as it is absent in the natural undisturbed vegetation and does not seem to be seed limited in the old field.

Results have shown that *D. rinocerotis* and *L. gnaphaloides* with wind adaptation for dispersal are not seed limited in the old field whereas the indigenous tussock grass *T. hispidum* could be seed limited in the old field. *Cynodon dactylon* and alien pasture grasses occur in significantly large quantities throughout the old field.

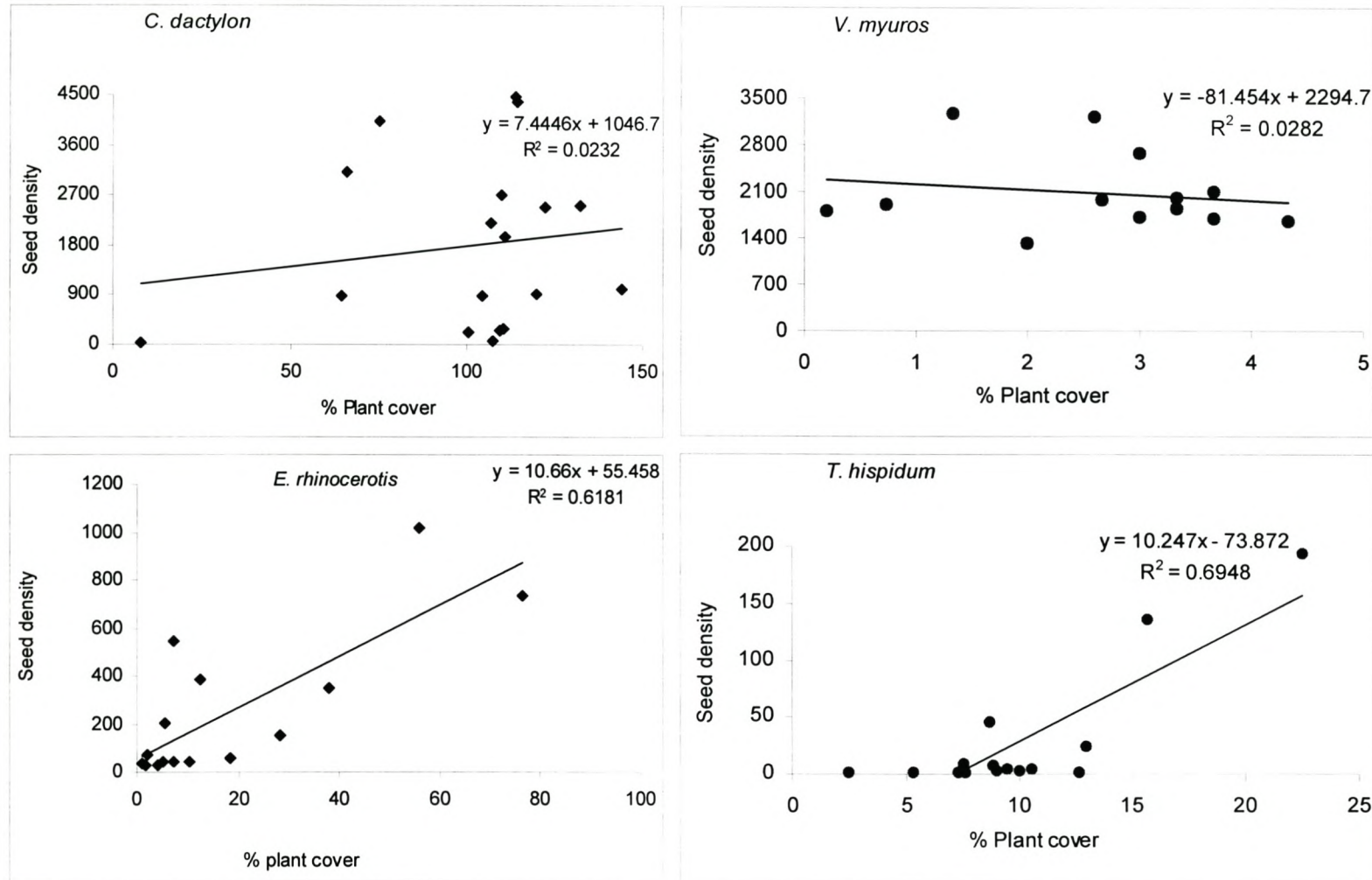


Figure 3.8 Correlation between seed density from pit traps and individual species cover of selected species, around traps.

3.3.3 Vermiculite trapping trays for fresh seed bank

3.3.3.1 Results

Seedlings belonging to 38 different taxa were identified from vermiculite trapping trays with 17 species of forbs, 11 grass species (including one sedge), 9 geophytes, and 1 shrub. The overall density of the seedlings increased with distance into the old field (Figure 3.9A) and the mean number of species was higher at the edge, decreasing both into the old field and into the natural vegetation, which had the least number of species (Figure 3.9 B). The seed rain was dominated by grass seeds, which accounted for 87% of the seedlings, of which 84% belonged to alien pasture grasses. Shrubs were poorly represented, with only one species, *Dicrothamnus rinocerotis* recorded only once at the edge of the natural vegetation (Table 3.4).

Geophytes

Two unidentified geophyte species (B2, 41% and B4, 22%) dominated the seedlings, followed by *Romulea* (12%). All three species were recorded in the natural vegetation or at the edge but not in the old field (Table 3.4). Mean seedling density of geophytes was highest (360 seedlings per m²) in the natural vegetation and dropped to less than 50 seedlings per m² at 40 m. Further than this distance, no geophytes were recorded in the fresh seed bank traps (Figure 3.10 A). The highest number of species in the fresh seed rain was found at the edge of the natural vegetation, and dropped off both into the old field and into the natural vegetation. The same number of species was found in the natural vegetation and old field (Figure 3.10 B). Species did not overlap between the two habitats. Geophytes recorded in the natural vegetation were not found in the old field, and species recorded in the old field (at 35 m) were not recorded in the natural vegetation (Table 3.4). The geophyte species recorded in the old field were *Ornithoglossum* sp., *Corycium* sp. and *Oxalis purpurea*.

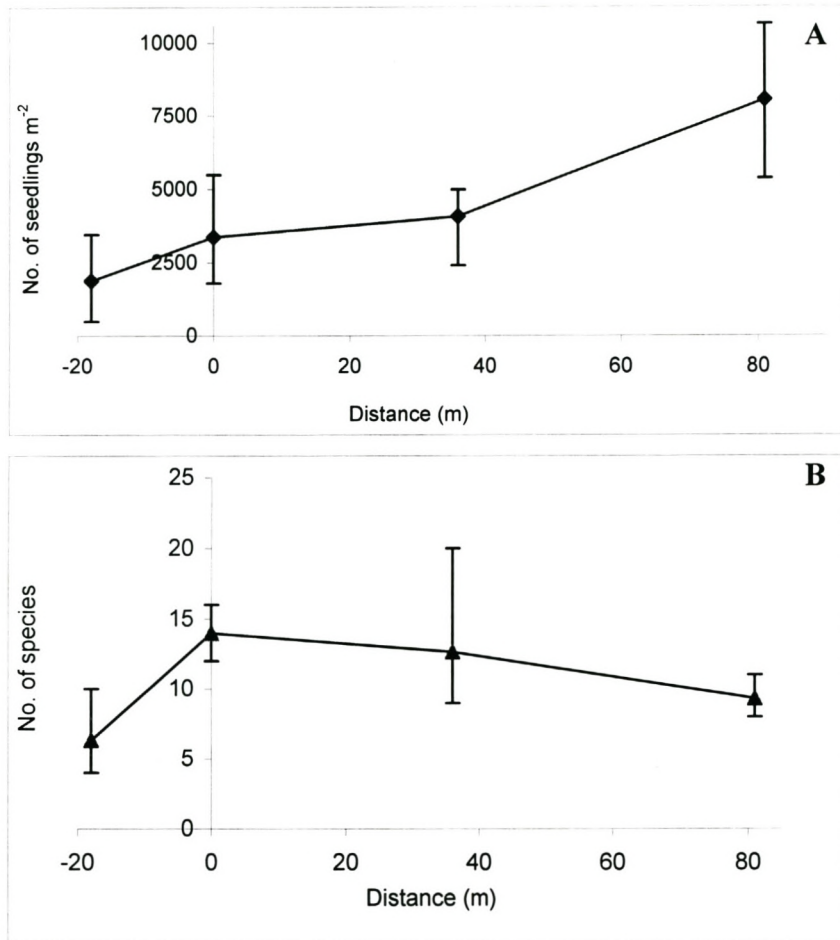


Figure 3.9 Changes in the density of seedlings (A) and number of species (B) recorded in the vermiculite traps along three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

Table 3.4 Represented taxa which emerged from the vermiculite trapping trays and their distribution across the field (*denotes alien species, values are total seedling number per m². ■ species recorded in the natural vegetation; ■ species recorded in the old field)

Growth form	Genus and species	Distance from edge (m)				Total
		-18	0	35	81	
Forbs	<i>Crassula</i> sp.3	29	29	29	0	86
	<i>Felicia echinata</i>	171	314	0	0	486
	<i>Diasca</i> sp.	0	86	0	0	86
	<i>Gazonia</i> sp.	0	29	0	0	29
	<i>Crassula</i> sp.2	0	600	0	0	600
	<i>Leysera gnaphaloides</i>	0	57	29	0	86
	<i>Hypochoeris radicata</i> *	0	29	86	1086	1201
	<i>Crassula</i> sp.1	0	800	0	114	914
	<i>Erodium botrys</i>	0	0	457	286	743
	<i>Dianthus</i> sp.	0	0	29	514	543
	<i>Ursinia anthemoides</i>	0	0	29	0	29
	<i>Cenia turbinata</i>	0	0	57	0	57
	<i>Anagallis arvensis</i> *	0	0	29	0	29
	<i>Spergula arvensis</i> *	0	0	29	57	86
	<i>Lactuca serriola</i> *	0	0	29	0	29
	<i>Gnaphalium</i> sp.	0	0	143	0	143
	<i>Erodium moschatum</i> *	0	0	0	29	29
	<i>Lobelia</i> sp.2	0	0	0	57	57
Geophytes	Unidentified species (B2)	657	29	0	0	686
	<i>Oxalis</i> (a weedy geophyte)	29	29	0	0	58
	<i>Othonna</i> sp.	29	0	0	0	29
	Unidentified species (B3)	0	29	0	0	29
	<i>Romulea</i> spp.	0	200	0	0	200
	Unidentified species (B4)	0	371	0	0	371
	<i>Ornithoglossum</i> sp.	0	0	29	0	29
	<i>Corycium</i> sp.	0	29	57	0	86
	<i>Oxalis purpurea</i>	0	57	57	0	114
Grass	<i>Vulpia myuros</i> *	486	4114	7543	17429	29572
	<i>Briza maxima</i> *	1400	1543	1800	1914	6657
	<i>Briza minor</i> *	143	0	29	29	201
	<i>Poa annua</i> *	343	57	29	57	486
	<i>Bromus diandra</i> *	0	0	457	257	714
	<i>Pentstemon airoides</i>	29	371	143	971	1514
	<i>Ficinia</i> sp.	1171	657	286	1000	3114
	<i>Tribolium unioalae</i>	1143	57	0	0	1200
	<i>Lolium</i> spp.*	0	29	0	29	58
	Unidentified species (G4)	0	114	743	229	1086
	<i>Tribolium hispidum</i>	0	257	29	0	286
Shrubs	<i>Dicerotheramnus rinocerotis</i>	0	114	0	0	114
TOTAL SEEDLINGS		5657	10000	12171	24086	51837
TOTAL SPECIES		12	25	23	15	39

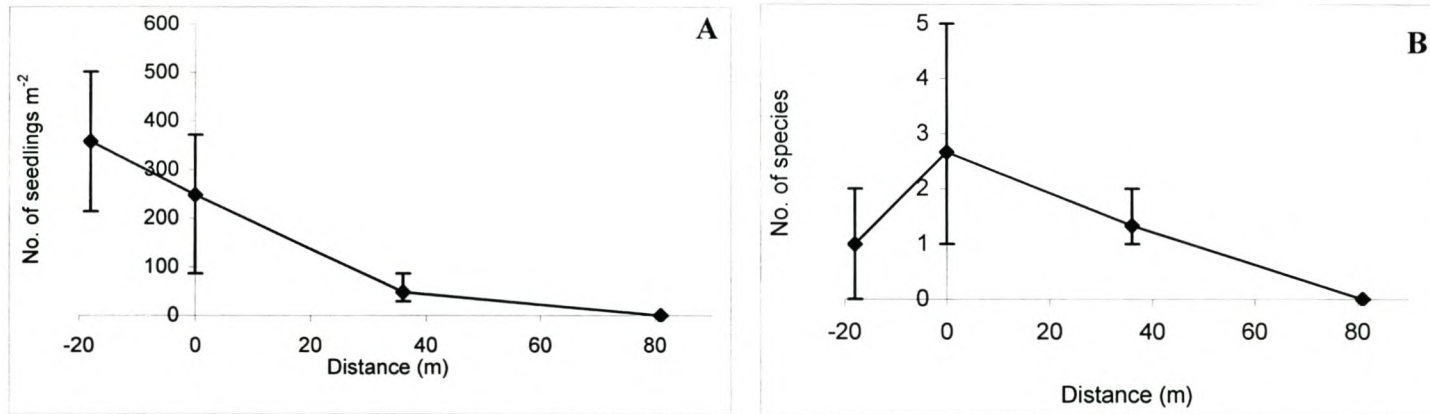


Figure 3.10 Changes in the density of geophyte seedlings (A) and number of species (B) recorded in the vermiculite traps along three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

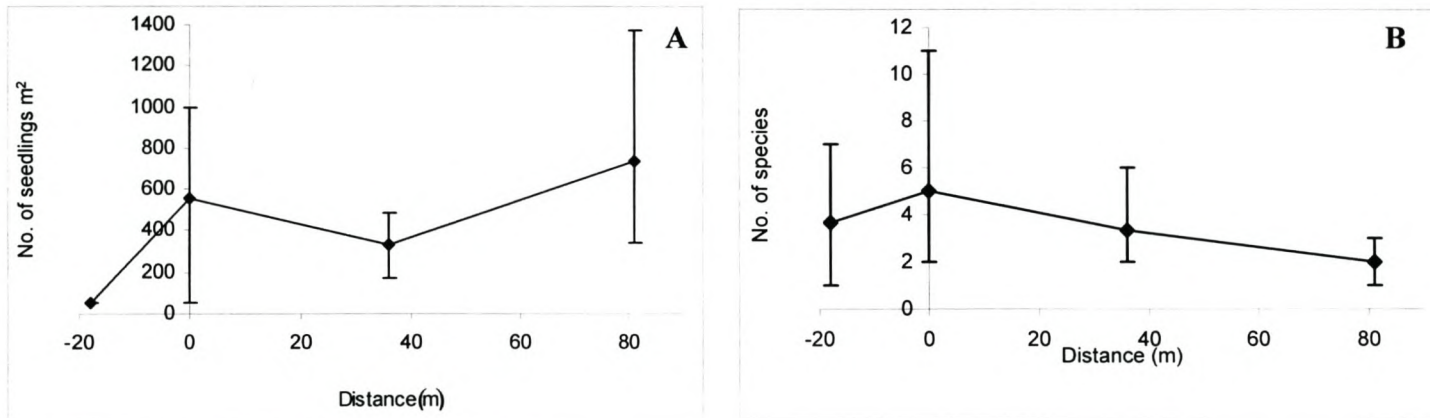


Figure 3.11 Changes in the density of forb seedlings (A) and the number of species (B) recorded in the vermiculite traps along the three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

Grass

Grass seedlings in the vermiculite trays were dominated by alien pasture grasses - *Vulpia myuros* (66%) and *Briza maxima* (14%) and together with 5 other alien pasture grasses made up 84% of all grass seedlings. These grasses, particularly *V. myuros* and *B. maxima* which occur at high densities, show an increase from the edge into the old field (Table 3.4). Indigenous grasses were dominated by *Ficinia* (a sedge) that occurs at high density both in the natural vegetation and in the old field. *Pentaschistis airoides* was also recorded at relatively high density among indigenous grass with highest density further in the old field (Table 3.4). The remaining two indigenous Renosterveld grass species *Tribolium uniolae* and *T. hispidum* were recorded in or close to the natural vegetation at high densities while limited in the old field (Table 3.4).

Forbs

The seventeen species of forbs recorded in the vermiculite traps were dominated by *Hypochoeris radicata* (an alien weed) (24%), *Erodium botrys* (15%), *Dianthus* (11%) the two *Crassula* species which made up 30% and *Felicia echinata* (9%). *Felicia echinata* was restricted to the natural vegetation while *Dianthus* and *E. botrys* were recorded only in the old field (Table 3.4). There are two peaks in seedling distribution; one at the edge and another one at the end of the trapping distance, 81 m. The least number of seedlings were recorded in the natural vegetation (a mean density of less than 10 seedlings per m²) (Figure 3.11 A). The first peak is due to *Crassula* and *F. echinata* (both indigenous) species and the second peak is due to the dominance of *H. radicata* (alien weed) and *Dianthus*. The least number of seedlings in the natural vegetation (Figure 3.11 B) is related to the least number of forb species there, represented only by two species, *Crassula* and *Felicia echinata*. Other species of the indigenous origin (*L. gnaphaloides*, *Diasca* and *Gazonia*) were recorded at the edge and absent in the old field whereas a number of others (*Dianthus*, *C. turbinata*, *Gnaphaium*) occupy the old field with alien weeds (*A. arvensis*, *Erodium*, *L. serriola*). As for the geophytes, there is also an observed non-overlap in forbs species composition between the old field and the natural/transition zone. All the alien weeds were recorded from the old field side of the transition zone except *H. radicata* while indigenous species occurred both in the natural vegetation and in the old field.

3.3.3.2 Discussion

Results have shown the dominance of alien pasture grasses in the fresh seed bank, which increased into the old field. The dominance of pasture grass species is related to the large percent cover of the same species in the old field reported in section 3.1. The large number of seeds from the old field compared to the natural vegetation was due to these alien pasture grass producing large numbers of seeds in the old field. The edge-transition zone supports a large number of species because being close to the seed source (natural vegetation) increases seed input from plants with short distances and also the dominance of the most competing species is excluded by the disturbance. This is the same pattern observed in vegetation surveys, and in seeds collected from pitfall traps.

Dicerotheramnus rinocerotis produces a large quantity of seeds that was recorded at all distances in the old field from pit traps (Chapter 3.2). Its poor representation in the vermiculite traps probably has more to do with the timing of the traps in the field and the seeding phenology of this shrub. Vermiculite traps were set up in the field in August and could have missed the seed release of this shrub which peaks in dispersal in June/July (Table 3.2; also see Levyns 1956). The second set of traps were set during the second year of dispersing seeds but these would not germinate because *D. rinocerotis* seeds need a year after dispersal to reach maturity for germination (Levyns 1956). Therefore, although the seed shadow for this species is provided from pit traps (Section 3.2, this Chapter), its germinability in the seed rain could not be provided from the vermiculite traps.

The absence of forbs in the natural vegetation could be ascribed to competition and shading by the dominant shrubs especially *D. rinocerotis*. *Dicerotheramnus rinocerotis* was shown to cover more than 80% of the vegetation cover within 1 m around the traps inside the natural vegetation (Table 3.1). A large number of indigenous species at the edge show a stage of succession in these disturbed sites and a number of indigenous species that was also recorded in the old field at further distances away from natural vegetation indicates that the seeds are not limited in the field. The dominance of *H. radicata* in the seed rain and the presence of other alien weeds further into the old field are unlikely to pose a threat to the indigenous forbs as it

seems that they are outcompeted by the encroaching indigenous species. Effective forb dispersal is facilitated by their possession of small seeds that are adapted to disperse long distances in wind. This method of assessing the fresh seed bank by seedling count was very successful in trapping small seeds that were not recognizable in pitfall traps although seeds with temporal dormancy might be underestimated.

Geophytes in the fresh seed rain are limited in the old field and were trapped only as far as 35 m from the natural vegetation. Species found in the natural vegetation are lacking from the old field and this might be explained by poor seed dispersal of geophytes (Kemper, Cowling, and Richardson 1999) and species recorded from the field that were lacking from the natural vegetation perhaps are pioneer species or shade intolerants. *Pentaschistis airoides* has small seeds that are adapted for dispersing in wind and is therefore not likely to be seed limited in the old field but the seeds of other indigenous grass of the *Tribolium* species are limited in the old field.

Vermiculite traps show high dominance by pasture grass seeds in the field whereas indigenous tuft grasses were limited in the field. Geophytes were also limited in the field but forbs were not seed limited.

3.3.4 Sticky traps

3.3.4.1 Results

Seeds representing 11 species were trapped, 7 grass species (3 indigenous and 4 alien), 3 forbs and one shrub. *Dicerotheramnus rinocerotis* (a shrub) dominated the seed rain, with up to 84% of all seeds trapped followed by *Vulpia myuros* (8%), *Briza maxima* (2.5%) and one unidentified forb (2%).

Spatial dispersal

Not enough seeds were trapped for all species to compile individual horizontal or vertical density patterns (Table 3.5). Species that were recovered in relatively large numbers were used to explore the effects of height above ground and distance from the natural vegetation on seed density (using Factorial, two-way ANOVA), Table 3.6). *Vulpia myuros* and *Briza maxima* represent seeds without a pappus whereas one species of unidentified forb (referred to as F1 in Table 3.5) and *Dicerotheramnus rinocerotis* represent seeds with a pappus, and these were the four species used for statistical analysis. Most of the seeds are dispersed at the lowest height, close to the ground especially in plants with seeds having no pappus (Table 3.5) and the test shows a significant effect of height on seed density on these species (Table 3.6). Pappus-bearing seeds show no significant difference in dispersal at all heights (Table 3.6). The non-significant effect of height on seed density for all seeds is perhaps due to the dominance of a pappus seeds in the test. Although the test did not show any significant effect by distance on the seed density, the spatial distribution of certain species shows trends similar to those obtained from the pit traps. For example *D. rinocerotis* had the most seeds at the edge, decreasing both into the natural vegetation and in the old field and *T. hispidum* was restricted to the natural vegetation.

Table 3.5 Represented taxa of seeds from sticky traps and their vertical and horizontal spatial variation of dispersal (*indicates alien species, values are total seeds per dm² over one year). Heights are: 1 (10 – 30 cm), 2 (45 – 65 cm), 3 (80 – 100 cm), 4 (115 – 135 cm)

Species	Seed morphology	Height	Distance m			
			-18	0	35	81
F1*	Pappus	1	4.9	7.4	7.4	12.4
		2	2.5	4.8	1.2	18.5
		3	3.6	2.5	8.7	7.3
		4	7.4	11.1	2.5	23.6
<i>Dicrothamnus rinocerotis</i>	Pappus	1	528.6	797.4	176.1	57.3
		2	616.2	766.2	139.8	61
		3	303.6	654.9	98.6	52.4
		4	384.8	602.4	177.3	53.6
<i>Hypochoeris radicata*</i>	Pappus	1	1.2	0	0	4.9
		2	1.2	0	0	1.2
		3	0	0	1.2	0
		4	2.5	0	1.2	0
<i>Leysera gnaphaloides</i>	Pappus	1	1.2	3.7	3.7	14.9
		2	2.4	1.2	2.4	1.2
		3	1.2	6.2	0	2.4
		4	1.2	0	2.5	1.2
<i>Briza maxima*</i>	No pappus	1	117.4	31.2	7.5	3.7
		2	0	1.2	0	0
		3	0	1.2	0	0
		4	0	0	0	1.2
<i>Vulpia myuros*</i>	No pappus	1	0	58.7	211.2	216.1
		2	0	3.6	13.7	9.8
		3	0	0	2.4	6.2
		4	2.5	0	0	3.7
<i>Briza minor*</i>	No pappus	1	37.5	0	0	0
<i>Bromus pectinatus*</i>	No pappus	1	0	0	1.2	0
<i>Cynodon dactylon</i>	No pappus	1	0	2.4	16.2	8.7
		2	0	0	0	1.2
<i>Pentaschistis airoides</i>	No pappus	1	15	13.7	11.1	18.7
		2	4.9	5	3.7	1.2
		3	2.5	5	0	2.5
		4	1.2	2.4	1.2	3.7
<i>Tribolium hispidum</i>	No pappus	1	1.2	2.4	0	0
		2	0	1.2	0	0
		3	1.2	0	0	0

Table 3.6 ANOVA models for effects of height and distance of sticky trap on number of seeds trapped

Seed morphology	Source of Variation	SS	df	F	P
All seeds	Model	617658.46	1	13.30	0.001*
	Distance	228567.68	3	1.64	0.192
	Height	45225.39	3	0.32	0.808
	Distance*Height	9057.82	9	0.02	1.000
	Error	2229370.80	48		
Without pappus	Model	14934.24	1	4.71	0.045*
	Distance	2145.80	3	0.23	0.877
	Height	37316.93	3	3.92	0.028*
	Distance*Height	4797.62	9	0.17	0.995
	Error	50747.05	16		
With pappus	Model	978600.50	1	10.60	0.005*
	Distance	519903.40	3	1.88	0.174
	Height	21467.77	3	0.08	0.971
	Distance*Height	22229.59	9	0.03	1.000
	Error	1477737.26	16		

*Significant at table-wide $\alpha=0.05$

Note: only four species (*D. rinocerotis* and *F1* = with pappus; and *V. myuros* and *B. maxima* = without pappus) were included in the model as others occurred at very low densities.

3.3.4.2 Discussion

The height at which seeds are trapped will determine how far are they likely to disperse (Bonn, Poschlod and Tackenberg 2000; van Dorp *et al* 1996). Seeds released from a greater height remained airborne for a longer period and would disperse over a long distance (Sinha and Davidar 1992). So the results show that seeds with pappus adapted for dispersing in wind have potential to disperse long distances than seeds without pappus. This is a characteristic of wind dispersed seeds. The height of the plant contributes to the seed-dispersal distance by affecting the terminal velocity of the seed (Howe and Westley 1997; Thiede and Augspurger 1996). Some of the non pappus seeds however would attain their long distance dispersal via animal dung, and this includes species adapted for endozoochory (e.g *Cynodon dactylon*).

3.4 References

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CHAPTER 4

Dung dispersal

4.1 Introduction

The role of seed dispersal by herbivores in generating spatial heterogeneity and influencing vegetation communities has recently been recognised (Milton and Dean 2001). Renosterveld occurs in the region that has been shaped by pastoralism for thousands of years in the Western Cape (Cowling and Richardson 1995). Due to high soil fertility that could have supported nutritious vegetation compared to Fynbos, Renosterveld is also thought to have supported the large herds of game in the Fynbos Biome a few hundred years ago (Rebelo 1996). The effect that herbivory might have had on the evolution of dispersal syndromes is not known nor has the role that the antelope that currently inhabit the region (introduced or reintroduced) play in dispersing seeds ever been addressed. Through herbivory, animals have the potential to transport seeds in their dung, making potential dispersers if they ingest diaspores of plants adapted to survive in digestive tracts (Janzen 1984). The aim of this aspect of the study was to quantify the contribution that large mammalian herbivores have in dispersing seeds into old fields in Renosterveld.

4.2 Materials and Methods

Animals at Elandsberg Private Nature Reserve

Large herbivores that occur in the reserve are listed in Table 2.1 (Chapter 2). Although this study focuses on large herbivorous mammals, other vertebrates, including herbivores, omnivores and insectivores (Table 2.2) could also play a role in dispersal of seeds or other propagules such as corms and bulbs. Tortoises, rodents and aardvarks are reported in the Karoo to disperse seeds (Jump 1988; Dean and Yeaton 1992; Milton 1992b in: Esler 1999). Ostriches are also reported to play a large role in dispersing seeds and mole rats could be dispersing corms of geophytes on which they feed. It would therefore be interesting to carry out a study determining the dispersal ability by these other animals.

Dung collection

In the same sampling area as seed traps (previous Chapter), dung was collected along six transects (2 m by 250 m) in the old field. Transects were 20 m apart and ran parallel to the natural vegetation (Figure 4.1). Each transect was divided into 25 subplots (2 m by 10 m) and from each subplot, dung was classified into one of the four animal groups: Eland, zebra, wildebeest and smaller antelopes ('Other'). The smaller antelope species included springbok, bontebok, red hartebeest, grey rhebok and gemsbok. Dung samples from these species were lumped because of the difficulty in distinguishing the dung between species. The first collection (September 2001) included both fresh and old dung that was present on the site within the sampled transects. After that, monthly dung samples were collected for a period of one year. Dung samples were immediately air dried after collection and their dry weight determined. For air-drying, the samples were spread on paper sheets and left open in a ventilated room, for seven days. The dry dung samples of each animal group were gently crushed and spread into nursery seed trays (maximum of three trays depending on the amount of dung obtained) and transferred to the nursery where they were kept well watered for germination.

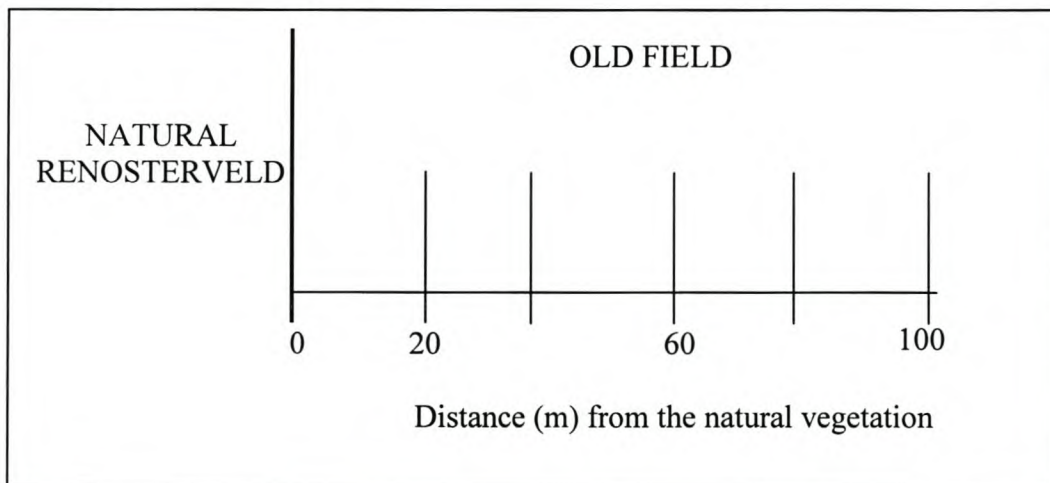


Figure 4.1 Sampling layout for collecting dung in the old field, showing vertical transects

Seedling counts

Germination of dung commenced in March 2002 when the nursery temperature cooled down, and simulated the conditions when Renosterveld plants germinate in the cooler winter rainfall period. Germinated seedlings were removed, recorded and identified, and any seedlings that could not be identified immediately were transplanted into pot plants for further development to the identifiable stage, or pressed after flowering. The nursery germination experiment was terminated at the end of September 2002 and data gathered were analysed. Earlier collected samples stayed in the nursery for at least 6 months and this period proved sufficient to complete germination. An attempt was also made to directly count seeds by physically dissecting the dung samples but no seeds could be identified (perhaps due to their small sizes).

Data analysis

Distribution patterns (both temporal and spatial) of dung for each animal group in the field were obtained and expressed as grams of dung per m². For temporal comparison, the September 2001 data are excluded because the first dung collection included an accumulation of fresh and old material. Since wildebeest and zebra seemingly deposited less dung at the shrubby edge (distance 0 m) compared to the open field, a one-way ANOVA was used to test for any differences, followed by Post Hoc Scheffe test (significant level of $p < 0.05$). Wildebeest, zebra and eland data did not meet the normality distribution assumptions for parametric statistical tests, so they were log transformed before the test. Normality was tested with Kolmogorov-Smirnov and Liliefors. Density of seeds for each species was determined in each of the animal groups and expressed as seedlings per 100 grams of dung. Again, seedlings were classified as forbs, geophytes, grasses and shrubs, and alien forbs and grasses noted. Statistical tests were performed in STATISTICA 6.0.

4.3 Results

Temporal and spatial dung density distribution in the field

There were differences both in temporal dung density distribution (Figure 4.2) and spatial density distribution (Figure 4.3) within and between all four groups of animals. Wildebeest were absent in the old field for most of the year during the wet winter season (March - July) resuming from August through to November during spring and

summer. Zebra foraged in the old field nearly throughout the year, avoiding the late dry summer months and early winter. Mixed herds of other antelopes foraged in the open old field throughout the year but also avoided wet winter months June and July. Eland also deposited dung in the field throughout the year, with a peak activity in autumn and early winter (May/June). Overall there was a higher animal activity in the field during summer than in winter. Summer months were also shown from the previous chapter, section 3.2 as the time when many plants are dispersing their seeds, so there is a potential to transport seeds to the old field by all of these large herbivores.

Dung was deposited throughout the old field, at all distances over the period of one year, with some spatial variation among and between animal groups (Figure 4.3). The spatial distribution and density of dung determines the patterns of distribution of seed dispersal, as shown by the germination trials of dung samples. Dung deposited by the mixture of other antelopes increased with distance from the natural shrubland into the grassy field. Wildebeest and zebra deposited less dung in the shrubby edge of the field than on the open grassy field, but it did not differ significantly from all other distances (Figure 4.3). For wildebeest, the amount of dung deposited in the shrubby edge only differed significantly from the amount deposited at 80 and 100 m from the natural vegetation. For zebra, the only significant difference found between the edge and the open field was at 40 m (Figure 4.3). Eland dung on the other hand showed that statistically there was no difference in dung density at different distances (one-way ANOVA; $F_{5,168} = 1.47$, $p = 0.20$). In other words, eland, wildebeest and zebra all deposited dung throughout the field at all distances and thus have potential to disperse seeds throughout the field.

Seedling densities and plant species emerging from dung

The first dung samples were put in the nursery for germination on the 27th October 2001 but the germination was slow due to hot summer temperatures, until March – 2002 when the temperature cooled down enough for seeds to successfully germinate. Thus the germination rate was greatest between March and June, ceasing in July (Figure 4.4). Variations could also be seen between forbs and grass emergence season; whereas grass started to germinate as early as January, forbs only emerged from March and the only shrub, *Hermannia* sp., emerged later in August. Temporal

or seasonal comparison in seed dispersed in dung deposited at different seasons could not be conducted, because of the differences in the period the samples remained under germination conditions. A few individuals died before proper identification to the genus or species level could be made but they were classified to their functional groups.

Fifty-three species germinated from dung including 30 species of forbs, 18 graminoids (4 sedges and 14 grasses), 4 geophytes and one shrub belonging to the genus *Hermannia* (Table 4.1). Common species include the lawn grass *Cynodon dactylon* that made up 36% of all seedlings, *Vulpia myuros*, an alien pasture grass (24%), *Romulea* sp., a geophyte (12%) and *Ficinia* sp., a sedge (7%). The most diverse group, the forbs were represented at low density among emergent seedlings, making up only 5% of all seedlings, whereas grass seedlings which emerged from dung made up 82%. The forbs in dung were dominated by *Plantago africana* (26%), but other common forbs include *Trifolium* sp. (17%), *Medicago lacinata* (12%), the two *Stellaria* species (11%), *Lobelia* spp. (7%), two *Amaranthus* species (6%), *Erodium moschatum* (5%), *Arctotheca calendula* (4%), *Cenia turbinata* (3%) and *Rumex actocella* (2%) (Table 4.1). One geophyte genus, *Romulea* was notably dispersed in animal dung, making up 92% of all geophyte contributions by large herbivores. *Cynodon dactylon*, together with seven alien pasture grass made up 85% of the grass seedlings, 11% were sedge seedlings and less than 4% comprised indigenous tussock grasses.

The two main groups of animals which dispersed seeds in their dung are zebra (117 seedlings per 100 g of dung) and 'other' antelopes (95 seedlings per 100 g dung), (Table 4.1). Although relatively few seeds are dispersed in wildebeest and eland dung, the two species disperse a relatively large number of species, 28 and 24 respectively (Table 4.1). Wildebeest are important in dispersing geophytes, especially *Romulea*. Although in low density, seedlings of *Amaranthus*, *Lepidium*, *Limeum*, *Hermannia* species and the two sedges – *Cyperus* and *Scirpus* were only recorded from eland dung, making these large mixed-feeding antelope also important in influencing the vegetation.

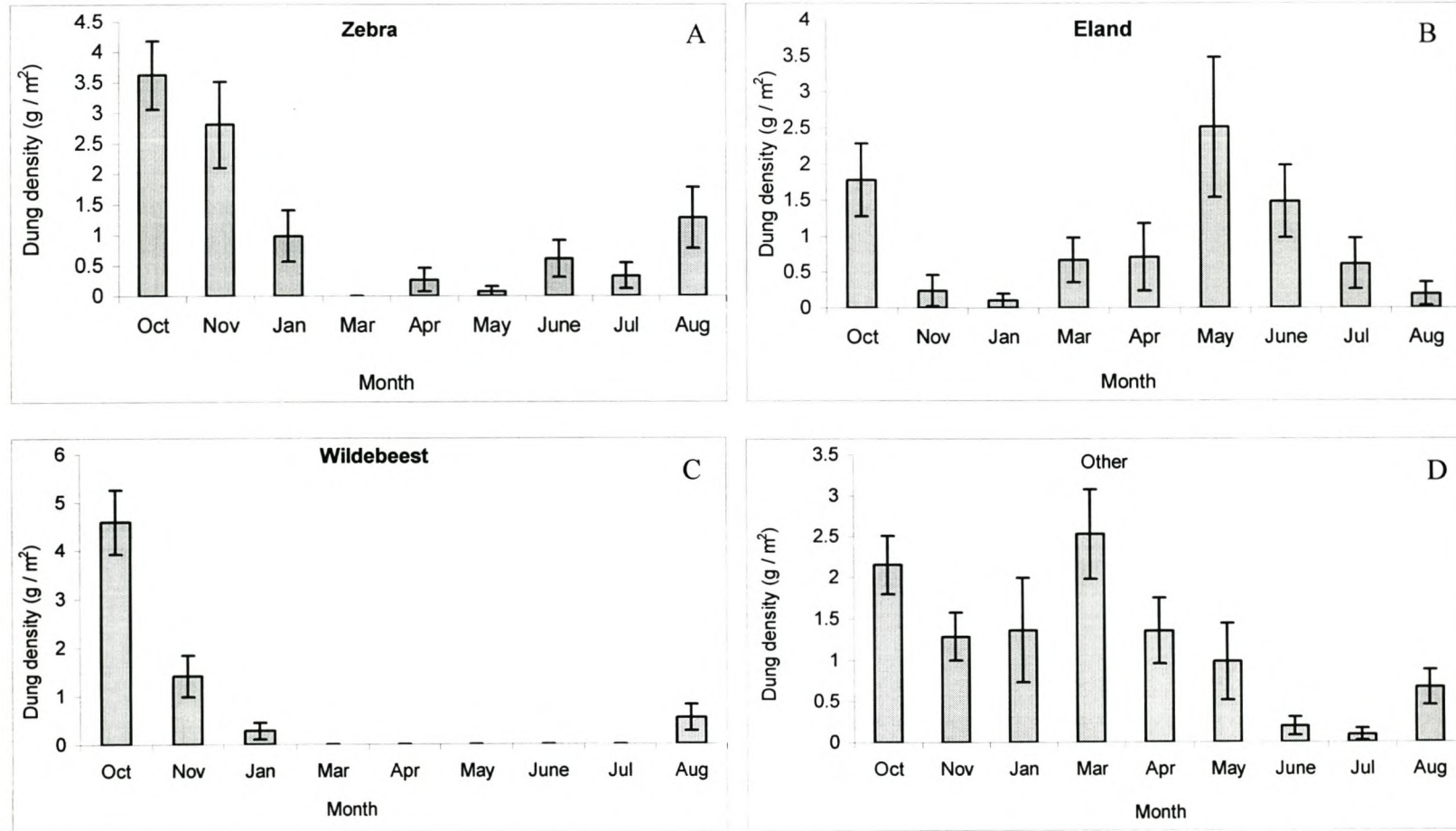


Figure 4.2 Temporal variations in amount of dung deposited (mean \pm S.E), calculated from subplots collected from six transects for (A) Zebra, (B) Eland, (C) Wildebeest and (D) other smaller antelope

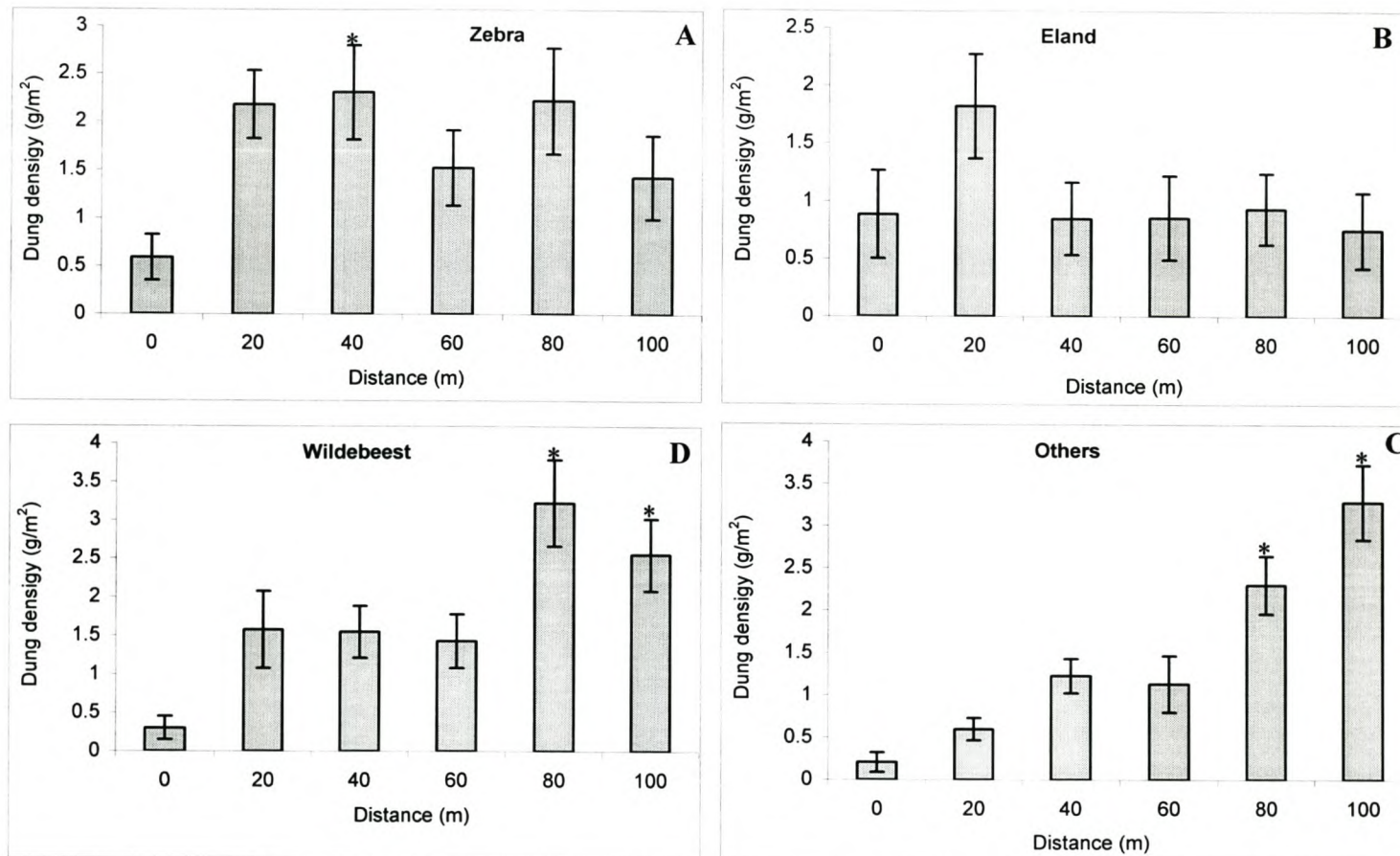


Figure 4.3 Spatial variations in amount of dung deposited (mean \pm S.E), calculated from subplots collected over 10 months for (A) Zebra, (B) Eland, (C) Wildebeest and (D) other smaller antelope. (* means that 0 m is statistically different from the marked distances; Post Hoc Sheffes test)

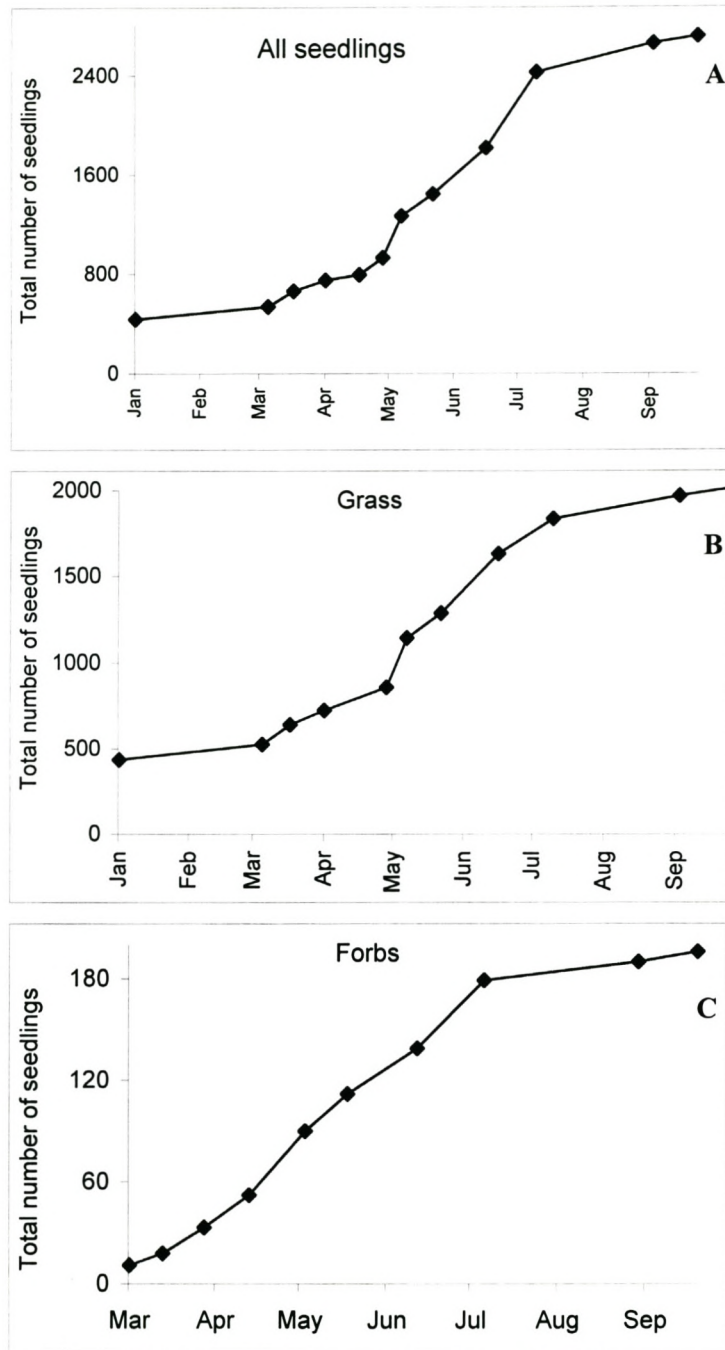


Figure 4.4 Cumulative counts of seedlings emerging from air-dried dung of the samples collected in September -01 to April-02 (A) all seedlings, (B) grasses and sedges, (C) forbs

Table 4.1 Densities (seedlings per 100 g of dung) of seedlings which emerged from animal dung; *indicates alien species

Growth form	Species	NAME OF THE ANIMAL GROUP				Total
		Zebra	Eland	Wildebeest	Other	
Forbs	<i>Amaranthus</i> sp.1	0	0	0	0.1	0.10
	<i>Amaranthus</i> sp.2	0	0.27	0	0	0.27
	<i>Amaranthus</i> sp.3	0	0.36	0	0.15	0.51
	<i>Amaranthus</i> sp.4	0	0	0	0.05	0.05
	<i>Anagallis arvensis</i> *	0	0	0	0.1	0.10
	<i>Arctotheca calendula</i>	0.13	0	0.2	0.1	0.43
	<i>Cenia turbinata</i>	0.13	0.09	0.1	0.1	0.42
	<i>Crassula</i> sp.1	0	0	0.03	0	0.03
	<i>Crassula</i> sp.2	0	0	0	0.1	0.10
	Unidentified species (F2)	0.07	0	0.3	0	0.37
	<i>Geranium molle</i>	0	0	0	0.1	0.10
	<i>Lepidium</i> sp.	0	0.09	0	0	0.09
	<i>Limeum</i> sp.	0	0.09	0	0	0.09
	<i>Lobelia</i> sp.1	0	0.09	0.1	0.66	0.85
	<i>Lobelia</i> sp.2	0.07	0	0	0	0.07
	<i>Medicago</i> sp.	0.88	0	0	0.56	1.44
	<i>Monopsis lutea</i>	0	0.09	0	0.05	0.14
	<i>Plantago africana</i>	2.53	0.45	0.03	0.26	3.27
	<i>Rumex actocella</i>	0.07	0	0.23	0	0.30
	<i>Silene</i> sp.	0	0	0.03	0	0.03
	<i>Nenax</i> sp.	0	0	0	0.05	0.05
	<i>Conyza</i> sp.*	0	0	0.03	0.05	0.08
	<i>Lactuca serriola</i> *	0.22	0	0	0	0.22
	<i>Plantago lanceolata</i> *	0.07	0	0	0	0.07
	<i>Spergularia</i> sp.*	0.07	0	0.03	0.1	0.20
	<i>Stellaria media</i> *	0	0.54	0	0.15	0.69
	<i>Stellaria</i> sp2.*	0	0	0.13	0.36	0.50
	<i>Trifolium</i> sp.*	1.18	0	0.03	0.83	2.05
	<i>Erodium moschatum</i> *	0.07	0	0.45	0.12	0.64

Table 4.1 -Continued

Growth form	Species	NAME OF THE ANIMAL GROUP				Total
		Zebra	Eland	Wildebeest	Other	
<i>Total forb species</i>		12	10	13	19	30
<i>Total forb seedlings</i>		5.48	2.06	1.72	4.01	13.27
Shrub	<i>Hermannia</i> sp.	0	0.18	0	0	0.18
Grass	<i>Briza maxima</i> *	1.12	0.27	0.14	2.8	4.33
	<i>Bromus diandrus</i> *	3.76	0	0.64	0	4.40
	<i>Bromus pectinatus</i> *	0.28	0	0.03	0	0.31
	<i>Vulpia myuros</i> *	49.19	7.98	3.22	3	63.39
	<i>Lolium</i> sp.1*	1.38	0.71	0.23	0.26	2.58
	<i>Lolium</i> sp.2*	0.22	0	0	0	0.22
	<i>Poa annua</i> *	2.86	0.09	3.14	1.24	7.32
	<i>Cynodon dactylon</i>	42.83	1.7	1.88	54.67	101.08
	<i>Scirpus</i> sp.	0	3.21	0	0	3.21
	<i>Cyperus</i> sp.	0	1.44	0	0	1.44
	Unidentified species (G4)	1.22	0	0	0.58	1.80
	<i>Eragrostis</i> sp.	0.07	0	0	0.62	0.69
	<i>Ficinia</i> c	1.59	3.04	0.25	15.17	20.05
	<i>Schismus barbata</i>	0	0	0.13	0	0.13
	Unidentified species (G6)	0	0.89	0	0	0.89
	<i>Pentaschistis airoides</i>	1.6	0	0.65	0.26	2.50
	<i>Tribolium hispidum</i>	0	0.09	0	0.48	0.57
<i>Total grass species</i>		12	9	10	10	17
<i>Total grass seedlings</i>		106.11	19.41	10.31	79.08	214.91
Geophytes	<i>Romulea rosea</i> .	5.14	1.11	16.53	9.51	32.28
	<i>Babiana</i> sp	0	0	0	0.1	0.10
	<i>Oxalis purpurea</i>	0.42	0	0.07	0	0.48
	Unidentified species (B4)	0	0	0	2.08	2.08
<i>Total geophyte species</i>		2	1	2	3	4
<i>Total geophyte seedlings</i>		5.55	1.11	16.60	11.68	34.94
	Total species	26	21	25	32	52
	Total seedlings	117.15	22.76	28.63	94.77	263.30

4.4 Discussion

High activity in the old field of large herbivores during summer indicates that these animals have the potential to disperse seeds as many of the plant species present dispersed their seeds during summer (Chapter 3.2). A substantial quantity and range of seeds were dispersed by large herbivores onto the old field in Renosterveld. According to Pakeman, Digneffe and Small (2002), dissemination of seeds by herbivores could have a significant effect on the dynamics and species richness in grazed ecosystems. Although no specific study on endozoochory by large herbivores has been done before in the area, studies from other areas in South Africa (Milton and Dean 2001) and from Europe (Welch 1985; Malo and Suarez 1995; Pakeman *et al* 2002) have also recorded large numbers of viable seeds dispersed in the dung of large herbivores and this makes endozoochory to be considered relevant in plant communities (Janzen 1984).

The dominance of graminoids and annuals in the dung of large herbivores has also been recorded in other studies (Welch 1985). Many of the alien forb species that germinated in the current study have been recorded, and especially relatively common *Stellaria media*, *Rumex acetosella* and *Trifolium* sp. were also among the species commonly found in Northern Hemisphere studies of endozoochory (Welch 1985). Also evident was that even species with certain apparent adaptations for dispersal by other means are capable of endozoochorous dispersal, an observation that was also reported by Pakeman *et al* (2002). This includes species with adaptations for wind dispersal such as *Arctotheca calendula*, *Ceniza turbinata* and others which have plumes adapted for flying in the wind. *Medicago* sp. has dispersal units with hooks or barbells, which are morphologically grouped as being dispersed externally by attaching to fur but it also germinated in dung in significant numbers in the current study. Generally, endozoochory helps to disseminate species that are classified as having no specific dispersal mechanism (Janzen 1984; Malo and Suarez 1995; Pakeman *et al* 2002) including *Poa annua*. These seeds are usually small, hard and adapted for survival in the digestive tract of an animal. These types of seed syndromes were the most recorded among the dung dispersed seeds (Appendix A) including the most obvious *Lepidium* sp., *Limeum* sp., *Plantago africana*, *Romulea* sp., and *Geranium molle*. Plants adapted for this dispersal syndrome not only have

tough small seeds but their specific location on the plant is also adapted for easy and undetected ingestion by the foraging animal. The seeds of *Amaranthus* and *Lepidium* species for example are distributed among the leaves or the seeds of *Rumex acetocella* are positioned on top of the herbaceous plant in such a way that they are unavoidable by the feeding herbivore (Janzen 1984). The data presented in this study thus support one of the 10 traits of endozoochorously dispersed plants predicted in the ‘foliage is the fruit’ hypothesis: ‘seeds are sufficiently small, tough, hard and inconspicuous to escape the molar mill.....’ (trait 7 of Janzen 1984).

Endozoochorous dispersal tends to be selective in that species with seeds with special adaptations for dispersal such as the plumes of most Asteraceae are less frequent in herbivore dung than species that lack any obvious adaptation to dispersal (Malo and Suarez 1995). Thus poor facilitation of shrubs by mammals in Renosterveld lies in the nature of dispersal syndromes of these shrubs. The shrubs are mainly characterised by parachute-type seeds that are dispersed by wind, e.g *Dicerotheramnus rhinocerotis* and *Helichrysum* sp., two of the common shrubs in Renosterveld. At maturity when shrubs are reproductive, shrubs in Renosterveld are also less palatable and thus attract fewer herbivores compared with some browsed non-reproductive young shrubs.

Not only do herbivores contribute to the dispersal of indigenous forbs and some geophytes but also disperse certain alien weed species. *Spergularia* sp., *Erodium moschatum* and *Trifolium* sp. for example are alien pasture weeds and were dispersed by almost all animal groups except for eland. The eland on the other hand disperse large number of seeds of *Stellaria* (another pasture weed that is not indigenous). In addition to these annuals, the seed rain of herbivore dung was highly dominated by *Cynodon dactylon* and alien pasture grasses. Dissemination of non-indigenous plants by game was also reported by Milton and Dean (2001) in semi-arid Karoo shrubland and Kalahari savanna. *Cynodon dactylon* dominated pastures are important in enhancing grazing capacity in Renosterveld (Coetzee 2002) and most grazing herbivores concentrate on such pastures (Janzen 1984; Young, Patridge and Macrae 1995; Coetzee 2002). Whereas this may reduce some of the pressure in the natural vegetation, it imposes difficulties on the restoration of these fields back to the natural vegetation as these grazing herbivores disperse large number of these grasses and thus maintain the lawn nature of pastures. *Cynodon dactylon*, like other lawn grasses

would dominate any pasture as soon as it is abandoned provided there are grazers (Mike Gregor pers.com) and it forms a dense mat which is difficult to penetrate by seedlings of other species. Herbivores prefer these open areas and thus maintain them (Janzen 1984; Young *et al* 1995; Posada, Aide and Cavelier 2000). However the presence of grazing animals are potential tool for reducing grass biomass and their exclusion from the areas can result in areas of high grass biomass that will inhibit the colonization by indigenous woody species (Posada *et al* 2000).

All four groups of animals observed in this study are important in influencing the vegetation in one way or the other by moving seeds of a wide range of species in their dung, around the reserve. Wildebeest and eland help disseminate seeds of indigenous species that are otherwise poorly dispersed while large number of grass seeds dispersed by zebra and smaller antelope do not really show to be dispersal-limited in the old field. Most of these seeds are alien pasture grass and *C. dactylon* that could possibly compete favourably with the under-represented indigenous tussock grasses and shrub species. Furthermore these grazers (zebra and small antelope) also disperse certain indigenous forbs that were not recorded in other animal dung.

Species with seeds dispersed in animal dung could not be seed limited in the old field as these herbivores deposit dung at all distances in the old field (Figure 4.3). Although animals disperse large number of seeds from lawn grass and alien pasture grasses, which dominate the old field there is also seed dissemination of indigenous forbs and a few species of geophytes. The results show that dispersal by large mammalian herbivores plays an important role in the dynamics of these plant communities by dispersing a wide range of species both alien and indigenous Renosterveld species.

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CHAPTER 5

Soil seed bank composition

5.1 Introduction

Studies of soil seed banks are important in plant population ecology, conservation, restoration and management of plant communities (Araki and Washitani 2000). For restoration processes, seed storage of the soil bank has the potential to contribute to the revegetation of the natural vegetation. Fields that have been transformed for extended periods are likely to have become depleted of the natural species seed bank. Under these conditions, the seed bank composition is usually largely made up of plants that are currently colonizing. The importance of seed bank dynamics to range management, conservation and restoration is addressed by, amongst others, Thompson, Band, and Hodgson (1993); de Villiers, van Rooyen and Theron (1994). The aims of assessing soil seed bank composition in this study were: a) to determine the soil seed bank composition in the old field, and b) to compare this information to the fresh seed rain from previous chapters. The first section of this Chapter describes the methods that were used and the last part of the Chapter present the results obtained, followed by the discussion. Comparison of the soil seed bank data with the new seed bank from fresh seed traps is presented in Chapter 6.

5.2 Materials and Methods

Along the same transect lines described in Chapter 3.2, soil samples were collected at six distance points (-18, 5, 9, 35,62 and 81 m) from the natural vegetation. A core soil sampler (5 cm deep and 5 cm diameter) was used and each soil sample was a collective of 18 cores of soil that covered a surface area of 0.035 m². The samples were spread onto the nursery trays up to the depth of 3.5 cm and were watered to allow seedlings to germinate. Seedlings were recorded, removed and identified where possible. Seedlings that could not be immediately identified were transplanted into individual pot plants for further development and later identification. The first soil sampling was done at the beginning of the study, in August 2001. However, due to very high summer temperatures, no germination was recorded for the period of three months, and the experiment was discarded as unsuccessful. The second set of soil samples was then collected in March 2002, at the beginning of the growing season,

just before seedlings emerged in the field. The samples remained in the nursery under germination conditions for the period of six months. Although the data were limited to one season of one year, the soils were collected right at the beginning of rainy season, before any seedlings started to germinate in the field (*sensu* Rand 2000; Bischoff 2002) and this should give an ideal indication of which last year's seeds survive up to the following year.

Data analysis

Seedlings were identified to genus or species where possible and classified into grasses, shrubs, forbs, and geophytes. Mean density of seedlings were calculated for each distance and expressed as the number of seedlings per m². The means for both species number and density of seedlings were calculated from the three transects. Data were tested for normality using Kolmogorov-Smirnov and Lilliefors test for normality and a one-way ANOVA was used to test for differences in the density of seedlings and species at different distances from the natural vegetation and a significant level of $p < 0.05$ was used. Statistical tests were performed in STATISTICA 6.0.

5.3 Results

Seedlings belonging to 53 different species emerged from the soil samples from the soil seed bank assessment. These included 26 species of forbs (a group containing all non-woody species), 13 species of grasses (including one sedge), 1 shrub, and 13 geophytes (Table 5.1). There was no significant difference in either density of seedlings or in the number of species between any two distances, (one-way ANOVA, $F_{5,12}=2.90$, $p=0.060$ for number of seedlings and $F_{5,12} = 2.21$, $p = 0.12$ for the number of species), although the maximum mean number of seedlings and species were recorded in the old field, comparing to the natural vegetation (Figures 5.1). Grass (mainly alien pasture grasses) dominated the soil seed bank, accounting for 74% of the total germinants.

Geophytes

There was a high rate of death among geophyte seedlings in the nursery, before they reached any development for possible identification. The maximum mean density of seedlings was attained at distances 9, 35 and 62 m, decreasing both into the natural

vegetation and further away to the distance of 81 m (Figure 5.2A), but there was no significant difference between different distances from the natural vegetation (one-way ANOVA, $F_{12,17} = 1.8$, $p = 0.18$). The maximum number of species was obtained from the natural vegetation (Figure 5.2B) although there was no significant difference with distance from the natural vegetation (one-way ANOVA, $F_{6,11} = 1.82$, $p = 0.24$). The geophytes in the soil were dominated by *Oxalis purpurea* (53% of the total geophyte seedlings) and *O. versicolor* (24%), followed by *Ornithoglossum* (12%) and *Corycium* (5%) and all other geophytes made up less than 2% (300 seedlings per m²) each (Table 5.1). There was also variation in seedlings distribution across the field among species. Two species, *O. versicolor* and *Ornithoglossum* were found throughout the sample area, from within the natural vegetation up to the end of the transect lines. There was also partitioning of species between the old field and the natural vegetation. Four species including *Corycium*, *Holothrix* and *O. purpurea* were recorded from the soil samples collected in the old field but did not occur in the natural stand of vegetation, whereas five species of geophytes including *Bulbinella* were restricted to the natural vegetation and were lacking from the old field (Table 5.1).

Grass species

Vulpia myuros, an alien pasture grass made up 60% of all grass seedlings that emerged from the soil samples, and together with six other alien grasses, took up 74% of grass seedlings. These alien grasses were distributed throughout the old field. Also recorded in relatively high density is a sedge, *Ficinia* which accounted for up to 21% of the total number of seedlings. It occurred at high density both in the old field and in the natural vegetation (Table 5.1). The two indigenous *Tribolium* species were not recorded beyond 40 m into the old field while *Pentaschistis airoides* was found throughout the trapping distance with maximum density at furthest from natural vegetation (Table 5.1).

Forbs

The most diverse group represented in the soil were the forbs, with 26 species. Seedling density and species density were higher in the old field compared to the natural and transition vegetation (up to a distance of 9 m) (Figure 5.4). Common species of forbs were three *Crassula* species which accounted for 41% of the

seedlings, *Lobelia* species (22%), *Hypochoeris radicata*, (an alien), (9%), *Erodium botrys* and *Cenia turbinata*, (6%). Although only four species occurred in the natural vegetation, indigenous species were recorded from the edge, and many occurred throughout the field. Nine of the forbs were alien weeds and were mostly recorded at distances of 62 and 81 m from the natural vegetation.

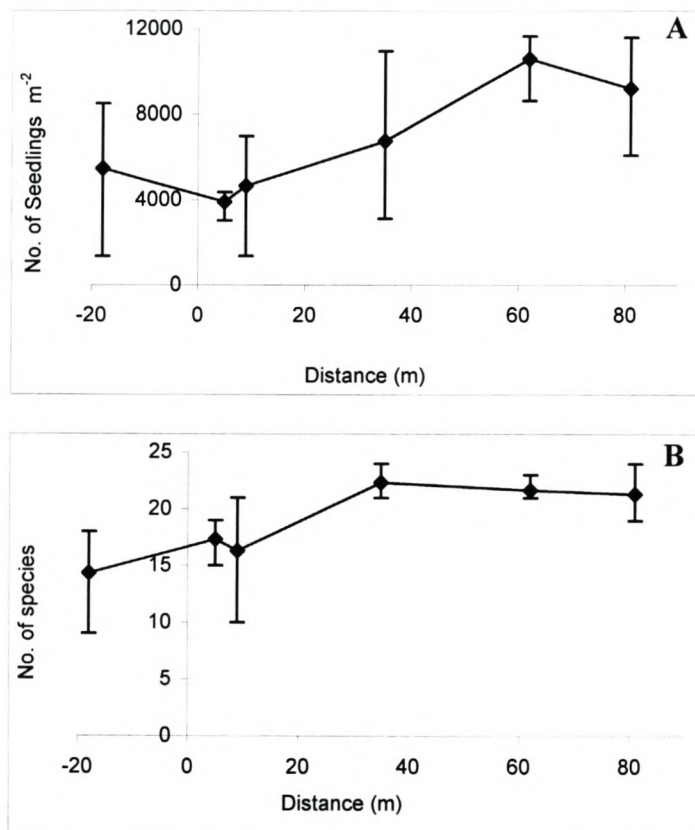


Figure 5.1 Changes in the density of seedlings (A) and number of species (B) recorded in soil samples along the three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

Table 5.1 Represented taxa which emerged from the soil samples and their density distribution across the transects; (*indicates alien species, values are total seedlings per m². ■ geophytes recorded in the natural vegetation; ■ geophytes recorded in the old field, ■ geophytes in both natural and old field vegetation)

Group	Species	Distance(m) from the natural vegetation						Total
		-18	5	9	35	62	81	
Forbs	<i>Cenia turbinate</i>	86	86	143	314	229	171	1029
	<i>Crassula</i> sp.3	143	286	0	86	486	1714	2715
	<i>Felicia echinata</i>	29	114	0	0	0	0	143
	<i>Drosera</i>	29	0	0	0	0	0	29
	<i>Crassula</i> sp.1	0	29	0	343	0	2486	2858
	<i>Erodium botrys</i>	0	86	29	400	371	0	886
	<i>Silene</i>	0	29	29	114	86	86	344
	<i>Lobelia</i> sp.2	0	29	171	1057	1343	914	3514
	<i>Gnaphalium</i>	0	29	29	57	57	86	258
	<i>Hypochoeris radicata</i> *	0	114	0	229	314	771	1428
	<i>Dianthus</i>	0	0	57	0	29	0	86
	<i>Diasca</i>	0	0	29	0	0	0	29
	<i>Ursinia anethoides</i>	0	0	171	114	29	114	428
	<i>Leysera gnaphaloides</i>	0	0	29	57	86	0	172
	<i>Plantago africana</i>	0	0	0	29	0	0	29
	<i>Crassula</i> sp.2	0	0	0	86	57	1143	1286
	<i>Stellaria</i> sp.1*	0	0	0	114	57	0	171
	<i>Spergula arvensis</i> *	0	0	0	29	86	0	115
	<i>Medicago</i>	0	0	0	0	171	0	171
	<i>Manulea</i>	0	0	0	0	29	29	58
	<i>Lactuca serriola</i> *	0	0	0	0	29	0	29
	<i>Salsola Kali</i> *	0	0	0	0	29	0	29
	<i>Trifolium</i> *	0	0	0	0	343	114	457
<i>Trifolium acutifolium</i> *	0	0	0	0	0	29	29	

Table 5.1 -Continued

Group	Species	Distance (m) from the natural vegetation						Total
		-18	5	9	35	62	81	
Grass	<i>Anagallis arvensis</i> *	0	0	0	0	0	29	29
	<i>Spergularia</i> *	0	0	0	0	0	229	229
	<i>Briza maxima</i> *	829	1571	1029	2171	1029	886	7515
	<i>Vulpia myuros</i> *	7771	3057	6543	6314	19686	10429	53800
	<i>Bromus diandrus</i> *	0	1629	171	514	571	143	3028
	<i>Poa annua</i> *	29	200	171	0	57	86	543
	<i>Briza minor</i> *	800	0	57	0	0	0	857
	<i>Lolium</i> *	0	229	86	171	86	0	572
	<i>Bromus pectinatus</i> *	0	486	57	0	0	57	600
	<i>Cynodon dactylon</i>	0	114	29	143	57	57	400
	<i>Ficinia</i>	4658	1600	1457	2400	2915	5914	18944
	G4	0	29	57	29	171	171	457
	Geophytes	<i>Pentaschistis airoides</i>	29	29	0	57	0	514
<i>Tribolium hispidum</i>		0	0	57	29	0	0	86
<i>Tribolium uniola</i>		686	171	0	1714	0	0	2571
Unidentified species (B1)		171	57	0	0	0	0	228
Unidentified species (B3)		29	0	0	0	0	0	29
Unidentified species (B4)		57	0	0	0	0	0	57
Unidentified species (B6)		114	0	0	0	0	0	114
Unidentified species (B7)		114	0	0	0	0	0	114
<i>Bulbinella</i>		114	0	0	0	0	0	114
Unidentified species (B5)		0	0	0	0	29	0	29
<i>Holothrix</i>		0	0	0	29	0	29	58
<i>Corycium</i>		0	200	86	86	229	143	744
<i>Oxalis purpurea</i>		0	1000	1971	2571	1686	714	7942
Unidentified species (B2)		29	0	0	0	0	57	86
<i>Ornithoglossum</i>		314	29	571	257	514	171	1856
<i>Oxalis versicolor</i>	286	514	943	714	914	171	3542	
Shrub	<i>Dicerotheramnus rinocerotis</i>	114	0	29	0	0	0	143
TOTAL SPECIES		20	25	25	29	31	29	54
TOTAL SEEDLINGS m ⁻²		16429	11714	14000	20229	31771	27457	121600

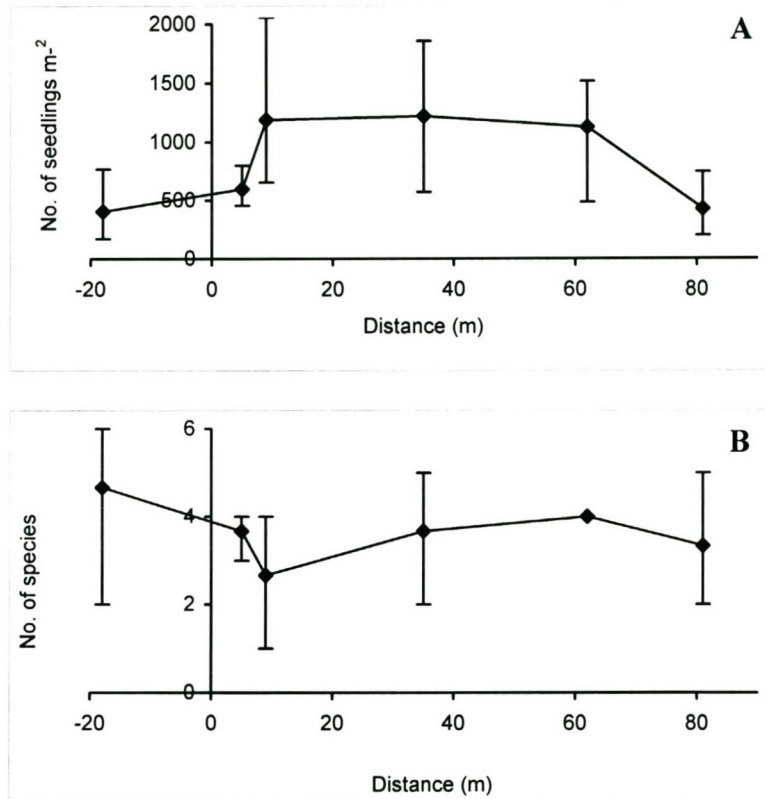


Figure 5.2 Changes in the density of seedlings (A) and the number of geophyte species (B) recorded in soil samples along the three transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

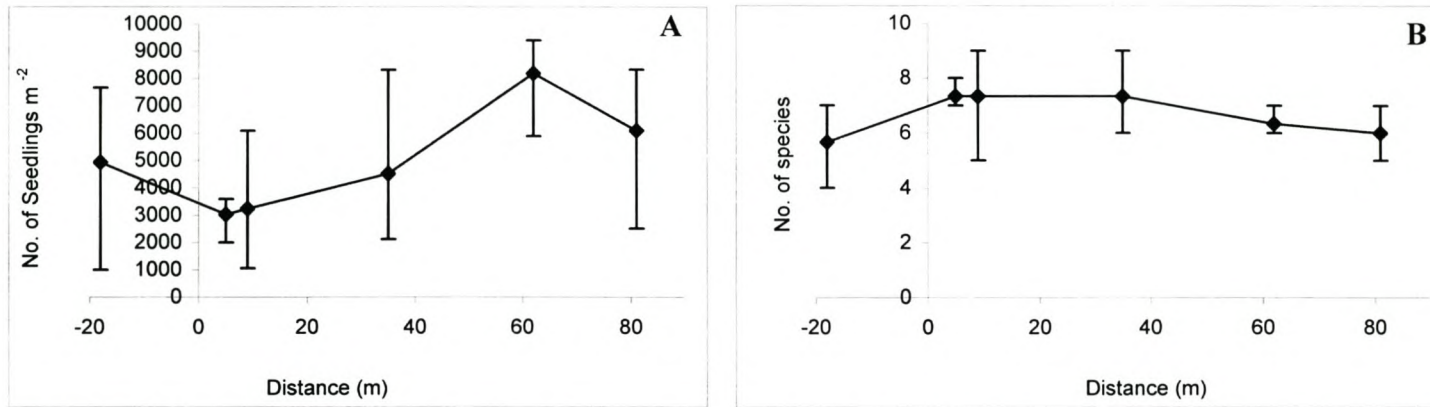


Figure 5.3 Changes in the density of grass seedlings (A) and species (B) recorded in soil samples along transects extending from the natural renosterveld into the old field. Means; maxima and minima were calculated from the three transects

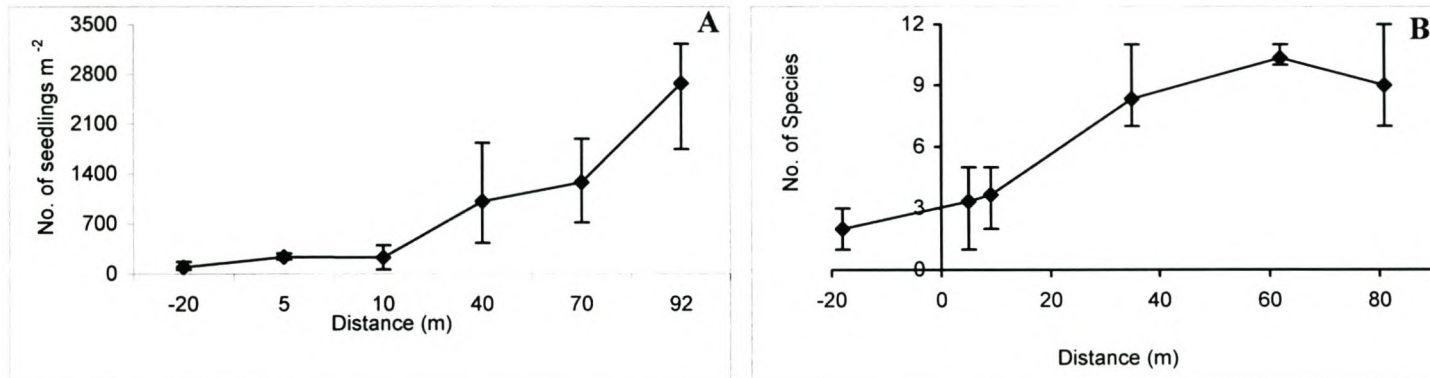


Figure 5.4 Changes in the density of forb seedlings (A) and species (B) recorded in soil samples along transects extending from the natural Renosterveld into the old field. Means; maxima and minima were calculated from the three transects

5.4 Discussion

It is unfortunate that there have been no other studies in literature, on Renosterveld seed banks that may be used for comparison with this study. Even Fynbos seed persistence has not been studied in detail (Pierce and Cowling 1991; Holmes and Foden 2001). High seed density and species richness in the old field was due to the dominance of the seed bank by herbaceous annuals and grasses and these were recorded in greater abundance in the open field than in the natural vegetation. Wijdeven and Kuzee (2000) in their seed bank study in Costa Rica have also found higher seedling density in a pasture comparing to the natural vegetation. Variation in geophyte species distribution can be ascribed to their dispersal mechanism and ability as well as vegetative reproduction from bulbs or corms that persisted in the soil. Geophytes with poor dispersal ability cannot directly move from the natural vegetation to colonise the old field. Partitioning of species between old field and the natural vegetation which were recorded in geophytes and some forbs is not unusual, as similar observations were made between a forest and a pasture (Holl 1999), where no species were found in sample plots in both the forest and pasture. Furthermore, the two species that were recorded throughout the trapping distances either have longer dispersal distances or have survived in the soil. The nonsignificant difference in number of geophyte species in the soil across all distances indicates that seed availability is not the main constraint for the return of certain geophytes to the old fields. With poor seed dispersal among geophytes (Kemper, Cowling and Richardson 1999), these geophytes have perhaps survived in the soil as bulbs.

The dominance of annual species in the seed bank has been noted by other studies in Mediterranean shrublands in the Western Cape Fynbos (Holmes and Richardson 1999) and elsewhere (Ferrandis, Herranz and Martinez-Sanchez 2001). These forbs either have small seeds adapted to wind dispersal or small tough coated seeds that are dispersed in animal dung. Although few species of forbs were found distributed throughout the study site, changes in species competition with distance could be due to different levels in succession among these species. Annual pioneers having well developed dormancy mechanisms that allow for germination only at favourable times (Tainton and Hardy 1999) as compared to later successional perennials. The restriction of alien weeds towards further distances from the natural vegetation could mean that they are out-competed by indigenous forbs if they once dominated the field.

A diverse array of indigenous forbs in the seed bank in the field therefore shows that the system is not seed limited for annual forbs.

Shrubs were poorly represented even in the soil samples from the natural vegetation where they were abundant above ground. Even *Dicerotheramnus rhinocerotis* that is shown to deposit thousands of seeds in the soil yearly (Chapter 3.2) was poorly recorded in the soil. Rarity of species that are abundant in aboveground vegetation in the soil of natural vegetation was also reported by Bischoff (2002). Other shrub species occurring aboveground both in the natural and the transition vegetation are also shown in Chapter 3.1. Whereas the restriction of these species to the natural vegetation might mean they are seed limited, their absence in the belowground soil bank could also be ascribed to their unknown germination ecology.

Alien pasture grass occurred throughout the field in the seed bank at high density. From the vegetation survey reported in section 3.1, it was also shown that the above ground cover of these grasses was high throughout the field and this could explain the high seed density in the soil. *Ficinia* is not dispersal limited, as shown by the large number of seeds both in the natural vegetation and in the old field. *Tribolium hispidum* and *T. uniolae* are limited at distances in the old field, away from the natural vegetation. The seeds of these indigenous grasses do not have any obvious adaptation to dispersal and seemingly do not have any seed bank. *Pentaschistis airoides* on the other hand has seeds that are adapted to wind dispersal and can fly long distances and therefore it was recorded at far distances in the seed bank.

From a good representative of forbs and geophytes recorded in the field conclusion can be drawn that that seed availability in the field is not the primary constraint to the return of these species to old fields.

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CHAPTER 6

General Discussion

This chapter is looking at overall patterns of seed distribution from the entire study, discussing and comparing fresh seed rain (seed traps and dung samples) with the soil seed bank. The relationship between dispersal ability in various seed morphologies, as well as the question of spatio-temporal dispersal trade-off is addressed. Other possible factors that are likely to influence the recovery of old fields in Renosterveld are also addressed in this chapter. Finally, the critique of methodology used in this study is discussed.

6.1 General patterns of seed distribution

Overall seed density from the seed rain increased with distance from the natural vegetation, illustrated in Figure 6.1. During plant succession, fields are initially taken over by pioneer species. These are mostly annuals, and they produce large number of seeds (Connell and Slatyer 1977). The observed high density of seeds and number of species of forbs, both in fresh seed bank and soil seed bank in old field compared to the natural vegetation can be explained by a high number of pioneer species that were abundant in the open old field. The large number of seeds on the old field was also due to the dominance of pasture grasses in the field that produce prolific seeds. Many annuals/forbs are shade intolerant (Tainton and Hardy 1999) and therefore prefer the open old field to the natural vegetation where competition from shrubs is high.

Observed species richness peaked in the transition zone, and decreased both into the natural vegetation and the old field (Figure 6.1). Transition zones are known to hold high species richness (Brooks, Hannah and da Fonseca 2001) as species from both communities co-exist (Peters 2002). The transition zone differs from that of the old field and the natural vegetation by having more species than the other two communities. A species-rich ecotone can be related to the hypothesis of intermediate disturbance (Connell 1978). The natural vegetation, the transition zone and the open field can be ranked on the scale of disturbance as least disturbed, moderately disturbed and heavily disturbed, respectively. The natural vegetation supports few

species due to the presence of competitive dominant species, whereas at the transition zone, diverse species coexist due to competition exclusion through disturbance (Brooks *et al* 2001). Results from Zimmerman, Pascarella and Aide (2000) also show a peak in number of species at the forest pasture transition zone. This supports the speculation that disturbance may promote the coexistence of similar species which would undergo competitive exclusion under more stable or undisturbed conditions (Hubbell and Foster 1986 in: Hovestadt, Yao and Linsenmair 1999).

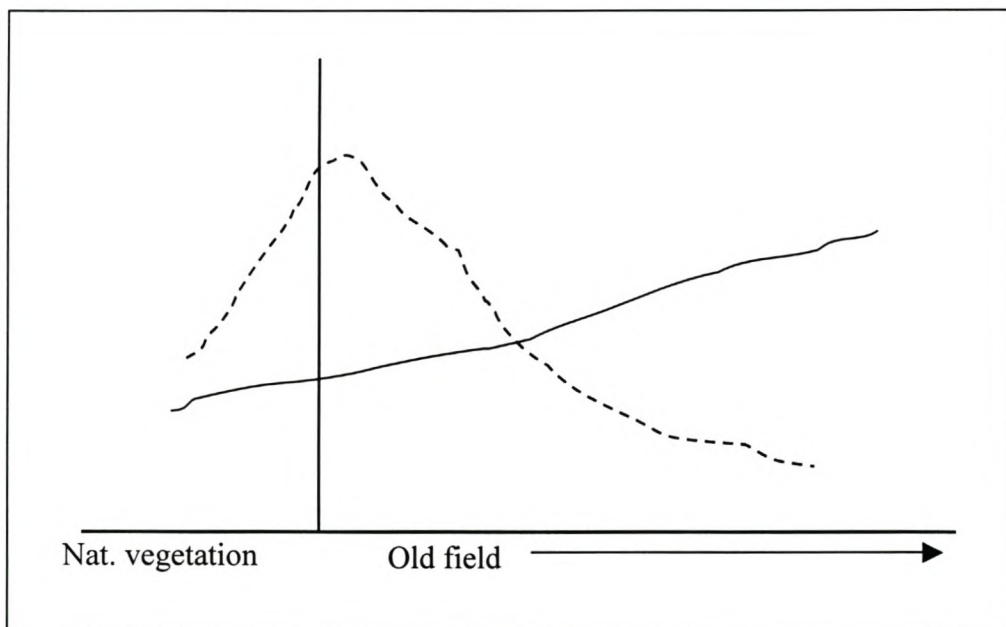


Figure 6.1 General patterns for species richness (---) and seed density (-), showing overall increase in seed density with distance from natural vegetation, and species-rich ecotone

6.2 Fresh seed rain and soil seed bank compared

Seeds collected in pit traps, sticky traps and seedlings found in vermiculite seed traps and in dung contributed to the number of fresh seed rain. All these measures of seed rain have the potential to contribute seeds to the soil seed bank. Species that were recorded in the soil seed bank but not in the fresh seed rain are (literally) considered to have a soil stored seed bank (*sensu* Garcia-Fayos and Verdu 1998; Ferguson and Drake 1999). All species of grass found in the soil seed bank were either recorded in dung samples or in vermiculite seed traps, indicating that grass depends on the fresh seed rain and is not likely to store seeds in the soil (Appendix A). In addition, all species of forbs in the soil seed bank were either found in dung or in fresh seed traps, except three species that were exclusively recorded in the soil bank (Appendix A), albeit at a very low density. This also shows that for forbs, the seed bank in the soil is not different from the fresh seed rain and thus a soil stored seed bank is unlikely. Furthermore, a large number of forbs recorded from dung samples were not recorded in the soil seed bank, indicating that seeds that are moved in animal dung germinate readily and therefore their limited return to old fields is rather due to poor establishment properties than poor seed dispersal. Less similarity was recorded between species that germinated from dung and those found in seed traps, demonstrating the importance of endozoochory in dispersing seeds that might otherwise be dispersal limited.

Geophytes were seed limited in the old field, as shown from the fresh seed traps. This is perhaps due to their poor dispersal properties (Kemper, Cowling and Richardson 1999). Seven species of geophytes recorded from soil seed bank were neither found in dung nor in fresh seed traps (Appendix A), indicating that they are not freshly deposited in the soil, but might have persisted in the soil. Survival in the soil (dispersal in time) could perhaps be the only way these poorly dispersed (in space) geophytes attain their dispersal. The other means for long distance dispersal is via herbivore dung, but only geophytes belonging to the genus *Romulea* germinated in animal dung at high densities. *Romulea* species have small roundish and hard-coated seeds that can survive in the digestive tract of animals. Endozoochory might therefore be the main mechanism for dispersal in this genus. *Romulea* is also one of the dominant geophytes in the fresh seed bank but was not recorded in the soil samples.

The poor representation of *D. rinocerotis* seedlings in the soil samples contradicts the large number of seeds that are deposited yearly into the soil (Levyns 1927; see also Chapter 3 this thesis). This indicates that this shrub does not store seeds in the soil and have to disperse to new areas every year to colonise. The seeds of *D. rinocerotis* are light with plumes, and therefore are well adapted for long distance dispersal.

In contrast to Renosterveld, where mainly geophytes have a soil stored seed bank, dispersal in time is well developed in Fynbos, either via a canopy seed bank (Bond 1988; Holmes and Richardson 1999) or in a soil seed bank (Holmes and Cowling 1997a in: Holmes and Foden 2001; Esler and Pierce 1990).

6.3 Seed morphology and dispersal patterns

Dispersal pattern and distances travelled by diaspores are, among other factors, influenced by seed morphology (Rabinowitz and Rapp 1981; Augspurger and Hogan 1983; Jongejans and Telenius 2001). Dispersal patterns that might be expected for various morphological seed types are discussed below, as well as suggestions as to which seed morphology type is or is not likely to be seed limited, as illustrated in Figure 6.2.

Wind dispersed seeds

Shrubs were poorly represented in the seed rain with only three species recorded. Two of these species (*Dicerotheramnium rinocerotis* and *Helichrysum* sp.) are adapted for wind dispersal and were thus recorded in the seed traps. The dispersal curve obtained from the seeds of *D. rinocerotis* followed that predicted for wind dispersed seeds (Harper 1977; Verkaar, Schenkeveld and Klashorst 1983; Green and Johnson 1989; Okubo and Levin 1989), and obtained in other studies (Rabinowitz and Rapp 1981; Manders 1986; Bond 1988; Howe and Westley 1997). The tail of the dispersal curve for *D. rinocerotis* did not drop to zero or near zero at the end of sampling distance (81 m from the natural vegetation), but continued at a constant seed density. This indicates that the seeds are capable of reaching long distances. This is supported by long distance dispersal models that have shown that these few seeds ('the tail of the curve') can travel long distances (Bullock and Clarke 2000). *Leysera gnaphaloides* is one of the indigenous forbs recorded both from seed traps and soil seed bank. The seeds are light with a feathery pappus adapted for wind dispersal.

Although this species was only recovered at low density and sparsely distributed, its seeds possess morphological characteristics of long distance dispersal. *Dicerotheramnus rinocerotis* and species with related seed morphologies thus are unlikely to be limited by seed dispersal.

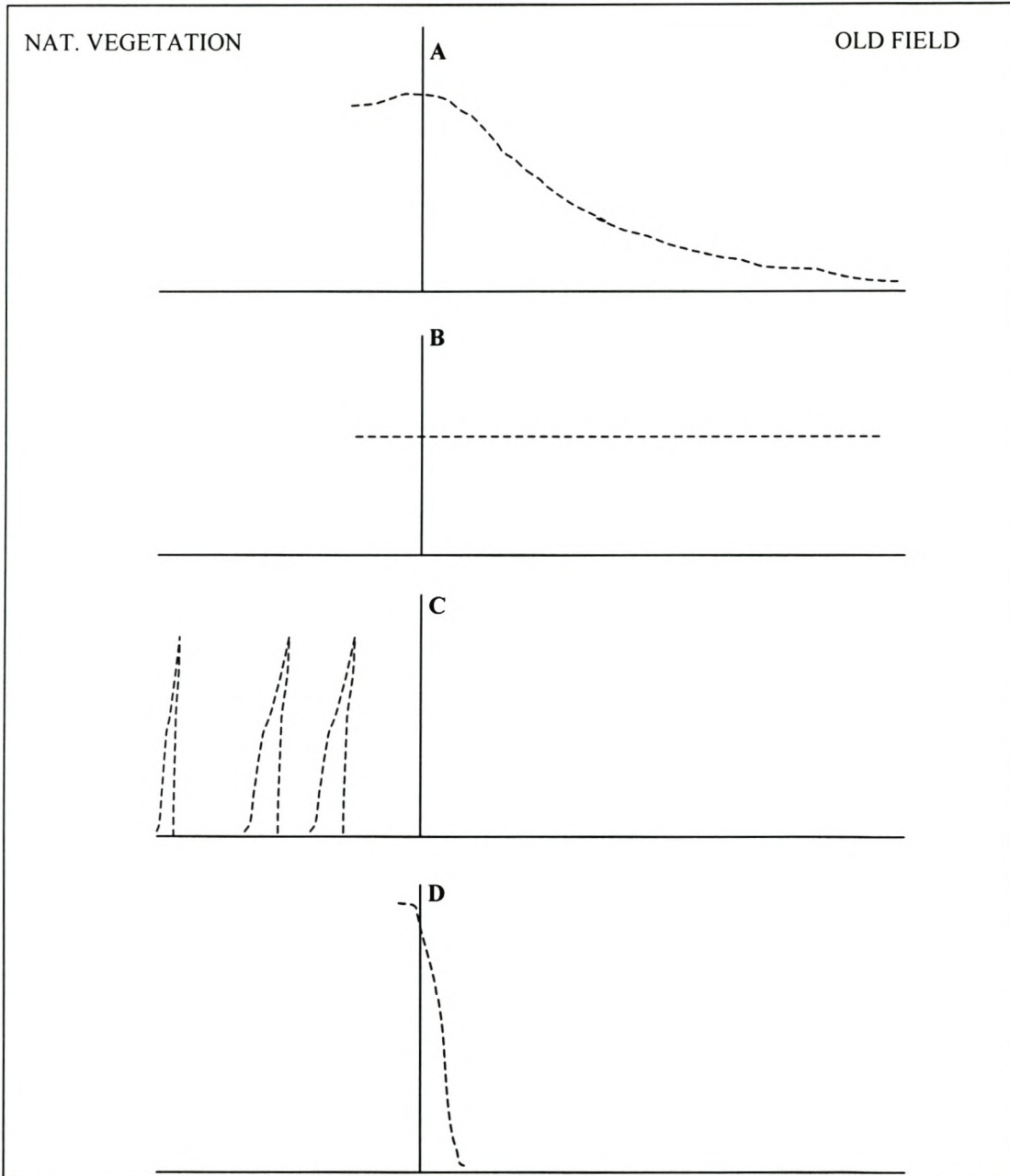


Figure 6.2 Expected seed shadows for wind dispersed seeds (A), seeds dispersed in herbivores (B), seeds dispersed by birds (C) and short distance dispersed seeds (D)

Seeds dispersed by herbivores

Plant species dispersed via the dung of large herbivores are expected to produce patterns related to dung distribution in the field, which depend on the foraging behaviour of the animal (Howe and Westley 1997). These plants have morphological characteristics and positioning of seeds that conform to the classical endozoochorous species described in Janzen (1984). Plant species that are dispersed by animals are not expected to be seed limited because animal dispersal provides long distance dispersal and expected dispersal patterns are not correlated to the distance from the natural vegetation (Figure 6.2 B).

Seeds adapted for dispersal by frugivorous birds

The absence of bird dispersed plants from seed traps and the soil seed bank indicates that this dispersal syndrome is not significant in the restoration of Renosterveld old fields. Bird behaviours follow available perches and food availability (Holl 1999; Zimmerman *et al* 2000). The vegetation structure can influence the perching behaviour of frugivorous birds and so may influence deposition patterns of bird-dispersed seeds (Ferguson and Drake 1999). In Renosterveld, species adapted for dispersal by bird are shrubs confined to *heuweltjies*, e.g. wild olive (*Olea europea africana*). *Heuweltjies* offer ample perches for birds in Renosterveld landscapes and fleshy fruits produced in these areas provide for food. In addition to feeding on fleshy fruits, birds also feed on termites that are abundant on *heuweltjies*. The open old fields, however, offer little to frugivorous birds (Chapman and Chapman 1999; Duncan and Chapman 1999; Holl 1999; Ferguson and Drake 1999), and therefore plants adapted to dispersal by birds are expected to be limited on old fields. A classic example for the expected seed shadow for bird dispersed species is illustrated in Figure 6.2 C, showing distinctive peaks in the natural vegetation around *heuweltjies*, and none in the old field. The graph is drawn according to the review by Ferguson and Drake (1999), who found that birds produce seed rain patterns characterised by distinct peaks where perches act as nuclei for deposition. In the tropical forest where frugivory by bird is an important dispersal syndrome, Holl (1999) suggested that artificial perches could be built in an open field to allow visitation by birds that will enhance the establishment of the otherwise limited plants. For Renosterveld, waiting for the natural development of perches in the open fields will obviously take

generations of succession, and establishment of artificial perches can be considered as an option to facilitate avian frugivory.

Seeds without long-distance dispersal adaptations

Small-seeded annuals that are generally classified as having no obvious adaptations to dispersal were among species that were recorded in the dung of large mammalian herbivores. Certain Renosterveld shrubs were abundant in the natural vegetation and at the transition zone (see the vegetation description in Chapter 3.1), but were not recovered in the seed rain, including *Relhania fruticosa* and *Athanasia trifurcata*. These shrubs do not readily shed their seeds but seem to keep them in the dead flower heads on the mother plant, perhaps dispersing them in the following years when the seed capsules rot away. This dispersal syndrome mimics serotiny (canopy stored seed bank) in Fynbos or in Karoo vegetation where the seeds of some species stay in their seed cones or capsules on the mother plant until a fire (Fynbos) or raindrops (Karoo) (Esler and Pierce 1990) triggers the opening of the seed capsules, and the seeds are released. It is, however, not clear as to what drives serotiny in Renosterveld. *Carpanthea* and *Lampranthus* species (Mesembryanthema) are found in the lowland Renosterveld where seasonal flooding is common and were also observed in the vlei (wetland) area in the natural Renosterveld at the current study site. These plants keep their seeds inside locules in the seed cone which are opened after flooding or heavy rain (Smith, Chesselet, van Jaarsveld, Hartmann, Hammer, van Wyk, Burgoyne, Klak and Kurzweil 1998). This rainfall-driven selection for canopy stored seed is a typical adaptation to arid regions (Karoo) where rainfall is unpredictable. Since rainfall in Renosterveld occurs predictably every winter this dispersal-prevention behaviour can rather be attributed to plants making use of temporal wetlands as a means of dispersal than this being an adaptation to prolonged droughts. Canopy storage by *A. trifurcata* and *R. fruticosa* might explain the absence of their seeds in the seed rain investigated here. Water dispersal does not provide these species with long distance dispersal to colonise the old field, and since these species seem to be lacking long distance dispersal adaptations, it can be concluded that they are likely to be seed limited in the old field (Figure 6.2 D).

The indigenous grasses *Tribolium hispidum* and *T. uniolae* also have seeds that have no obvious adaptation to dispersal, and as they are also not represented in the dung samples, these species can be regarded as seed limited in old fields.

Trade-off between dispersal in time and space

This hypothesis states that seeds evolved for long distance dispersal are unlikely to be stored in the soil seed bank whereas seeds with poor dispersal in space have a soil stored seed bank (Thompson 2000). The theory of resource allocation assumes that allocation of resources to various plant structures is equivalent to allocation to corresponding functions (Bazzaz, Ackerly and Reekie 2000). Plants with poor dispersal allocate their resources to develop soil persistence of seeds. Dispersal in time allows seeds to disperse and germinate only when conditions for establishment are appropriate. Good dispersers on the other hand allocate resources to well developed seed structures for long distance dispersal. *Dicerotheramnus rinocerotis* from this study represents plants with seeds that have evolved to disperse in space. This shrub was poorly represented in the soil seed bank, indicating that *D. rinocerotis* does not disperse in time. This form of trade-off was also observed among the geophyte species. Common geophytes from the fresh seed rain were either absent (*Romulea*) or occurred at a very low density in the soil seed bank, while common species in the soil seed bank were either absent (*O. versicolor*) or occurred at a very low density (*Ornithoglossum*, *O. purpurea* and *Corysum*) in the fresh seed bank. *Romulea* attains its long distance transportation by being readily dispersed in animal dung, especially by Wildebeest, at high density (Chapter 4). This negative relationship between species dispersed in fresh seed rain and species found in the soil seed bank could be explained by the trade-off hypothesis.

6.4 Other factors influencing vegetation recovery on old fields

Although it has been pointed out that seed dispersal is ubiquitous barrier to plant regeneration (Zimmerman *et al* 2000), other factors have also been reported to delay or stop the regeneration of plant communities (Chapman and Chapman 1999; Holl, Loik, Lin and Samuels 2000; Holl 1999; Zimmerman *et al* 2000). Pasture species that dominate the seed rain are reported as barriers for the recovery of abandoned pastures (Chapman and Chapman 1999; Holl 1999; Holl *et al* 2000; Zimmerman *et al* 2000) and can impose a similar establishment constraint on the Renosterveld species in old-

fields. The current study has shown that lawn grass *Cynodon dactylon* and alien grasses did not only dominate the total grass seed rain but dominated the entire seed rain from seed banks, pits and herbivore dung, making up about 80% of the total seed density. Martinez-Garza and Gonzalez-Montagut (1999) in their study of seed rain in pastures suggested that of the seeds of those species arriving at the pasture, only few will establish due to the hard conditions in pastures. Pasture species proliferate with herbivore activity, overgrazing and lack of appropriate management (Guevara *et al.* 1997; in: Martinez-Garza and Gonzalez-Montagut 1999) and are thus well represented in the seed rain. *Cynodon dactylon* (a dominant pasture grass in Renosterveld) for example will take over any field as soon as it is abandoned, in the presence of grazing (Mike Gregor pers.com). Joubert (1984) has dealt with similar situation whereby an area was infested by large number (more than half of the total seed bank counted) of seeds of nasella tussock (*Stipa trichotoma* Nees; Poaceae), a noxious weed in South Africa. He recommended that over-sowing the site with seeds of indigenous species accompanied with pre-burning the surface litter would kill off a large number of the nasella seeds, or cultivating the field to bury the nasella seeds.

Attempted removals of pasture grass and herbaceous weeds have yielded contradicting results (Zimmerman *et al* 2000). Whereas some studies showed positive improvement in seedling establishment, other studies did not show any difference, while yet others have shown negative effects of weeding on the survival of indigenous seedlings (reviewed by Zimmerman *et al* 2000). This option (pre-burning or cultivating the field) is however not encouraged in Renosterveld old fields, as this will destroy all seeds in the soil seed bank, including rare indigenous forbs and the sparsely distributed shrubs that take time to establish themselves. Posada, Aide and Cavelier (2000) suggest that seed addition would be more successful when the grass biomass is still low, e.g. immediately after abandonment. However, since soil tilling especially over extended periods changes soil properties, it is unlikely that immediate sowing will lead to successful establishment. The concept of succession (Connell and Slatyer 1977; Tainton and Hardy 1999) states that early species (pioneers) that take over immediately after abandonment modify the field condition during the first few years of abandonment. According to the predictions of the mechanisms of succession, earlier successional species can either modify the condition and thereby facilitate the colonisation of later species, or suppress the colonisation of the later succession

species (Connel and Slatyer 1977). The latter is especially true if the former species propagate vegetatively as well as sexually, because under these conditions, the opportunities for a new seedling of any species to establish in a dense stand of perennial grass is virtually nil. *Cynodon dactylon* reproduces both sexually and vegetatively and forms a non-penetratable mat. Studies looking at competition and seedling establishment in Renosterveld are currently being undertaken in the study area, to explore alternative explanations for the poor recovery of these fields.

Water stress: Martinez-Garza and Gonzalez-Montagut (1999) suggested that even though many species arriving at pastures might not establish in early stages of natural regeneration, their presence in the seed rain enhances the regenerative potential of those sites. This is supported by the observed wave-like patterns of returning *D. rinocerotis* that are concentrated along the drainage lines on the study site. The establishment of this shrub might then be constrained by other factors, e.g. water stress. Levyns (1956) has shown that seedling growth of *D. rinocerotis* is very much influenced by the environment and even a temporary drought is sufficient to kill the seedlings. In her experiments, Levyns (1927) found that unless the pots in which the seedlings were growing were kept standing in water, a hot dry day kills off large numbers of seedlings. Seasonal floodplains at Elandsberg are reported as being essential for the survival of rare plants such as *Oxalis natans* and *Isoetes stephansenii*, the former being an aquatic species found only on Elandsberg Nature Reserve (Smuts 1996; in: Diemer 2000). The well-drained old fields will therefore not offer suitable conditions for the survival of seedlings of these species and their return to these sites is unlikely.

Seed predation: Another fate for seeds arriving in the field is predation. The few seeds that arrive on pastures are commonly subjected to high rates of predation (Chapman and Chapman 1999; Holl 1999). Chapman and Chapman (1999) show that seed-eating rodents were almost twice as abundant in a pasture as in a mature stand in a tropical forest. Seed predation in Renosterveld has not been investigated yet but contradicting results between the prolific yearly deposition of seeds by *D. rinocerotis* and its absence from the soil samples might indicate seed predation, in addition to unknown germination constraints. Seed predation is also reported in the tropical

forest to seriously limit the available pool of species for forest regeneration (Wijdeven and Kuzee 2000).

6.5 Critique of methods used in this study

Results in the seed rain from different trapping sources were comparable in terms of the patterns of seed distribution, and this shows the success of the methods used. For example there was a similarity in the distribution of forb species from the fresh seed bank and from the soil seed bank. Species that were recorded from the natural vegetation in the fresh seed bank are also found in the soil seed bank of the natural vegetation. There was also a similar dominance of species among forbs between the soil seed bank and the fresh seed bank. However, the seedling count technique used in estimating the soil seed bank might not give full information and therefore its comparison to the fresh seed bank might be obscured. The seedling count method is limited in such a way that only those species whose germination cues are met will be recorded (Simpson, Leck and Parker 1989; Carey and Watkinson 1993; de Villiers, Van Rooyen and Theron 1994; Guo, Rundel and Goodall 1999). Similarly, determining the potential contribution of large herbivores to seed dispersal using the method of seedling count is associated with uncertainty in that species with specific germination requirements might be missed. Dung collection throughout the year, however, covers all species during their individual seasons of setting and shedding seeds. Future improvement in similar methods could include the timing for fresh seed bank traps. These traps should be set up at the beginning of dispersal in the first year of the study, to allow enough time for germination in the nursery. Seed traps rarely yield sufficient seed densities for statistical analysis for all species (Fort and Richards 1998).

6.6 References

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CHAPTER 7

Conclusions and Synthesis

This study has shown that seed dispersal is not a primary constraint to the return of a number of geophytes, indigenous forbs as well as *Dicerthamnus rhinocerotis* as shown by the availability of their seeds in the old ploughed field either via physical seed rain, seeds in animal dung or their presence in the soil seed bank. The presence of seeds of these Renosterveld species in the old field shows that there is a good potential for the regeneration of these fields should other primary constraints be overcome. However, the fact that a number of Renosterveld species, including common characteristic shrubs and endemic geophytes that are not dispersed by wind or in dung, are not represented in the seed rain shows that these might be limited by seed dispersal and will therefore delay the recovery of these sites even when there are no other limitations. According to Zimmerman, Pascarella and Aide (2000) dispersal limitation is an easily managed barrier that can be overcome with broadcast sowing should there be no other significant barriers to the re-establishment. However, it is important that for these species that were not recovered in the seed rain, limitations be determined for successful sowing. Lack of proper perches in the old field explains little avian dispersal to these sites and dispersal to these sites was mainly by wind-dispersed species and from those species that are dispersed in the dung of large herbivores. Other possible factors that might explain poor regeneration are yet to be investigated in Renosterveld.

Large herbivores are important in the area as they contribute to the dispersal of some important Renosterveld species that would otherwise be limited due to poor seed dispersal (e.g. the geophyte, *Romulea* and certain forbs). However these animals are also dispersing large number of seeds of competitive alien pasture grasses but yet it is their presence that help reduce the grass biomass in the field.

There were also signs of trade-off between dispersal in time and in space among the geophytes that were recorded in the soil bank, although no detail was given to what extent. Therefore this study was one of the basic studies important both to the

ecological knowledge of Renosterveld as well as to the Renosterveld Restoration Project.

To the Renosterveld Restoration Project currently underway on, this study has provided essential information on the availability or absence of propagules to restored sites. More specific questions have also arisen as a result of this study. For example the ecological behaviour of the dominant shrub in Renosterveld, *Dicerotheramnus rinocerotis* that produces thousands of seeds yearly, but no seeds were recovered even from the soil samples collected just underneath the shrubs in the natural vegetation. The investigation of seed predation in Renosterveld is just one of the many questions that are relevant not only to the knowledge of the ecology of this vegetation type but also to restoration of old fields. As far as dispersal ecology in Renosterveld is concerned, there are still a number of unanswered questions. Which factors trigger the dispersal of seeds in serotinous species in Renosterveld and how do *Relhania fruticosa* or *Athanasia trifurcata* disperse their seeds? Furthermore, this study has also shown that there is more to the restoration of these old fields than the mere limitation by seed dispersal. In other words, whereas dispersal might limit some of the species, other species are not seed limited and seeds are found in abundance on old fields. The return of these species might be inhibited by competition from alien grasses, changes in soil chemistry, herbivory or other possible constraints. A study on competition and establishment of indigenous seedlings has just been initiated in the same study area and this together with other upcoming research would provide further information.

For the consideration of the importance of seed availability and accessibility to the restored sites, recommendations to future landuse management in Renosterveld are as follow: Any disturbance practise should consider the availability of a potential nearby seed source. The size of both the disturbed area and the seed source is also important. The disturbed sites should be small enough to permit adequate dispersal of seeds across the sites, and to avoid restoration sites being taken over only by species that are good dispersers like *D. rinocerotis*, or by certain geophytes that survive in the soil seed bank. Therefore it is recommended that landuse managers avoid intense disturbances that cover large areas, to facilitate natural dispersal to these sites, and to prevent expensive and tedious restoration projects of sowing. To protect the seed

source, minimum viable populations of key species should be maintained, large enough to provide a good representation of all indigenous species. These recommendations are similar to those given by Wali (1999) for tropical forest regeneration.

However the journey towards recovery is long, and has been estimated in studies in tropical forests, to range from between 30-40 years to 100 and even 200 years on moderately used pastures (review by Chapman and Chapman 1999). As this study has shown, successful restoration does not only depend on seed availability but a number of (unknown) factors are involved and need to be considered. Therefore I hope that studies in the same area that are looking at other aspects of limitations will provide further understanding of the ecological processes of Renosterveld for a successful restoration of this endangered vegetation type.

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Appendix A. List of all species found in seed rain, together with morphology of dispersal unit. Media in which the seeds were recorded are indicated as D (dung), SI (soil), V (vermiculite traps), P (pit traps), St (sticky traps).

Species or Genus name	Seed description	D	V	SI	P	St
<i>Amaranthus</i> sp.1	Small hard, shiny	1				
<i>Amaranthus</i> sp.2	Small hard, shiny	1				
<i>Amaranthus</i> sp.3	Small hard, shiny	1				
<i>Amaranthus</i> sp.4	Small hard, shiny	1				
<i>Anagallis arvensis</i> * L. (Scarlet Pimpernel)	Small, winged	1	1	1		
<i>Arctotheca calendula</i> (L.) Levyns	Medium, plumed achene	1				
<i>Avena</i> sp.*	Large barb				1	
<i>Babiana</i> sp.	Medium, spherical, hard	1				
<i>Briza maxima</i> * (L.)	Small, winged	1	1	1	1	1
<i>Briza minor</i> * (L.)	Small, winged		1	1	1	1
<i>Bromus diandrus</i> * Roth	Large, barbs and awns	1	1	1	1	
<i>Bromus pectinatus</i> * Thunb.	Large, barbs and awns	1		1	1	1
B1				1		
B2			1	1		
B3			1	1		
<i>Bulbinella</i> sp.	Medium, winged			1		
<i>Cenia turbinata</i> (L.) Pers	Small, winged achene	1	1	1		
<i>Conyza</i> sp.*	Small, plumed achene	1				
<i>Corycium</i> sp.	Dust seed		1	1		
<i>Crassula</i> sp.1	Dust seed		1	1		
<i>Crassula</i> sp.2	Dust seed	1	1	1		
<i>Crassula</i> sp.3	Dust seed	1	1	1		
<i>Cynodon dactylon</i> (L.) Pers.	Small, hard above foliage	1		1	1	1
<i>Cyperus</i> sp.	Small, hard, triangular	1				
<i>Dianthus</i> sp.			1	1		
<i>Diasca</i> sp.	Dust seed		1	1		
F2		1				
<i>Drosera</i> sp.				1		
<i>Dicrothamnus rinocerotis</i> (Lf) Less	Small, plumed achenes		1	1	1	1
<i>Eragrostis</i> sp.	Small, hard	1				
<i>Erodium botrys</i> (Cav.) Bertol.	Barbed awn		1	1		
<i>Erodium moschatum</i> * (L.) L'Hér.	Medium barbed awn	1	1		1	
<i>Felicia echinata</i> (Thunb.) Nees	Medium, plumed achene		1	1		
<i>Ficinia</i> sp.	Small, hard	1	1	1		
G4		1	1	1		
G5					1	
<i>Gazania</i> sp.	Medium, fluffy achene		1			
<i>Geranium molle</i> (L)	Medium, barbed awn	1				
<i>Gnaphalium</i> sp.	Small, plumed achene		1	1		
<i>Helichrysum</i> sp.	Small, plumed achene				1	1
<i>Hermannia</i> sp.	Small hard	1				
<i>Holothrix</i> sp.	Dust seed			1		
<i>Trifolium</i> sp.*	Small, hard	1		1		
<i>Ursinia anthemoides</i> (DC.) NE.Br.	Small winged achene		1	1		
F1	Plumes (wind)					1

Appendix A -Continued

Species or Genus name	Seed description	D	V	SI	P	St
B4		1	1	1		
B5				1		
B6				1		
B7				1		
G1					1	
G2					1	
G3					1	
<i>Hypochaeris radiata</i> * (L.)	Parachuted achene		1	1	1	1
<i>Lactuca serriola</i> * (L)	Medium parachuted achene	1	1	1		
<i>Lepidium</i> sp.	Small, hard	1				
<i>Leysera gnaphaloides</i>	Plumed achene + barbed achene		1	1	1	1
<i>Limeum</i> sp.	Small, hard	1				
<i>Lobelia</i> sp.1	Dust seed	1				
<i>Lobelia</i> sp.2	Dust seed	1	1	1		
<i>Lolium</i> sp.*	Medium,oval, hard in foliage	1	1	1	1	
<i>Manulea</i> sp.	Dust seed			1		
<i>Medicago</i> sp.	Medium, barbs or hooks	1		1		
<i>Monopsis lutea</i>		1				
<i>Nenax</i> sp.	Medium, spherical, hard	1				
<i>Ornithoglossum</i> sp.			1	1		
<i>Othonna</i> sp.	Medium, plumed achene		1			
<i>Oxalis</i> (a weed)	Explosive capsule		1			
<i>Oxalis purpurea</i> Thunb.	Explosive capsule	1	1	1		
<i>Oxalis versicolor</i> (L)	Explosive capsule			1		
<i>Pentaschistis airoides</i> (Nees)	Small, hard	1	1	1	1	1
<i>Trifolium angustifolium</i> *	Small, hard			1	1	
<i>Plantago africana</i>	Medium, oval, shiny, hard	1		1		
<i>Plantago lanceolata</i> * (L)	Small, hard	1				
<i>Poa annua</i> * (GK)	Small hard in green leaves	1	1	1		
<i>Romulea</i> sp.	Small, spherical, hard	1	1			
<i>Rumex acetocella</i> (L)	Medium, triangular, hard	1				
<i>Salsola kali</i> * (L)	Medium, winged			1		
<i>Schismus barbata</i> (L.) Thell.	Small, hard in foliage	1				
<i>Scirpus</i> sp.	Small triangular	1				
G6		1				
<i>Silene</i> sp.	Dust seed	1		1		
<i>Spergula arvensis</i> * (L)	Small, winged		1	1		
<i>Spergularia</i> sp.*	Small, winged	1		1		
<i>Stellaria media</i> * (L.) Villars	Small, spherical, rough	1				
<i>Cerastium</i> sp.*	Small round	1		1		
<i>Tribolium hispidum</i> (Thunb.)	Medium burr	1	1	1	1	1
<i>Tribolium uniola</i> e (Lf) Renvoize	Small in foliage		1	1		
<i>Vulpia myuros</i> * (L.) CC Gmel.	Medium barbed awn	1	1	1		1