Using ecological concepts to restore the drylands of Namaqualand, South Africa

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Declaration

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Abstract

This thesis investigated the impact of cultivation, and the efficiency of passive and active restoration of fallow fields, in Namaqualand's Hardeveld and Renosterveld vegetation communities. The core theory of this thesis lies in the ecology of semi-arid environments and the concept of patch dynamics. In such areas plants grow together, creating communities with a distinct patch/inter-patch structure. Patches of vegetation concentrate more organic matter, nutrients and moisture, in 'islands of fertility' as well as providing protection for seedlings from harsh elements, trampling and herbivory. The objectives of this thesis are to assess the efficacy of passive restoration and why it might not work, and to explore the value of patch dynamics as a theoretical framework for developing restoration approaches.

I used these ideas in three separate studies as they pertain to two main vegetation types in the Kamiesberg area of Namaqualand, South Africa. These are the Kamiesberg Mountain Renosterveld surrounding the village of Leliefontein, and Hardeveld vegetation surrounding the village of Tweeriver. Both vegetation types are located within the Leliefontein commonage, are subjected to the same disturbance patterns and occur on the same underlying geology with similar soils, but are differentiated by their altitude and rainfall.

In the first study I tested the hypothesis that cultivation had removed and compromised the structure and functioning of patches, and that these features do not improve over time. In each vegetation type, I surveyed a 100 m vegetation transect on four fields in two age classes respectively. The age classes represented fallow lands that had not been cultivated for a period of 7 – 20 years ("young fields") and 30 – 60 ("old fields") years. This was compared to eight, 100 m transects taken from intact communities under two different grazing pressures. These are communal land which was exposed to regular, even daily, grazing and private farms which experience rotational grazing and lower grazing pressure. The transects recorded all perennial species in the growth forms of herbs, grasses, small and medium leaf succulents, stem succulents, and small and medium non-leaf succulent shrubs. The results indicated that passive restoration is not effective in either vegetation type, as fallow fields rested between 7 to 60 years were not distinguishable from each other, suggesting that there had been no improvement over time. The removal of a diverse community through ploughing leads to the establishment by pioneer plants of *Dicerothamnus rhinocerotis* (renosterbos) and *Galenia africana* (kraalbos), with few other species occurring in the landscape. The dominance of these two species persists for decades.

In this first study I also tested the hypothesis that the recovery of vegetation on fallow fields in Namaqualand is hindered by a decline in soil condition and the removal of fertile islands in the landscape. In each vegetation type, on three old fields, and on three intact communities, soil samples were taken from between shrubs (three samples) and from under the dominant patch-forming shrubs (three samples) respectively, to determine the role that plant patches have on the formation of fertile islands beneath their canopies. Results indicate that soil characteristics are substantially altered after cultivation. Even after decades, the levels of organic matter and nutrients in old lands of both vegetation types are lower than in the intact community. In Hardeveld there was evidence that the pioneer shrub, kraalbos, does create a fertile island under its canopies, gradually accumulating organic matter and carbon, but at very low levels. *G. africana* also increased the pH and phosphorus levels beyond levels found in the pre-disturbed system. In Renosterveld vegetation, soils on fallow fields showed no signs of fertile island formation or improvement in soil nutrients.

In the second study, which was undertaken in a greenhouse, I tested the hypothesis that the recovery of fallow fields is hindered by a depleted perennial soil seed bank. In each vegetation type, seedlings that germinated from the top 5 cm of soil collected from beneath and around the edge of 12 plant patches from four land types (young and old fields, and communal and private reference farms) were identified and classed into the same growth forms as listed earlier. The results supported the hypothesis, as the seed bank on fallow fields consisted almost entirely of annuals with kraalbos and renosterbos the only perennial plants to germinate.

In the final study I set up factorial restoration experiments in the field at three sites in each of the two vegetation types, and tested the efficacy of different restoration interventions on perennial species over a three year period. Each treatment contained 45 replicates. The species were grouped into four growth form types: grasses, herbs, leaf succulent shrubs and non-leaf succulent shrubs. In Hardeveld, succulent shrubs and grasses established well, whilst in Renosterveld it was grasses and herbs that were most successful.

The experiment used pioneer plants to establish the original community. The thesis hypothesized that pioneer plants create a fertile island under their canopies and that this could be used to improve seedling establishment success. This was done by sowing seeds in open

control plots and plots where the above ground portion of kraalbos and renosterbos were removed. The results did not support this hypothesis as there was no noticeable benefit to seedlings growing on a fertile island plot as compared to an open area. I also hypothesized that adding fertilizer (nutrients) would increase the success of seedling establishment because this would re-create the more nutrient rich patch environment seedlings would be growing in. Results show that it was only succulent shrubs (Hardeveld) and grasses (Renosterveld) that responded significantly to nutrient addition. The other growth forms had no noticeable benefit. The most unexpected result was that this treatment resulted in a decline of herb seedlings in Renosterveld.

To test the hypothesis that nurse plants or shelters play an important role in restoration success, unsheltered control plots were compared to plots sheltered with brush packs, square boxes or a pioneer nurse plant. Results supported this hypothesis, as box and brush pack treatments were successful in increasing seedling numbers. In the Hardeveld, boxes were very effective for non-succulent shrubs, succulent shrubs, and grasses. In Renosterveld, there was a clear preference by all growth forms for brush pack shelters, whilst the open boxes did not have much influence. Finally, I hypothesized that a nurse plant would facilitate seedling establishment, if there is no competition between the seedling and the nurse plant. Kraalbos, as a nurse plant, provided no noticeable benefit to seedling establishment as they had similar results to unsheltered controls for all growth forms. The only indication of facilitation by a nurse plant was with renosterbos and herb seedlings.

In this thesis, I contribute conceptually and theoretically to our understanding of patch dynamics, by analysing their role in intact systems and how these dynamics recover over time after degradation. Passive recovery of Renosterveld and Hardeveld has not occurred in the vegetation types and areas that I surveyed. Without active re-introduction of perennial seeds to fallow lands seed will not reach these fields. Although soil condition was seen to be improving under kraalbos, the high pH and phosphorous restrict plant growth of the original community. In Renosterveld, the fertile island does not re-form.

Results from this study show that different treatments have different outcomes in different vegetation types. Restoration practitioners should carefully consider the environment they are working in, as well as consider the requirements of different growth forms in restoration planning. Some growth forms establish well initially and focus should be to return these first, in order to improve cost effectiveness. In the Hardeveld succulent shrubs and grasses established well over the three years and in Renosterveld it was grasses and herbs.

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Chapter 1 General Introduction

1.1 Problem statement

Arid and semi-arid regions cover approximately 30 – 40 % of the earth's surface and more than 38% of the global population relies on services provided by these systems *(Maestre et al.*, 2016). Desertification, which is the continuous expansion and increase of drylands, affects millions of people (UNCCD, 2003). Drylands, which encompass dry sub-humid, arid, and semi-arid regions, have been and continue to be, damaged by mismanagement. Most of the degradation is a result of farming practices (Clemente *et al*., 2004). Overgrazing, overcutting for firewood, inappropriate farming techniques, and poor irrigation management are the leading causes of desertification (Bainbridge, 2012). In drylands the dominant land use is grazing (Schmiedel *et al*., 2016) which is also considered as the key driver of biodiversity loss in such areas (Bösing *et al*., 2014). Agriculture has transformed large parts of semi-arid and arid regions (Clemente *et al*., 2004; Hobbs & Walker, 2007), particularly low-lying, fertile land that is suitable for cultivation. Cultivation and grazing can lead to the complete removal of natural vegetation, changes in biodiversity and disruption of vital ecosystem services (Allsopp, 1999). Today, these are some of the most threatened ecosystems (Curtis, 2013).

When agriculture is no longer practiced, the land is left fallow, but it rarely returns to its original state. Passive restoration, where the source of disturbance is removed and natural succession is allowed to occur, has limited success in arid lands. Extreme temperatures, high winds, limited moisture and low soil fertility restrict recovery. The favourable conditions needed for plant re-establishment occur irregularly, and it can take hundreds of years to recover fully. Even after minor disturbances, recovery periods are long (Bainbridge, 2012). The recovery of plant communities in Karoo and Renosterveld is uncommon and a lengthy process, even after the source of disturbance is removed (Heelemann *et al*., 2013; Kemper *et al*., 1999; Midoko-Iponga *et al*., 2005; Whisenant *et al*., 1995), although the details of recovery rates following rest are not well described. The resilience of a system is negatively affected by the removal of vegetation and major functional groups (Suding & Hobbs, 2009), but the ecological processes of degradation, recovery, and succession are poorly researched topics in arid regions (Otto *et al*., 2006). Management interventions rely on an understanding of community dynamics (Zhang & Dong, 2010), and these abandoned fallow lands provide ample opportunities for understanding ecological succession and recovery (Hobbs & Walker, 2007).

The restoration of degraded agricultural fields is encouraged in order to restore biodiversity, improve agricultural productivity, and build resilience in ecosystems (Roberts *et al*., 2012). There is increasing pressure that restoration must be part of land management, but degraded arid and semi-arid vegetation communities respond unpredictably to management efforts (Hobbs & Harris, 2001). Management efforts are also hampered by insufficient ecological understanding of the ecosystem (Bourne *et al*., 2017; Hobbs & Harris, 2001). The knowledge of ecosystem drivers for restoration in Karoo and Renosterveld vegetation communities is limited, which poses problems for land managers.

One of the major limitations to rangeland recovery is the lack of indigenous perennial plant seeds in the soil (Milton 1994), and thus re-introduction via seeding is common practice. However, restoration methods involving sowing seeds have often proved disappointing, because of failed germination or poor seedling establishment (Merino-Martín *et al.*, 2017; Saayman *et al.*, 2017; Swart, 2019). Broadcasting seeds and fertilizer, a common restoration technique is ineffective in semi-arid regions, because it ignores the natural processes and dynamics of arid systems. Seeds require safe and favourable microsites where there is protection from the harsh elements. Restoration practices that mimic natural recruitment processes are more likely to be successful (Galatowitsch, 2008) and calls for better research into factors governing seedling establishment have emerged (Call & Roundy, 1991).

In degraded landscapes, the patch dynamics and associated resource accumulation are absent or severely compromised. Therefore, the resource-rich islands that seeds would naturally establish on are compromised, which affects seedling establishment and growth (Whisenant *et al*., 1995). The restoration of arid lands needs to focus on concentrating scarce resources (water, organic matter, nutrients, and propagules) into patches to improve the micro-climate for seedling establishment. By artificially creating safe sites that provide protection, trap water, sediments, and litter, one may be able to assist in the formation of fertile patches that facilitate the establishment of seedlings. A fairly new concept, and with little evidence published to date, in restoration planning is the use of vegetation to facilitate the establishment of seedlings (Callaway & Walker, 1997; Castro *et al*., 2002; Padilla & Pugnaire, 2006).

1.2 Dryland dynamics in a global context

Drylands occupy 47% of the earth's land surface and are increasing in extent under changing climates (Y. Li *et al*., 2019; Prăvălie *et al*., 2019). Drylands are ecologically distinct areas with low precipitation and therefore little water availability for organisms inhabiting them (M. Verstraete *et al*., 2008; M. M. Verstraete *et al*., 2009). More than 38% of the global population depends on dryland services (Maestre *et al*., 2016). Therefore, desertification, the persistent expansion of drylands, directly impacts millions of people, and has partly been attributed to human activities (UNCCD, 2003).

In South Africa, almost 91% of the land is considered arid, semi-arid, or dry sub-humid (Hoffman & Ashwell, 2001). Degradation and desertification have received substantial of desertification (W.RJ. Dean *et al*., 1995). In order to conserve and restore these landscapes, it is critical to understand the underlying ecological processes of arid regions.

1.2.1 Patch dynamics as an organising concept in drylands

Plants in arid ecosystems have adapted to extreme environmental conditions through various survival strategies and growth characteristics (Ward, 2009). Unlike plants growing in resource rich environments, plants in arid environments generally occupy less than 60% of the available ground surface area (Aguiar & Sala, 1999; Ward, 2009). In arid environments, shrubs often grow together, or are 'clumped', creating a mosaic of patches of plants separated by open, un-vegetated space (Desmet, 2007; Eccles *et al*., 1999). This suggests that certain resources determine where plants can grow, yet the high productivity and diversity of these patches indicate that this mosaic pattern is critical for the functioning of arid systems (Val *et al*., 2020). These plants have access to more nutrients and water from the soil, which in-turn improves the environment under their leaves (Howard *et al*., 2012).

The patch and mosaic pattern are the result of competition and facilitation between plants in environments low in resources (Aguiar & Cipriotti, 2014). The most obvious limited resource in a dry environment is water (Sala & Lavenroth, 1982). However, nutrients also play a crucial role, especially given that arid zone soils have low levels of nutrients and organic matter (Garcia-Moya & McKell, 1970; Watkeys, 1999). Nutrients play a largely underestimated role in the functioning of patches (Carrick, 2001; Austin, 2011). There is a delicate interplay between these two factors, and Grubb (1992) suggested that in semi-arid systems, plants tend to compete for water when it is scarce, and for nutrients and light when water is abundant. In support of these ideas, Carrick (2001) found that in Namaqualand, the survival of most shrub seedlings is determined by the availability of water, but that for some species, such as *Galenia africana* and the succulent shrub *Ruschia robusta*, survival is determined by nutrient availability (Carrick, 2001).

Patches accumulate resources via a number of mechanisms. In windy conditions, the plant canopy traps airborne particles of soil, plant debris, and seeds which are then deposited on the soil under the plants. This process has been recorded for trees that have higher abundances of mycorrhizae,which aid in nutrient uptake, (Camargo-Ricalde & Dhillion, 2003). Plants in the northern Sinai desert accumulate mounds of nutrient rich soil sediment under their canopies (El-Bana *et al*., 2003). In North and South America, exchangeable nutrient concentrations increase (Rostagno *et al*., 1991; Schlesinger *et al*., 1996), and in arid China and South Africa, organic matter and total nitrogen increase in patches (Carrick, 2001; J. Li *et al*., 2007; Stock *et al*., 1999). This trend has also been recorded in Renosterveld, where soil carbon and nitrogen levels are significantly higher under *Dicerothamnus rhinocerotis* (formerly *Elytropappus rhinocerotis*) plants compared to open sites (Mills & Fey, 2004). Leaf litter from the plants within the patch, as well as from outside the patch, is deposited on the soil surface and contributes to higher nutrient levels in the soil (Ludwig & Tongway, 1996). Small animals and arthropods can also contribute to the nutrients in patches due to the decomposition of their faeces, fallen nests and carcass remains which accumulate under plants (Noble *et al*., 2007; Sagi & Hawlena, 2021; Schlesinger *et al*., 1996). Soil micro-organisms on plant roots contribute to higher nutrient levels in the soil below plants (Aguilera *et al.*, 1999). These factors contribute to a greater diversity of microbes in the soil (Bachar *et al*., 2012). Plant roots also extend beyond the canopy (Esler, Cowling, & Eccles 2002) and draw nutrients into the patch, reducing nutrients in the inter-patch space and resulting in an uneven distribution of soil resources across the landscape (Aguiar & Sala, 1999; Schlesinger *et al*., 1996).

Patches also increase water input under their canopies. In semi-arid vegetation types in Australia, Europe, and North America, patches have been shown to store more water and have better infiltration rates than inter-patch areas (Ludwig *et al*., 2005; Vandandorj *et al*., 2016). This is thought to be due to leaf litter accumulation and the presence of biological crusts (Eldridge & Greene, 1994), which increase infiltration rates. Patches also obstruct the flow of water, and organic matter across the soil surface, thereby gaining greater access to moisture and reducing the loss of soil (Ludwig *et al*., 2005). The burrowing activities of small mammals and arthropods help to loosen the soil to improve infiltration (Sagi & Hawlena, 2021). Finally, plants harvest water from fog or mist that condenses on their leaves and falls to the soil below

(C. E. Martin & von Willert, 2002). This process ensures higher productivity and subsequently promotes the persistence of those shrubs in the community (Hook *et al*., 1991; Schlesinger *et al*., 1990; Tongway & Ludwig, 1991).

1.2.2 Islands of fertility and their role in facilitation and competition

This process of resource accumulation under canopies results in 'islands of fertility' or "resource islands" (Garcia-Moya & McKell, 1970; Schlesinger *et al*., 1990), which occur within an area of resource poor 'inter-patches'. The formation of fertile islands is a well-documented concept in semi-arid ecosystems internationally. This has been recorded in North America (Butterfield & Briggs, 2009; Titus *et al*., 2002), in South America (Bisigato & Bertiller, 1999; Camargo-Ricalde & Dhillion, 2003), in Australia (Facelli & Brock, 2000; Noble *et al*., 2007), as well as in Southern Africa (Allsopp, 1999; Carrick, 2001; Lechmere-Oertel *et al*., 2005). However, fertile islands are created by the individual plants in a patch and are not permanent. Once the individual plants which comprise the patch are removed, the levels of nutrients decline over time (Stock *et al*., 1999; Esler, Cowling & Eccles, 2003).

This unequal distribution of resources also influences seed germination, by offering seedlings a variety of potential establishment niches, that can be exploited by seeds with different ecological traits (Harper, 1977). Apart from catching soil particles and organic matter, patches also trap wind-borne seeds as well as seeds from the adult plants within the patch. This in turn increases seed density and the diversity of seeds in the soil (Erfanzadeh *et al*., 2014). In addition, the canopies of adult plants provide shelter from harsh environmental elements and, in combination with the increased water and nutrient accumulation in a patch, create a beneficial environment for seedling establishment (Callaway *et al*., 2000; Valladares & Gianoli, 2007). Adult or 'nurse' plants reduce soil temperature, and increase relative humidity, water and nutrient availability (Saayman *et al*., 2017). They also provide protection from browsing and trampling by animals, allowing seedlings under a canopy to grow faster and more likely to reach adulthood (Callaway & Walker, 1997; Flores & Jurado, 2003). This role of facilitation that plants play for seedlings is important in the structuring of semi-arid plant communities.

This 'nursing' environment is beneficial for the germination of most shrub species. However, in the case of succulent species, 65% prefer to establish in the inter-patch areas (Yeaton & Esler, 1990). In due course, these plants will create new patches (Callaway & Walker, 1997; Milton, 1995b). This has been recorded in the Succulent Karoo, where non-succulent shrubs have their seedlings established under succulent shrub nurse plants (Yeaton & Esler, 1990).

Patch dynamics and their functioning in the Succulent Karoo has been observed and documented (Yeaton & Esler, 1990). However, it is not known to what extent this process occurs in the Renosterveld and, as well as the more arid forms of the Renosterveld. West Coast Renosterveld and some forms of Shale Renosterveld contain thicket like bush-clumps consisting of *Olea europea*, *Searsia laevigata* and *Euclea racemosa* (Rebelo, 1996). There have been no studies dedicated to the topic of patch dynamics, but given Kamiesberg Renosterveld's close affinities to Karoo vegetation, the low rainfall and the high presence of succulents, it is plausible that this type of Renosterveld may function in similar ways to Succulent Karoo vegetation communities. There have been very few studies on nurse plants in Renosterveld. Those studies that have been conducted have focused on the dominant shrub known as renosterbos (*Elytropappus rhinocerotis*), which have shown it to has a nurse plant role for several different species (Allsopp *et al*., 2014; Levyns, 1927; M. Simons, 2017; Walton, 2006).

Although there are benefits to plants establishing in patches, they may also encounter competition for resources with other plants. Competition may be intraspecific, between individuals of the same species, or interspecific, between individuals of different species (Begon *et al*., 1996). Competition between individuals over a common limited resource will lead to a decline in the survivorship and growth of individuals (Begon *et al*., 1996). Whether patches are beneficial or not to seedlings will depend on the balance of positive and negative effects (Callaway & Walker, 1997). The role of competition in patches in resource-limited environments has been a debated topic. Grime (1974) believed that competition is not an important influence on arid plant communities. This notion was thought to hold true in the Succulent Karoo as well, but competition was important in the role of plant communities in the Nama Karoo (Esler *et al*., 1999). However, numerous researchers have contested this view. In arid areas, soil water availability is a critical factor for plant establishment, and as soil water is depleted, competition may become more apparent (Fonteyn & Mahall, 1981) and may regulate the spacing of perennial plants (Milton *et al*., 2003). There is sufficient evidence supporting the notion of competition in the Succulent Karoo, observed among perennial shrubs (Carrick 2003; Esler & Cowling 1993; Yeaton & Esler 1990) and between perennial shrubs and annuals (Dean and Yeaton 1993).

In Namaqualand, competition between succulent shrub species (Carrick, 2003) and between grass and succulent shrub species (Shiponeni *et al*., 2011) has been observed. In Renosterveld, shrub seedling survival was negatively influenced by competition from annuals and grass (Midoko-Iponga *et al*., 2005; Shiponeni *et al*., 2011; Von Hase *et al*., 2003).

Competition and facilitation are important role players in the vegetation dynamics of arid communities (Yeaton & Esler, 1990). Multi-species patches are very common in Namaqualand, indicating that the benefits of facilitation are greater than the costs of competition in these environments (Eccles *et al*., 1999). Plant species are able to co-exist in a niche through resource partitioning, through the pattern of spacing, and through the differentiation of rooting depths (Callaway & Walker, 1997; Carrick, 2003; Cody & Martin, 2014; Yeaton & Esler, 1990). Plant's rooting morphologies allow them to co-exist as some have deep descending taproots whilst others have shallow but lateral roots (Carrick, 2003).

It is therefore clear that patch dynamics influence fundamental ecological processes within ecosystems in arid and semi-arid regions and should be considered in ecological and restoration research (Kruger, 2010; Valladares & Gianoli, 2007).

1.2.3 Disturbance and processes of succession in arid landscapes

Disturbance is regarded as an event that changes resources, disrupts an ecosystem, community, or population structure, alters the physical environment, reduces primary production, lowers the resilience of the ecosystem, and results in the mortality of selective individuals (Rapport & Whitford, 1999). Disturbance is an important cause of variablity in vegetation communities (Midoko-Iponga, 2004). It is a driving element in the evolution of plant life histories, morphology, and defences, and shapes the composition of plant communities (Grime, 1974). Fire, grazing, trampling, burrowing, and digging, as well as human activities such as agriculture and land clearing, are all examples of disturbance.

Over the past 200 years, large parts of the world's arid and semi-arid regions, including parts of Australia, southern Africa, China, and North and South America, have been transformed by agriculture and farming practices (Clemente *et al*., 2004; Hobbs & Walker, 2007). Low-lying, fertile land, especially, has always been the most suitable for cultivation and has been heavily exploited. Due to severe fragmentation, these are some of the most threatened ecosystems today (Curtis, 2013). Cultivation and tilling of the soil results in the complete removal of the vegetation community and impacts the soil in a significant and long lasting way (Allsopp, 1999). These impacts disrupt key ecosystem functions, services, and dynamics. A recurrent or severe disturbance will impede many species from re-colonising an area, especially if return intervals are shorter than generation times which in turn reduces diversity and has the potential to shift the system into states of simplicity, characterized by a shortage of life forms. The removal of vegetation provides space for opportunistic colonisers to move in, some of whom were present in the original community, but were weak competitors. These species are generally characterised by high reproductive rates, relatively short life cycles, and small size (Rapport & Whitford, 1999). Disturbance can reduce water availability as well soil nutrients and organic matter, to a point where vital resources are below the requirements of the original vegetation (Whisenant *et al*., 1995).

However, ecological, social, and economic factors on a global scale have resulted in the decline of cultivation. Fluctuations in the global markets and technological advances to increase production have led to a loss of economic viability and relevance of traditionally produced crops. This, together with the rural-urban migration trend, has depopulated rural areas, leaving vast areas of transformed land to lie fallow (Hobbs & Walker, 2007; Hoffman *et al*., 2018; Scott & Morgan, 2012).

In South Africa's Renosterveld and Succulent Karoo areas, wheat and lucerne are the two most important crops grown (in combination with smaller amounts of oats, barley, and rye) (Hoffman *et al*., 2018), and this region has undergone significant vegetation changes over the past 200 years (Milton *et al*., 1994). During European settlement of Renosterveld areas, there was large-scale removal of shrubs and suppression of fire for cultivation and grazing (Von Hase *et al*., 2003). Cultivation peaked between the late 1940's and early 1970's. South Africa has reflected global trends in declines in agriculture due to increased production costs and other social factors (Schmiedel *et al*., 2010). By the mid 1990's, the cultivated area in Namaqualand had declined by nearly two-thirds (Hoffman & Rohde, 2007), and by 2007 the area under wheat production in the Karoo had declined to around 14%, and by 2002 the area under Lucerne was down to under 30% (Hoffman *et al*., 2018).The Namaqualand Granite Renosterveld, has seen over 20% of its area transformed by agriculture (Helme & Desmet, 2006). The other vegetation type, Hardeveld, has 5 - 6% of the area transformed by cultivation (Hoffman *et al*., 2018; Mucina & Rutherford, 2006). However, in the past, lands on the periphery would also be cultivated for a couple of years and then abandoned, suggesting that the total area of cultivated land since the 19th century is considerably greater than the area of land cultivated in any particular year (Hoffman & Rohde, 2007). This has resulted in many abandoned croplands scattered throughout the Namaqualand landscape (Schmiedel *et al*., 2010).

Croplands are also used for grazing, which increases the total production per unit area, as livestock graze on crop residues, an inexpensive source of feed (Samuels, 2013). In drylands, livestock grazing is the main type of land use (Schmiedel *et al*., 2016) and is also regarded as a key driver of biodiversity loss in such areas (Bösing *et al*., 2014). Herders in Leliefontein have managed to maintain and support large livestock populations for decades (Todd & Hoffman, 2000), but most of the commonage has been degraded by goat and sheep browsing. The commons are surrounded by private farms where livestock farming methods differ greatly compared with those that occur on the commonage. The government administration prior to 1994 gave considerable support to private landowners, who are dominantly white, which has allowed them to stock their farms according to the National Department of Agriculture's recommended stocking rate of 0.1 Small Stock Unit/ ha (Hoffman *et al*., 1999). These farms are often run by a single owner who divides the rangeland into fenced camps and practices rotational grazing, allowing the vegetation periods of rest. In contrast, multiple famers in the communal areas share equal access to the rangeland for their livestock. As a result, communal area rangelands are browsed continuously throughout the year and, on average, are stocked between 1.6 to 1.85 times the governments recommended rate (Todd and Hoffman, 1999, 2009; Hoffman & Aswell, 2001; Nenzhelele *et al.*, 2018). This practice transforms rangelands far more than the rotational grazing practices that occur on private farms, and in Namaqualand has been found to influence plant species composition over time (Anderson & Hoffman, 2007; Nenzhelele *et al*., 2018; Todd & Hoffman, 2009). Continuous browsing grazing contributes to the degradation of both uncultivated and cultivated land in communal areas.

Renosterveld, being part of the Fynbos Biome, is a fire driven ecosystem. Fire plays an important role as a landscape scale disturbance that shapes vegetation communities in this vegetation type. Fire creates gaps in plant communities which provide space for plant establishment and contributes towards maintaining the diversity (Van Der Merwe & Van Rooyen, 2011a). However, post-fire vegetation recovery is poorly documented in Renosterveld (Rebelo *et al*., 2006) and is not known for Kamiesberg Renosterveld.

1.2.4 Novel ecosystems and processes of recovery in drylands

Once agriculture has ceased and the land has been left fallow, the vegetation community that arises may resemble that which existed before agriculture occurred, or it may create an entirely new, novel, or alternative ecosystem. This new ecosystem contains unique abiotic and biotic components with a new complement of species that, due to human influence, differ from those that prevailed historically (Suding & Hobbs, 2009; Perring *et al*., 2013). Cultivation and grazing impacts range from simple losses in vegetation cover, to changes in diversity and complete compositional shifts. The species-rich plant communities of the Succulent Karoo and Renosterveld undergo a shift towards an alternative stable ecosystem which is unlikely to return to its pre-disturbed state without some form of intervention (Hobbs *et al*., 2013; Bosco *et al*., 2018). The alternative state is dominated by annual or more generalized species with similar traits that are more tolerant to disturbance, as wel as increased bare ground cover (Bosco *et al*., 2018, Redhead *et al*., 2018).

In the Succulent Karoo, there is a significant shift in the vegetation of communal rangelands towards a more ephemeral community (Milton, 1995; Anderson & Hoffman, 2007; Nenzhelele *et al*., 2018). There is a reduction in biomass, with vegetation composition and cover becoming increasingly homogenous (Hoffman & Cowling 1990; Hoffman & Cowling 1991). In Namaqualand, the original vegetation, which is dominated by perennial and palatable plants, changes to a community dominated by less palatable plants and those with annual life histories (Todd and Hoffman, 1999; Anderson & Hoffman, 2007; Nenzhelele *et al*., 2018). In the Renosterveld uplands, disturbed areas are dominated by *Dicerothamnus rhinocerotis* (renosterbos) and in the lower-lying areas by *Galenia africana* (kraalbos). In the interstices between the two dominant species, a wide vaireity of annuals and short lived plants occur. This is consistent with grazing impacts experienced more generally in the drylands of Southern Africa, where an increase in annual plant richness occurs after grazing occurs (Rutherford *et al*., 2012; Hanke *et al*., 2014). In Namaqualand, the impact of different stocking rates has been demonstrated, whereby low stocking rates allow the vegetation to support animal numbers, while heavy stocking rates over decades result in greater variability in biomass between years. The perennial plant-dominated ecosystem (equilibrium) is transformed into an annual forb-dominated ecosystem (disequilibrium). This is enabled by the large pool of annual species that are successful colonisers of disturbed rangelands (Nenzhelele *et al*., 2018). The complete removal of vegetation, the loss of major functional groups, and changes in diversity negatively affect the resilience of the ecosystem (Suding & Hobbs, 2009).

Renosterveld has been extensively transformed by agricultural activites (Kemper *et al*., 1999). Historically, grazing was localised by indigenous herbivores and fire frequency was variable (Cowling *et al*. 1986). Following settled agriculture, the fire and grazing disturbance regime has changed. Deliberate burning of Renosterveld has occurred to promote grazing for livestock and wildlife in parks (Kraaij, 2010). There are indications that the fire regime in Kamiesberg Renosterveld was around 4 years (Simons, 2017), followed immediately by grazing. However, this has weakened the competitive ability of grasses, making it possible for renosterbos shrubs to establish (Radloff *et al*., 2014) quickly due to the ability of its seedlings to colonise disturbed areas and grow rapidly once established (Van der Merwe & Van Rooyen, 2011).

The recovery of perennial plant communities in the Karoo and in Renosterveld is uncommon and may take decades. Removing the source of the disturbance may also not result in improvement in either of these vegetation types (Whisenant *et al*., 1995; Kemper *et al*., 1999; Midoko-Iponga *et al*., 2005; Heelemann *et al*., 2013), particularly since water is a limiting factor to re-vegetation (Von Hase *et al*., 2003), and saline soils delay vegetation recovery (Milton *et al*., 2003). The persistence of kraalbos and renosterbos indicates that rest from grazing alone is not enough to restore landscapes that have been greatly transformed (Radloff *et al*., 2014; Saayman & Botha, 2008; L. Simons & Allsopp, 2007), although the details of recovery rates following rest are not well described. The most notable example of slow recovery is from the pre-European sheep kraal sites of indigenous herders, which have remained un-vegetated and eroded for the last 250–300 years (Milton & Dean, 2015). Secondary succession of old fields in Namaqualand is slower than on grasslands (van Rooyen, 2002; Hongslo *et al*., 2009). For example, in the Namaqua National Park (NNP), van Rooyen (2002) found that secondary succession on old fields proceeds very slowly, and that these plant communities are still clearly distinguishable from those in natural, unploughed areas 50 years after the area has been ploughed. This is similar to findings from the Goegap Nature Reserve (Allsopp, 1999). The only study to record that vegetation on an old field, which had lain fallow for 80 years, resembled intact vegetation was in NNP (Schmiedel *et al*., 2010). However, it should be noted that this field was inside a protected area and was not exposed to continuous grazing, as is the case for rangelands in commonage areas.

The slow recovery of Renosterveld is in line with other Mediterranean-type ecosystems (Krug & Krug, 2007). In Overberg Renosterveld, natural recolonisation of old fields is very slow, with some species never recovering, even after 30–50 years (Von Hase *et al*., 2003), and the trajectory of secondary succession is not straight forward (Cowan & Anderson, 2019). However, in the West Coast region of Renosterveld, old lands of 30 years are reported to be similar to unploughed lands (Walton, 2006). In Roggeveld Mountain, Renosterveld, annuals and small woody shrubs dominate throughout the phases of succession (Van der Merwe and Van Rooyen, 2011). These types of Mediterranean ecosystems have low resilience to major disturbances, and recovery cannot be foreseen in the short term (Du Toit, 2011).

Several factors affect the rate of recovery of old fields. Recovery depends on rare rainfall events that promote flowering, seeding, germination, and seedling survival (Beukes & Cowling 2003, Botha *et al*. 2008). Bare soil, loss of organic matter (Milton *et al*., 1994), competition from dominant herbaceous plants and continuous browsing (Midoko-Iponga *et al*., 2005) hinder perennial vegetation's ability to recover. In some Renosterveld areas, nutrient enrichment from commercial agriculture is followed by the invasion of competitive alien grasses (Sharma *et al*., 2010; Heelemann *et al*., 2013; Low, 2015). Other factors include the number of times the area was ploughed, the time since the area was last ploughed, as well as soil fertility, climate, and grazing history (Milton, 1995; De Villiers *et al*., 2003; Botha *et al*., 2008). However, one of the most significant barriers to recovery is the lack of indigenous seeds in the soil of old fields (De Villiers *et al*., 2003; Shiponeni, 2003; Midoko-Iponga *et al*., 2005; Saayman and Botha, 2008) and no patches, obstructions, or means to trap seeds. The proximity of the disturbed area to intact, unploughed vegetation, from where seeds can disperse and from where colonisation can begin, is compounded by the limited seed dispersal properties of the dominant shrub species (van Rooyen, 2002; Hongslo *et al*., 2009).

The loss of vegetation is well documented, but the role of seed limitation as a driving force for retaining habitats in a degraded state is not (Suding & Hobbs, 2009). Soil seed banks play a vital role in rebuilding biodiversity and increasing the resilience of plant communities after disturbance (Donnell *et al*., 2014), but can be destroyed by extreme events (Suding and Hobbs, 2009). Only a few studies on the seed banks of old fields and neighbouring native vegetation have been done in Renosterveld, and these showed depleted seed banks and low recovery potential of old fields (Saayman and Botha, 2008; Heelemann *et al*., 2013). Lastly, an important factor influencing vegetation recovery is current land-use practices (Kellerman and van Rooyen, 2009). Continual subjection to grazing means these fields remain barren and dominated by unpalatable shrubs (Hoffman & Rohde, 2007).

1.3 Restoring dryland ecosystems

The need to restore agricultural land to a state of ecological functioning, increased biodiversity, and with the ability to provide forage for wildlife and domestic animals has become desirable in recent years (Gabriels *et al*., 2003; Huber-Sannwald & Pyke, 2005; Schmiedel *et al*., 2010; Simons & Allsopp, 2007). The restoration of abandoned fields will also increase the sizes of fragments and establish links among fragments (Krug, 2004b).There is increasing pressure that restoration must be part of land management, but it is hampered by insufficient ecological understanding in each region or ecosystem (Bourne *et al*., 2017; Hobbs & Harris, 2001). The challenge for restoration ecologists and land managers is that due to the scale of degradation and the economic cost, restoration of arid and semi-arid land is not attractive. There is also the lack of policies, lack of political will, and the challenge of finding cost effective techniques that are labour intensive (Bourne *et al*., 2017; Mills *et al*., 2007; Milton *et al*., 2003). In countries such as South Africa this provides opportunities for employment, skills development, ecological monitoring and research (Aronson & Vallejo, 2006; Le Maitre *et al*., 2009; Roberts *et al*., 2012). The aim is to initiate recovery that does not require constant management (Whisenant *et al*., 1995).

Ecological restoration is the process of assisting the recovery of an ecosystem by increasing structure and function (Society for Ecological Restoration International Science & Policy Working group, 2004). The aim is to provide the ecosystem with sufficient biotic and abiotic resources for it to be able to recover with little further assistance. Restoration is not simply about changing species numbers or diversity, but requires the return of function, as well as resilience to fluctuations in environmental conditions (Hobbs & Walker, 2007). With the absence of these elements, restoration efforts do not result in long term success (Kruger, 2010). The ecological concepts described here are universally found in semi-arid ecosystems, and they provide the context for more specialized research to be conducted.

In order to create restoration goals, ‘reference ecosystems’ are used. This consists of using land that has not been degraded as a model to refer to, in combination with gathering information from other locations and other sources such as historical accounts, aerial photography, and herbarium specimens (Hobbs & Harris, 2001; Society for Ecological Restoration International Science & Policy Working Group, 2004). It also needs to be recognised that there could be a range of possible short and long term outcomes after the implementation of restoration projects (Perring *et al*., 2013; Suding & Hobbs, 2009), and that there is no fool-proof recipe for restoring arid areas within a matter of decades (Milton & Dean, 2015).

The concept of returning the natural vegetation is well-intentioned, but needs careful consideration, and must be based on an understanding of the ecosystem processes that shaped the ecosystem (Suding & Hobbs, 2009; Von Hase *et al*., 2003). Using locally adapted plant species and maximizing the effectiveness of rainfall is key for the recovery of natural vegetation (Carrick & Kruger, 2007; Coetzee, 2005; Tinley & Pringle, 2014).

In general, restoration methods have aimed to reduce competition from existing pioneer vegetation by eradicating them, in order to promote the establishment of favourable species (Gómez-Aparicio, 2009; Huber-Sannwald & Pyke, 2005). However, removal of these pioneer shrubs entails a great deal of time and effort and can actually decrease the success of the project and create an even greater restoration shortfall. This is because it has ignored the principle that later succession species often require the cover of a pioneer plant, as discussed earlier with the principles of facilitation (Kruger, 2010). The complete removal of all pioneer vegetation is in itself a form of degradation that will shift the landscape into another novel system (Morris *et al*., 2011). This system will have less structure and function than the previous one, and thus have more threshold barriers to cross on its road to recovery. An attempt to restore desert grasslands in the southwest United States is an example of this scenario. Extreme attempts, with the use of a bulldozer and herbicide, were made to remove shrubs, but this failed in the long term, because the cause of the initial invasion of shrubs was not considered (Rapport & Whitford, 1999). Methods have changed recently to encourage retaining some woody plants and inter-seeding grasses (Huber-Sannwald & Pyke, 2005).

1.3.1 The role of patch dynamics

One of the major limitations to rangeland recovery and plant establishment is the lack of indigenous perennial plant seeds in the soil (Milton, 1994) and ecologists cannot rely on the seed bank for recovery of sites. Colonisation from natural areas is usually very slow and cannot be relied on (Esler, 1999; Holmes & Richardson, 1999). Introducing seeds of preferred perennial species artificially by seeding is common practice (Epanchin-Niell *et al*., 2009; L. M. Martin & Wilsey, 2006) and should be seen as a vital first step of restoration. This has been noted in several Namaqualand studies (Bourne *et al*., 2017; Carrick & Kruger, 2007; Simons, 2005). This will help to restore back the species diversity, abundance, cover, and biomass, improve the ecological stability, and re-establish the ecological structure and functioning of the area (Bertiller & Carrera, 2015; Seymour *et al*., 2010). Shrub re-establishment in particular on an abandoned field, is vital, because shrubs provide important ecosystem services and functions (Porensky *et al*., 2014). Sowing seeds of herbaceous species will be necessary for successful revegetation in parts of Namaqualand (De Villiers *et al*., 2002).

However, restoration methods involving the sowing of seeds have often proved disappointing, because of failed germination or poor seedling establishment (De Malach *et al*., 2014; Hanke *et al*., 2011; Merino-Martín *et al*., 2017; Saayman *et al*., 2017; Swart, 2019). This could be due to a number of factors, such as insufficient rainfall, incorrect timing of seed sowing in relation to rainfall, seed predation, competition from pioneer plants, or poor seed quality (Milton, 1995b; Porensky *et al*., 2014; Saayman *et al*., 2017). A common problem with reseeding efforts is that agricultural techniques are applied to restoration activities, whereby seeds and fertilizer are broadcast. In most semi-arid regions, this practice is wasteful as the majority of the seeds require safe and favourable microsites and will thus not establish when spread widely over the landscape. Broadcast seeds and seedlings are usually exposed and vulnerable to desiccation, wind erosion, temperature fluctuations, and predation (Swart, 2019).

Seedlings have different biotic needs to those of adult plants, which poses a major constraint for plant regeneration in the landscape (Bertiller & Carrera, 2015). Restoration practices that mimic natural recruitment processes are more likely to be successful (Galatowitsch 2008). Before the 1990's, research emphasized the establishment of vigorous exotic grasses on arid rangelands instead of biologically diverse plant communities, and calls for better research to understand factors governing germination, seedling establishment, and plant community development began to emerge (Call & Roundy, 1991). Active intervention may be needed to provide suitable microsites (Bosco *et al*., 2018; Morris *et al*., 2011), via the use of mulching or brush packing (covering the soil surface with woody branches that have been collected). These actions increase seedling survival in the Karoo (Saaed *et al*., 2018; Saayman *et al*., 2017; Saayman & Botha, 2008; Simons & Allsopp, 2007). Prioritizing where and how these seeds are sown may improve efficiency (Davies *et al*., 2020; Swart, 2019).

The patch dynamics of resource distribution in an area are absent or severely compromised in degraded landscapes. The plants present on these sites are likely pioneer or early succession plants and probably do not create long-lived, heterogeneous patches in the landscape (Stock *et al*., 1999). Grazing also results in the loss of perennial shrubs and their associated resource patches. The resource rich islands that seeds would naturally establish on are compromised, which in turn affects seedling establishment and growth (Whisenant *et al*., 1995). The restoration of arid lands needs to focus on concentrating scarce resources (water, organic matter, nutrients, and propagules) into patches and fertile islands, to establish keystone species and improve the micro-climate for plant establishment. It is also essential to prevent resource loss (Whisenant *et al*., 1995).

Water is the easiest resource to gather, and since it transports organic matter, soil particles, and nutrients, effectively collecting it can greatly assist in creating resource patches. Restoration trials in the Karoo have attempted various ways to increase water infiltration and retention. Examples are ripping, digging of hollows, brush or stone packing, mulching, use of erosion mesh and vegetation "sieves" to slow down runoff water and trap seed (Snyman, 2003; Visser *et al*., 2004; van den Berg & Kellner, 2005; Simons & Allsopp, 2007; Burke, 2008). Harvesting methods like pitting and contour furrowing have short-lived benefits. The use of micro-catchments for water collection is far more effective. Simple manipulations in the soil topography allow water to collect in depressions or catchments. Slight soil disturbance, or loosening of the soil, is needed, and has been effective in the restoration of kraalbos dominated fields in the Cederberg (Saayman *et al*., 2017). These catchments can range in size from large 0.4 ha circular ridges found in New South Wales Australia (Thompson, 2008) to smaller micro-catchments found in the Negrev Desert (Whisenant *et al*., 1995). In the uplands of Namaqualand, 0.3 m^2 micro-catchments constructed on severely overgrazed rangelands were effective in collecting higher amounts of organic matter, which resulted in higher rates of natural recruitment (Simons, 2005).

By artificially creating safe sites that trap water, sediments, and litter, one may be able to assist in the formation of fertile patches that facilitate the establishment of seedlings. These structures may act to capture resources and provide protection without seedlings competing with the nurse plant for resources. The use of plant debris was effective in increasing soil water moisture and plant growth in Australia (Ludwig & Tongway, 1996); in the Karoo (Beukes & Cowling, 2003); and near Steinkopf in Namaqualand (Bourne *et al*., 2017), although Simons (2005) found that this method was ineffective near Paulshoek in Namaqualand.

1.3.2 Use of nurse plants

Adult plants alter soil resource distribution in degraded landscapes, but this is a gradual process that occurs over the lifetime of a plant (Stock *et al*., 1999). In a harsh environment, sowing seeds into exposed soil limits germination, but using pioneer shrubs together with seed sowing could be effective (Mills *et al*., 2007). Shrubs capture windblown organic materials, nutrients, and soil microorganisms (Suding & Hobbs, 2009; Whisenant *et al*., 1995). Pioneer shrubs can reduce seed lost to wind and animals, and can be used as nurse plants that provide protection to seeds from the harsh conditions (Aguiar & Sala, 1999; Callaway, 1995; Saayman *et al*., 2017). The use of vegetation to facilitate the growth of other plants in dryland and Mediterranean ecosystems has been considered in restoration planning (Callaway & Walker, 1997; Castro *et al*., 2002; Padilla & Pugnaire, 2006), but is a fairly new concept, with little published evidence to date (Padilla & Pugnaire, 2006). In Spain, nurse plants were found to decrease seedling mortality in mountain pines (Castro *et al*., 2002). In semi-arid China, higher seedling densities were attributed to improved organic matter, soil moisture, and levels of nitrogen and phosphorus (Zhoa *et al.*, 2007). In the U.S. sagebrush survival increased by 40% in former canopy microsites (Davies *et al*., 2020). On mine rehabilitated sites in Namaqualand, seedling emergence was higher under transplanted shrubs but not significantly so (Schmidt, 2002). Established vegetation such as kraalbos and renosterbos, although undesirable, could provide favourable germination microsites, as opposed to seeding in barren, vegetation free areas (Carrick, 2003; Merino-Martín *et al*., 2017; Simons & Allsopp, 2007). It has been reported that renosterbos could function as a nurse plant for geophytes, herbs, dwarf shrubs, and perennial grasses (Walton, 2006). Allsopp (1999) indicated that kraalbos does create a fertile island which can be used to facilitate the re-establishment of the original community without the need for expensive soil intervention. Overall, seeding trials in arid areas have not recognised the importance of patch dynamics in the functioning of natural ecosystems.

In conclusion, understanding the intricate relationships between abiotic factors and the needs of different plant traits at the microsite scale is important (Bertiller & Carrera, 2015; Bosco *et al.*, 2018). Researchers are striving to improve the efficiency and effectiveness of dryland restoration (Bourne *et al.*, 2017; Carrick & Kruger, 2007; Erickson, 2015; Erickson *et al.*, 2016; Madsen *et al.*, 2012; Turner *et al.*, 2013).

1.4 Thesis overview

1.4.1 Research themes and objectives

The focus of this thesis is on the vegetation dynamics of the low-lying Hardeveld of the Succulent Karoo and the uplands of Kamiesberg Renosterveld (Ladislav *et al.*, 2006). The aims of this thesis are to understand the impact of cultivation, how secondary or passive restoration occurs, and whether it is effective; as well as to asses the effectiveness of active restoration interventions. The latter has been doen with a view to inform the drafting of feasible, landscape-scale ecological restoration strategies for the two vegetation types.
as well as to grow the knowledge base of ecological restoration for these ecosystems. The core hypothesis of this thesis is that in arid ecosystems, the concentration of scarce resources (water, organic matter, nutrients, and propagules) into patches and fertile islands is essential to the functioning of these ecosystems. The key objectives of this thesis are based on broad ecological concepts and are therefore applicable to both local and other semi-arid ecosystems. The objectives are:

1. To understand the role and efficacy of passive restoration and why it might not work (chapters 2 & 3);
2. Explore the value of patch dynamics as a theoretical framework for developing restoration approaches to arid and semi-arid ecosystems (chapter 4)

Chapters 2 and 3 explore the following two hypotheses, that a) cultivation destroys these patches and the associated underground fertile island, and b) that passive recovery and establishment of vegetation on old fields is hindered by a lack of suitable fertile patches and poorer soil quality. In order to understand the impact of grazing and the possible trajectory of recovery, a good understanding of the pre-disturbed community is required, which includes the influence of grazing pressures on the vegetation. The approach taken in this study is to attempt to understand the impact of cultivation, and the possible process of succession through a patch dynamics model. Studying dynamics on lands with known ages since abandonment has proved an effective tool to understand the sequence of succession (Hobbs & Harris, 2001). An analysis of patches and their associated fertile islands at certain sites allows for a comparison of the abundances of plants and soil dynamics of patch and inter-patch areas. Chapter 3 also explores the hypothesis that the recovery of cultivated fields is further restricted by a depleted perennial soil seed bank. Sites for these chapters were selected from intact remnants under two different grazing pressures and fallow fields (ranging in age from 7 to 60 years since abandonment) and were compared to each other. A number of key questions were formulated and can be largely broken into three main sections:

1) How do the vegetation, seed bank, and fertile island function in patches in the intact community
2) The effect of cultivation on soil properties, vegetation community composition, and the composition of the soil seed bank
3) is the vegetation which establishes on old fields assisting in the ecosystem recovering to a natural state and is this vegetation also creating fertile islands

The aim of chapter 4 is to inform restoration efforts of cultivated lands via the reintroduction of seeds of perennial plant species. Many seed based restoration projects in arid areas have provided disappointing results, which leads one to question if these strategies are still applicable for the future. The restoration of arid lands needs to focus on concentrating scarce resources into patches and fertile islands, to establish keystone species and improve the micro-climate for plant establishment (Whisenant *et al*., 1995). The experiment consisted of re-creating and mimicking aspects of patch formation and structure, with the use of natural and artificial structures, nutrient addition and living nurse plants, to explore the response of different plant growth forms to different microhabitats. I hypothesized that different growth forms' recruitment rates would respond differently to abiotic scenarios.

The dominance of kraalbos and renosterbos on fallow lands poses another, potentially costly, obstacle to restoration. However, these plants are also a feature that can be exploited. I hypothesized that by using the resource islands and former shrub canopies created by these unwanted dominant plants, the establishment of a diversity of perennial sown seedlings would be greater on resource island patches, than on inter-patch (open) microsites.

A variety of different sheltering structures, which included adult shrubs (nurse plants) of kraalbos and renosterbos as well as artificial shelters, such as cardboard boxes and brush packs, were analysed for their effectiveness on seedling establishment. I predicted that the establishment of seedlings would be greater in sheltered micro-sites than in unsheltered micro-sites. Nutrients are a limited resource in arid areas, and I hypothesised that seedling establishment would be increased by the addition of nutrients.

1.4.2 Thesis structure and outline

This thesis has been divided into five chapters. This first chapter is devoted to a broad literature review on the ecology of arid ecosystems, and introduces the Renosterveld and Succulent Karoo vegetation types including the regional context and historical influences. Literature supporting the rationale behind Chapter 2 (Community dynamics and post-cultivation succession), Chapter 3 (Seed bank dynamics and post-cultivation succession) and Chapter 4 (Restoration of post-cultivated fields) is presented in each of the respective chapters.

Chapters 2 and 3 endeavour to understand the impact that cultivation and extended fallow periods have had on the two vegetation communities in the upland and lowland environments of the Kamiesberg. These chapters investigate the secondary successional processes occurring on fallow fields ranging in age from 7 to 60 years since abandonment. It compares above ground vegetation, soil seed bank composition, and the soil properties of intact or unploughed remnants of Karoo and Renosterveld vegetation with that of fallow fields.

Through the collection of soil samples, the first aspect of Chapter 2 focuses on the effect of cultivation on the physical and chemical properties of the soil, the role that plant patches have in the formation of fertile islands beneath their canopies in intact, uncultivated vegetation; and whether pioneer plants that establish on old fields also create fertile islands. Chapter 2 uses vegetation surveys to assess the effect of cultivation on vegetation community composition and dynamics over time in relation to intact, uncultivated land on both communal and private land. Chapter 3 consisted of a greenhouse study to determine the impact that cultivation has had on the composition and dynamics of the soil seed bank by comparing it to seed banks of intact, uncultivated land subjected to different grazing pressures.

Chapter 4 focuses on the in-field experimentation, which tested the role of patch dynamics on seedling recruitment responses to 13 different restoration interventions (including the control). Given that large-scale removal of pioneer plants is costly, this thesis explored the notion that these unwanted pioneer shrubs can be used to recreate patches to facilitate the establishment of diverse perennial plant communities. Potential benefits of patches such as facilitation, provision of nutrients and physical shelter provided by nurse plants were linked to seedling establishment. The impact of competition between nurse plants and seedlings was also explored. The interventions are substitutes for ecological drivers of recruitment in patches in arid areas and include the creation of micro-depressions, seeding, and addition of fertiliser, physical shelter provided by two different types of structure and seeding under a living pioneer plant. Understanding seedling ecology is valuable in developing guidelines for restoration interventions. Recommendations for restoring cultivated fields in this region, based on findings from this study are discussed.

Chapter 5 provides the study synthesis by highlighting the key findings and giving recommendations for future research and implementation of restoration of the uplands and lowland communities of the Kamiesberg in Namaqualand. The findings of this thesis can be applied locally and to other semi-arid ecosystems, since they are based on broad ecological concepts.

1.5 Description of the study area

1.5.1 Introduction to two vegetation types along an altitudinal gradient

Namaqualand is located in the Northern Cape Province of South Africa and comprises about a quarter of the Succulent Karoo biome (Figure 1.1). The research in this thesis was conducted in the Kamiesberg area of Namaqualand. The Kamiesberg mountain range links the lowland coastal plains in the west, to the start of the interior plateau to the east. The highest point of the mountain range is the Rooiberg peak (reaches 1706m), which is also the highest point in the broader Namaqualand region. The land above the 1200 m contour is defined as the Kamiesberg Centre (KBC), one of several foci of high endemism within the Succulent Karoo (Helme & Desmet, 2006; Van Wyk & Smith, 2001).

The study area for this thesis is located within the Leliefontein Communal Area of Namaqualand. This area straddles the Kamiesberg range, and contains Fynbos (on the high peaks), Renosterveld (on the flatter plateaux) and Karoo vegetation (on the escarpment and low-lying areas) in close proximity to each other. The Leliefontein communal area comprises some 192 000 ha, and spans the Kamiesberg mountain range in an east-west band of about 50 km. It is one of six communal areas (formerly known as Coloured Reserves under the apartheid government of South Africa before 1994) in Namaqualand. The Leliefontein communal area is divided into 10 unfenced village commons. There are 77 adjacent private farms with an average size of 1 615 ha (Samuels, 2013). Villages located in the lowlands (altitude about 250 m above sea level) are Spoegrivier, Kheis, and Klipfontein. In the uplands near the village of Leliefontein, the altitude is about 1 350 m above sea level. The villages of Kharkams, Tweerivier, Nourivier, and Paulshoek villages are located on the Kamiesberg escarpment

1.5.2 Land use

In Namaqualand, private farms occupy 52% of the area and communal lands occupy 30% of the area (May & Lahiff, 2007). On private farms, meat from livestock farming is for national and international agricultural markets. Animals are managed by practices that were promoted to white farmers through subsidies from the 1950s onwards, whereby multiple enclosures, or ‘camps’, are used to rotate grazing animals. Communal tenure in the Northern Cape consists of municipal commonages, owned by local municipalities, as well as six historic communal areas, held in trust by the Minister of Land Affairs and serviced by local municipalities (Samuels, 2013). In municipal commonages, a fenced camp is rented out to an individual or a group of farmers, but as all the camps are rented out at the same time, farmers cannot practice rotational grazing (Samuels, 2013). Between 1974 and 1997, the six communal areas were stocked at 1.6 times the recommended stocking rate (Northern Cape Veterinary Services, Unpublished data). Small stock herds are often concentrated at stockposts scattered around the rangeland. This is a common practise in the communal areas of Namaqualand (Hendricks *et al*., 2004).

Dryland cropping comprises 12 % of the total area, with cropland units or ‘sowing plots’ (Afrikaans: ‘saaipersele’) ranging from less than 1 ha to 302 ha in size (Samuels, 2013). An annual rental fee is paid to retain access rights to the unit. Currently, the majority of these sowing plots are not actively used, but the right is customarily inherited by a family member (Samuels, 2013). Crop farming in the area is constrained by low rainfall, and farmers will usually only sow and plough if there have been good rains by August, with harvesting occurring in early December. After harvesting, croplands are generally regarded as open grazing land and around 80% of croppers own livestock. Oats is the most commonly crop grown while wheat is cultivated on a relatively small scale. Other crops grown are barley, rye and lucerne, but these are grown mainly for livestock fodder (Samuels, 2013). Other land-use activities in the communal area include firewood harvesting, medicinal plant collection, harvesting of reeds to build traditional reed mat houses and food gardening.

1.5.3 Climate

Namaqualand falls within a typical winter (May to September) rainfall area, with an extended summer drought period. Rainfall in Namaqualand is unique in that it is predictable (Hoffman & Cowling, 1987) relative to other winter rainfall regions (Esler & Rundel, 1999), and follows both an altitudinal and west-east gradient. The Kamiesberg mountain receives orographic rainfall, resulting in relatively moist western and upper slopes (Anderson *et al*., 2010). Rainfall ranges from about 126 mm MAP (mean annual precipitation) in Garies at 200 m, to 160 mm in Tweeriver at 600 m, with periodic droughts (well below 100 mm per year) of one or two years in succession. Leliefontein at 1350 m receives 380 mm MAP (South African Weather Service Unpublished data). The unrelenting southern breeze off the cold Atlantic Ocean that dominates the coastal climate of Namaqualand has a significant effect of moderating the temperatures of the south-west facing slopes for the majority of the year. The occurrence of dew and fog which occur as a result of this oceanic influence contribute to the predominant west-east moisture gradient (Helme & Desmet, 2006).

Apart from increasing moisture, the altitude of the mountain results in cooler average temperatures on the plateau than the surrounding areas. Summer maximum temperatures are high, even on the upper plateau, and many days are over 30 °C, with occasional peaks of over 40 °C. In winter and spring, strong easterly berg-winds rapidly raise ambient temperatures and lower humidity (Helme & Desmet, 2006).

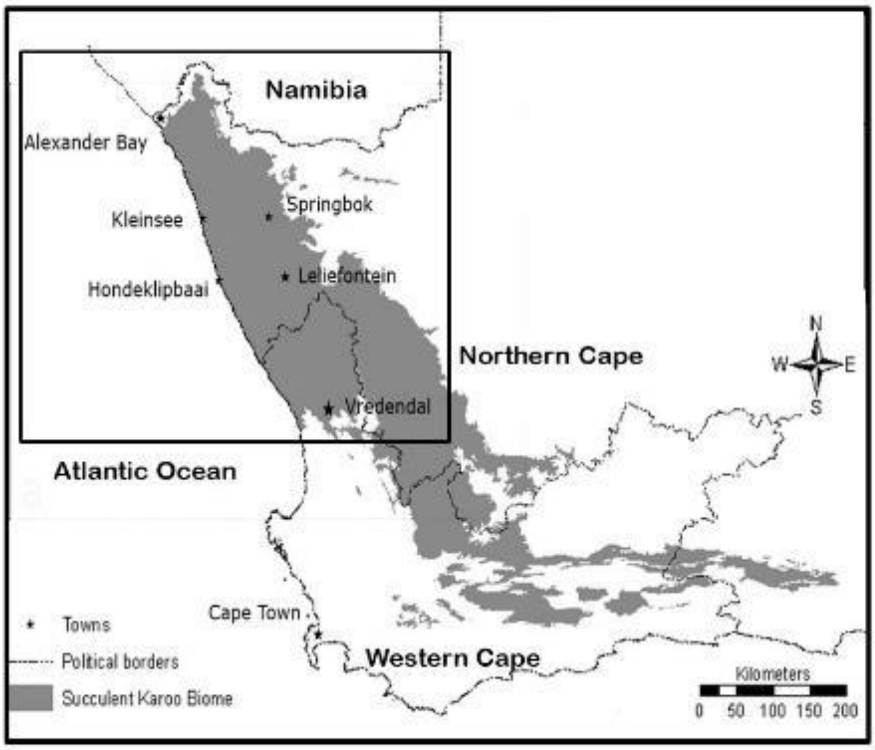


Figure 1.1 Extent of the Succulent Karoo biome within South Africa, showing the location of the study sites near Leliefontein within the context of Namaqualand (box)

On the escarpment around the village of Tweeriver mean annual winter temperature is 16 °C. Minimum daily temperature from June to August spans 3 – 5 °C. Summer temperatures (December to February) may exceed 40 °C, particularly in the lower-lying areas. Mean maximum daily temperature from January to February range 29 – 32 °C (Ladislav *et al*., 2006). On the plateau, around Leliefontein village, the mean annual winter temperature is 10 °C. Minimum daily temperature from June to August spans 2 – 4 °C and snow falls on average once or twice a year, mainly above 1200 m, with occasional sleet. In summer the mean maximum daily temperature range is 24 – 28 °C.

1.5.4 Soils and vegetation

The Kamiesberg consists of a large granite-gneiss intrusion is surrounded by relatively uniform red and yellow, free draining, variably grained, sandy to loamy, weakly-structured apedal soils, derived from underlying granites and gneiss (Cowling *et al*., 1999; Watkeys, 1999). The deepest soils (sandy loams) are found in the valleys and on the plateau, where fine-grained silts may accumulate. As is typical in the more arid areas of South Africa, the A horizon is orthic (lack of organic, humic topsoil), free from waterlogging and is typically very sandy (W. Dean & Milton, 1999).

The study area forms part of the Succulent Karoo and Fynbis Biomes. The Succulent Karoo biome, which is a recognized biodiversity hotspot of global significance. Namaqualand contains 75% of the plant species in the biome (Cowling & Pierce, 1999). The Kamiesberg is host to a number of different vegetation types, but this thesis focuses on the two vegetation types surrounding the villages of Tweeriver and Leliefontein (Figure 1.2). One of these vegetation types includes Renosterveld, which is one of the most threatened vegetation types in South Africa and is also one of the least understood vegetation types (Jacobs & Jangle, 2008). Kamiesberg Mountain Renosterveld is replaced by Fynbos at a higher rainfall and altitude, and by Succulent Karoo at lower rainfall and altitudes. However, there is a complex relationship between elevation and rainfall, resulting in patches of Renosterveld occurring as low as 800 m and above 1200 m (Helme & Desmet, 2006).

Renosterveld has a complex classification history. It is mostly classed as part of the Fynbos biome (Rebelo *et al*., 2006) , as both Fynbos and Renosterveld are subject to recurring fires and therefore fire adapted, with the frequency, season, intensity and size of fires being important determinants of species composition, vegetation structure and successional patterns (Kraaij, 2010). However, floristically and ecologically Renosterveld is quite different from Fynbos. The fundamental difference is that Renosterveld is a fire-prone shrubland occurring on nutrient-rich soils, whilst Fynbos is fire-prone shrubland occurring on nutrient-poor soils. Renosterveld is divided into two broad groups based on their geographical distributions -West Coast Lowland Renosterveld and Mountain Upland Renosterveld, and both contain several different types of Renosterveld communities within themselves (Rebelo *et al*., 2006). Fire ecology has been researched in Fynbos, but little is documented on the fire regimes in Renosterveld and there is virtually no peer reviewed literature on desirable fire intervals (Bond *et al*., 2004; Curtis, 2009; Kraaij, 2010). The natural fire frequency for Mountain Renosterveld is undefined, but a study by Simons (2017) in Kamiesberg Renosterveld suggests that a fire frequency of seven years is beneficial for forage production and biodiversity. This is similar to the fire management cycle of no less than eights years in Overberg Renosterveld in Bontebok National Park (Kraaij, 2010), whilst findings on Roggeveld Mountain Renosterveld found that vegetation condition declines after ten years (Van Der Merwe & Van Rooyen, 2011a). Kamiesberg Renosterveld is classified as part of the granite Renosterveld group, whilst most other Renosterveld vegetation units occur on shale. Granite Renosterveld contains only three units which occur in the Kamiesberg, Swartland and Robertson area. All three of these units are quite distinct and unrelated to one another (Mucina

& Rutherford, 2006). The Renosterveld in this study falls within the more arid zone of Renosterveld distribution, receiving approximately 380 mm per year, whereas other Renosterveld vegetation types receive well over 400 mm per year.

In the literature, Renosterveld is distinguished from the Succulent Karoo because it is fire-prone (Bergh *et al*., 2014). However, several authors have recognized Mountain Renosterveld's affinities with Karoo vegetation (Campbell, 1985; Van Der Merwe & Van Rooyen, 2011b), particularly Kamiesberg mountain Renosterveld (Taylor, 1978), including Crassulaceae and Aizoaceae lineages (Bergh *et al*., 2014). The two study areas used in this thesis are situated on an altitudinal and rainfall gradient but occur on the same underlying geology with similar soils, and are subjected to the same disturbance patterns. Studies of land-use and grazing of these two vegetation types, have been compared along this gradient as well (Anderson & Hoffman, 2007; Anderson *et al*., 2010).

The village of Tweeriver is located in Namaqualand Klipkoppe Shrubland, with patches of Namaqualand Blomveld vegetation type in lower areas. Both of these vegetation types form part of the Succulent Karoo Biome (Mucina & Rutherford, 2006), but are not viewed as separate vegetation types in this study and are forthwith defined as 'Hardeveld' (Figure 1.2). Vegetation consists of small to medium-sized shrubs, and a high proportion of these shrubs are succulent species from the Aizoaceae family (Cowling *et al*., 1999). Non-succulent woody shrubs from the Zygophyllaceae, Asteraceae, and Fabaceae families make up most of the remaining vegetation, with a component of bulbs, annuals and herbaceous plants.

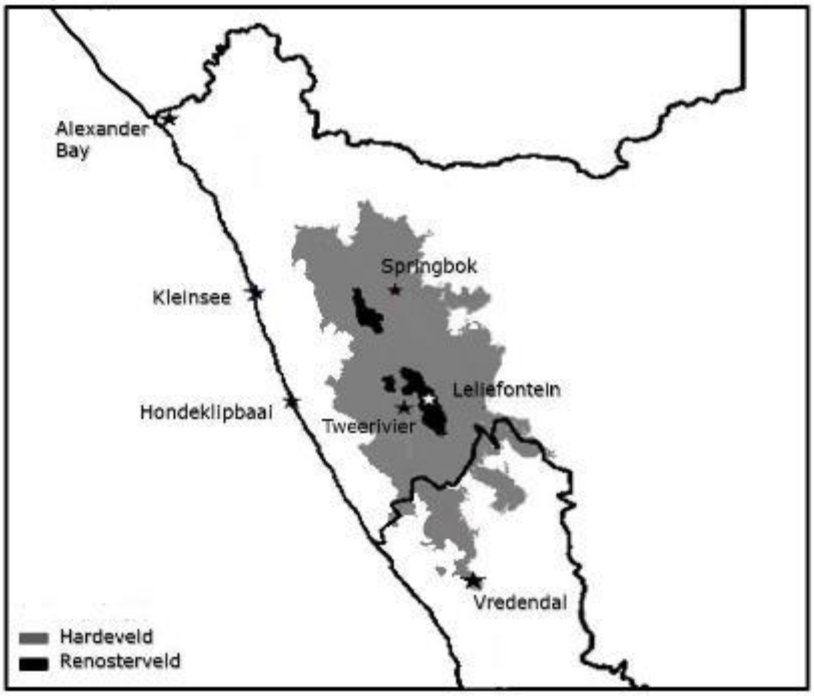


Figure 1.2 Location of the settlements of Tweerivier and Leliefontein within the two vegetation types of Hardeveld and Renosterveld.

The area around the village of Leliefontein is floristically defined as Namaqualand Granite Renosterveld (Figure 1.2). It is characterized by large stands of the woody shrub *Dicerothamnus rhinocerotis* (Asteraceae) and is also dominated by other Asteraceae shrubs. The relative abundance of Asteraceous shrubs and grasses prior to European settlement in the late 18th century is still under debate (Krug *et al*., 2004; Stock *et al*., 1993). Bergh *et al.*(2014) argue that Renosterveld prior to European colonisation was more grassy, due to evidence of grazing by native mammals, and that this dynamic was drastically altered by the extermination of mammals and the introduction of modern farming systems. This occurred before any studies of the ecosystem could be undertaken, thus little is known about the dynamics and ecology (Bergh *et al*., 2014).

Chapter 2 Community dynamics and post-cultivation succession in two arid vegetation types in the Kamiesberg, South Africa

2.1. Introduction

This chapter describes the impact that cultivation has had on upland and lowland vegetation and the efficiency of passive restoration of fallow fields in the two vegetation communities in the Leliefontein commonage in Namaqualand.

2.1.1. Cultivation and grazing

Extensive areas of the world's arid and semi-arid landscapes have been transformed by agriculture (Hobbs & Walker, 2007), and most of the degradation occurs as a result of farming practices (Clemente *et al*., 2004). Cultivation results in the complete removal of the vegetation community and disrupts key ecosystem processes and vegetation dynamics, which impact the soil in a significant and long-lasting way (Allsopp, 1999). This results in large tracts of fallow land with little recovery of the original vegetation community (Schmiedel *et al*., 2010). In the winter rainfall region of Namaqualand, cereal crops were widely grown during the course of the 20th century (Hoffman and Rohde, 2007), but by the 21st century, the area under cultivation in Namaqualand had declined significantly.

Ecosystem dynamics are complex and nonlinear (Suding & Hobbs, 2009). In Namaqualand, where a heavy disturbance, such as cultivation occurs, recovery to the original state does not always occur without active intervention. Instead, the vegetation in Namaqaualand changes from a diverse community dominated by palatable shrubs to one shaped by unpalatable and semi-toxic woody shrubs and annuals (Allsopp, 1999; Helme & Desmet, 2006; Simons & Allsopp, 2007). Recovery and secondary succession of old fields in arid regions is a poorly researched topic (Otto *et al*., 2006), and in Namaqualand specificially, little is known about how landscapes have changed following land abandonment (Hoffman and Rohde, 2007; Schmiedel *et al*., 2010). Research into the croplands of Namaqualand has only occurred in three areas, namely, Namaqua National Park (van Rooyen, 2002; Schmiedel *et al*., 2010), around Concordia near Springbok (Hongslo, Rohde & Hoffman, 2009), and near Paulshoek (Simons & Allsopp, 2007). Research in the Kamiesberg area of Namaqualand has not explored the role of abandoned fallow farmland in providing opportunities to further our understanding of succession and vegetation recovery (Hobbs & Walker, 2007; Krug & Krug, 2007).

The autogenic recovery of perennial plant communities in the Karoo is uncommon and may take centuries if at all (Seymour *et al*., 2010; Van der Merwe & Van Rooyen, 2011; Bourne *et al*., 2017). In Renosterveld, the trajectory of secondary succession is not necessarily fixed (Cowan & Anderson, 2019). Recovery is limited by rare rainfall events, loss of seeds and organic matter, and the absence of patches to trap resources (Milton *et al*., 1994). Factors that influence the rate of recovery include the proximity of the disturbed area to intact vegetation, the condition of the seed bank, how intensively the area was farmed, as well as soil fertility, climate and grazing history (Milton, 1995; De Villiers, Van Rooyen & Theron, 2003; Botha, Carrick, and Allsopp, 2008). Slow secondary succession lasting more than 50 years has been recorded in the Namaqua National Park (van Rooyen, 2002), in Goegap Nature Reserve (Allsopp, 1999) and in West Coast Renosterveld (Walton, 2006). There has only been one reported study of recovery after 80 years where the vegetation in old fields in Namaqua National Park resembled intact vegetation (Schmiedel *et al*., 2010). Further studies are needed on the rate of recovery of old lands in other areas of Namaqualand. It would be of particular interest to assess the recovery in Kamiesberg Renosterveld, where such studies have not been conducted.

Apart from cultivation, grazing by goats and sheep has also contributed towards degradation. Livestock farming methods differ greatly between communal agricultural land, which is browsed continuously throughout the year by multiple farmers, and bordering private commercial farms, with one owner practicing rotational grazing. This continual heavy grazing pressure in the communal areas of the Succulent Karoo biome has been found to influence plant species composition over time, leading to a reduction of palatable perennials as well as a reduction of biomass and vegetation cover (Anderson & Hoffman, 2007). Therefore, this continual browsing also contributes to the degradation of uncultivated and cultivated land in communal areas.

2.1.2 Patch dynamics

A core theory in this thesis is the importance of patch dynamics in the functioning of arid, resource-poor environments. In such areas, plants grow together, creating communities with a distinct patch/inter-patch structure (Eccles, Esler & Cowling, 1999; Stock *et al*., 1999; Desmet, 2007). These patches are functional units concentrating more organic matter, nutrients, seeds, and, in some cases, more water than the surrounding bare soil areas (Aguiar and Sala, 1999; Bisigato & Bertiller, 1999). For the recovery of vegetation, the importance of creating favourable micro-sites, or "safe sites," for seedling establishment has been recognized (Galatowitsch 2008). Activities that affect the structure and dynamics of vegetation patches would affect the recruitment opportunities of different species.

Fertile islands can develop in the soil beneath a patch (Stock *et al*, 1999). This concentration of nutrients and biotic activity under shrubs is a well-documented concept in semi-arid ecosystems internationally (Garcia-Moya & McKell, 1970; Schlesinger *et al*., 1996; Aguiar and Sala, 1999; Stock, Dlamini & Cowling, 1999; Wezel, Rajot and Herbriga, 2000; Li *et al*., 2007), as well as in Southern Africa (Allsopp, 1999; Carrick, 2001; Lechmere-Oertel, Cowling & Kerley, 2005). However, fertile islands are not permanent features. Once the individual plants which comprise the patch are removed, the levels of nutrients decline over time (Stock *et al*., 1999; Esler *et al*., 2003). Studying the dynamics of old lands with known ages since abandonment has proved an effective tool to understand the sequence of succession (Hobbs & Harris, 2001). An analysis of patches and their associated fertile islands at certain sites allows for a comparison of the abundances of plants and soil dynamics of patch and inter-patch areas. The approach taken in this study is to attempt to understand the impact of cultivation and the process of succession through a patch dynamics model.

In arid areas, where the role of patch dynamics and resource allocation under patches is crucial for vegetation survival, I hypothesized that the recovery of old fields in Namaqualand is hindered by a decline in soil condition and disruption of the underground fertile island. I also hypothesized that the lack of suitable patches and poorer soil quality hinder the establishment of perennial shrub communities. A second limitation in plant establishment is due to seed bank restrictions, which are explored in Chapter 3.

In this study, I investigated secondary successional processes in two previously unstudied vegetation types by comparing vegetation characteristics and soil of intact or unploughed remnants and fallow fields ranging in age from 7 to 60 years since abandonment. Specifically, I examined the dynamics of plant communities on ploughed fields and intact areas in both the Hardeveld lowlands and the Kamiesberg Renosterveld uplands in order to ascertain the following:

In terms of soils:

1. The effect of cultivation on the physical and chemical properties of the soil;
2. The role that plant patches have on the formation of fertile islands beneath their canopies in intact, uncultivated vegetation;
3. Whether pioneer plants which establish on old fields also create fertile islands and if so, how they compare with those on intact, uncultivated vegetation.

In terms of the vegetation:

1. The effect of cultivation on vegetation community composition and dynamics over time in relation to intact, uncultivated vegetation.
2. The effect of different grazing pressures on vegetation community composition on intact, uncultivated vegetation.

2.2 Materials and Methods

2.2.1 Location of sites

For this chapter, I surveyed abandoned (i.e., previously ploughed) sowing plots (Afrikaans: ‘saaipersele’) and unploughed or "intact" vegetation around the villages of Leliefontein and Tweeriver in order to test the key objectives and hypotheses outlined in Chapter 1. A map of the sampling sites in relation to the villages is displayed in Figure 2.1, whilst Tables 2.1 and 2.2 provide information regarding the GPS co-ordinates, location, land-use history, and elevation of all the sites used in the study.

Ploughed fields

Local community members assisted in the selection of sowing plots to be used in this study by providing information about ownership, the ploughing history, and the year of abandonment (when all cultivation ceased and the community member usually took no further action). In most cases, these dates can be verified with the use of aerial photographs. Sowing plots were grouped into one of two age classes; those where cultivation ceased relatively recently, 7–20 years ago (hereafter referred to as "young fields") and those where cultivation ceased 30–60 years ago (hereafter referred to as "old fields"). For each of these two age classes, four sowing plots were selected, and an area within each sowing plot, roughly in the centre (to avoid roads, rivers, and fences), was selected for sampling. All abandoned field sites had been exposed to grazing by domestic livestock on a regular, sometimes even daily, basis.

In the Hardeveld, these sites were located around the village of Tweerivier (Table 2.1, Figure 2.1), and were dominated by relatively open ground and a vegetation community consisting primarily of *Galenia africana* (hereafter called kraalbos) with scatterings of *Conicosia elongata* and *Pharnaceum confertum*. In Renosterveld, the sites were located around the village of Leliefontein (Table 2.2, Figure 2.6). Most sites had occasionally been burnt or slashed to control the encroachment of *Dicerothamnus rhinocerotis* (hereafter called renosterbos). The vegetation communities were characterized by species within the Asteraceae, such as renosterbos, *Chrysocoma ciliata* and *Leysera gnaphalodes*. One of the old field sites (known as "OLD 2") had to be removed from the study after the data had been collected because later discussions with local farmers revealed that although the site was degraded, it was not due to cultivation activities.

Reference sites

In both Hardeveld and Renosterveld vegetation, two types of reference sites were found to represent the range of grazing conditions that unploughed, or "intact," vegetation would be subjected to. The first set of sites was located on communal land, while the second was located on privately-owned land. In Namaqualand, commercial farms occupy about 52% of the area, while communal lands occupy 30% of the area (May & Lahiff, 2007). There are six communal areas, one of which is the Leliefontein commonage (192, 000 ha), where this study was based. Together, the reference sites provide an understanding of how uncultivated vegetation functions overall, how it responds to grazing, and suggest an end goal for recovering vegetation. The major limitation in the location of these reference sites is that there is very little level ground (or plains) that has not been ploughed. Intact, uncultivated vegetation is often restricted to steeper hillsides and rocky outcrops, where accessibility by tractor and plough is not possible. Furthermore, such remnant patches of intact vegetation are often small in size. Despite these limitations, four sites of unploughed vegetation were located within the communal areas (hereafter referred to as "communal reference farms") and within close proximity to the two settlements. It was assumed that these reference sites were exposed to grazing on a daily basis, as livestock were observed moving through them. Four sites were located on privately-owned farms (hereafter referred to as "private reference farms") bordering the communal area. For these areas, it was assumed that grazing pressure was lighter, and that the vegetation was periodically rested, due to more managed rotational grazing systems and fences. Private farms were often located a substantial distance away from the sites, which were all located on communal land.

In the Hardeveld, reference sites on privately-owned farms were located on the farms Grootvlei and Brakkies along the N7 highway near Kamieskroon, ca. 30 km west of Tweerivier (Table 2.1, Figure 2.1). In all cases, sites were selected based on a variety of factors such as species composition, rockiness, and openness. The Hardeveld sites consisted mostly of succulents, such as *Leipoldtia schultzei* and *Ruschia goodiae* (Aizoaceae) and *Euphorbia mauritanica* (Euphorbiaceae), with some non-succulent perennial shrubs such as *Eriocephalus* sp. (Asteraceae) and *Calobota sericea* (Fabaceae).

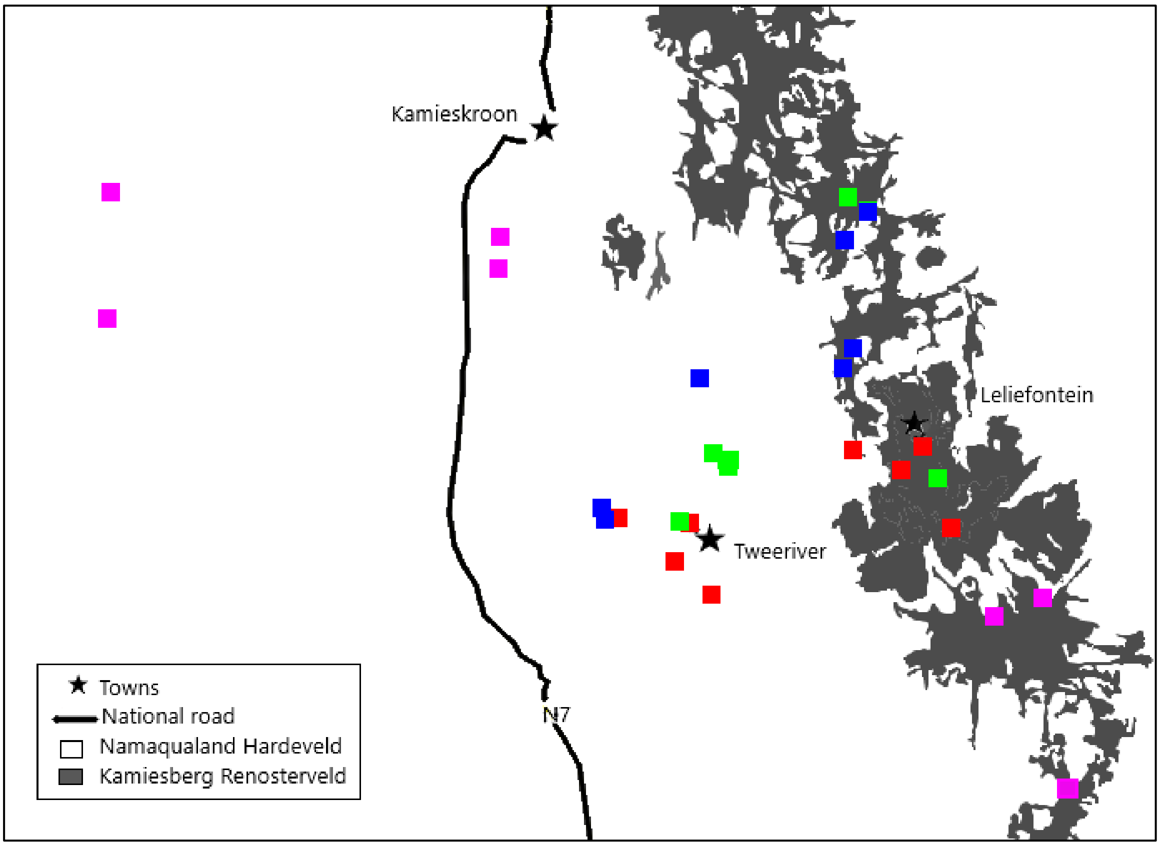


***Figure 2.1** Map of the sampling sites around the villages of Leliefontein and Tweerivier, in relation to Kamieskroon and the N7 road. Sites sampled within the two vegetation types of Hardeveld and Renosterveld. Colours of the squares indicate the land use: young fields (7-20 years since cultivation) (blue), old fields (30-60 years since cultivation) (green), private reference farms (pink) and communal reference farms (red). Map compiled in Cape Farm Mapper, scale 1:288 895.*

In Renosterveld, reference sites on private farms were located on the farms Koornlandskloof, Wolfhok, and Ezelfontein near Studer's pass, ca. 18 km south of Leliefontein (Table 2.2, Figure 2.1). These sites consisted largely of non-succulent perennial shrubs such as renosterbos, *Euryops lateriflorus*, and *Oedera genistifolia*. Due to misinformation received from a farmer, one of the reference sites on private lands (RFPV 4) in Renosterveld was removed from the study post data collection as it was deemed unsuitable as a reference site due to its land-use history.

Table 2.1 Location of sampling sites across four different land uses in Hardeveld, presented together with their relevant GPS co-ordinates, elevation and year of abandonment (when ploughing ceased), as well as the name of the landowner (if known, otherwise named after a geographical point). The previously ploughed fields are denoted by: young = fields abandoned 7 – 20 years ago, old = fields abandoned 30+ years ago. Unploughed intact land is used as a reference, whereby RFPV = private reference farms, and RFCOM = communal reference farms.

Sampling site	Location/ ownership	GPS	Elevation (m)	Year of abandonment
YOUNG-1	Koos Beuke plot # 207	S 30.29656; E 017.99239	689	2006 - 2007
YOUNG-2	Unknown ownership, known as the "koppie"	S 30.32615; E 018.00314	638	2001 - 2003
YOUNG-3	Meissenheimer plot #248	S 30.34330; E 17.95154	670	2000
YOUNG-4	Meissenheimer plot #251	S 30.34769; E 017.95333	689	2000
OLD-1	Old Meissenheimer plot near to river	S 30.32380; E 017.99750	632	Mid 1970's
OLD-2	Unknown plot by reservoir	S 30.32634; E 018.00442	644	early 1970's
OLD-3	Unknown land near Cloete's drift	S 30.34823; E 017.98414	654	Late 1960's
OLD-4	Unknown plot underneath telephone poles	S 30.32879; E 018.00429	631	Mid 1970's
RF-PV-1	Grootvlei farm	S 30.27528; E 017.74751	400	Reference site
RF-PV-2	Grootvlei farm	S 30.22992; E 017.74955	401	Reference site
RF-PV-3	Farm Brakkies	S 30.24614; E 017.90972	775	Reference site
RF-PV-4	Farm Brakkies	S 30.25758; E 017.90903	770	Reference site
RF-COM-1	Main junction into Tweeriver	S 30.34871; E 017.98850	612	Reference site
RF-COM-2	The big curve on the road to Kharkams	S 30.34707; E 017.95894	688	Reference site
RF-COM-3	Plateau behind Tweeriver	S 30.37443; E 017.99702	650	Reference site
RF-COM-4	Besiehoogte	S 30.36253; E 017.98190	645	Reference site

Table 2.2 Location of sampling sites across four different land uses in Renosterveld, presented together with their relevant GPS co-ordinates, elevation and year of abandonment (when ploughing ceased) as well as the name of the landowner (if known, otherwise named after a geographical point). The previously ploughed fields are denoted by: young = fields abandoned 7 – 20 years ago, old = fields abandoned 30+ years ago. Unploughed intact land is used as a reference, whereby RFPV = reference areas on private farms and RFCOM = reference areas in the communal area. Note that "OLD2" and "RFPV4" were removed due to land-use history errors.

Sampling site	Location/ ownership	GPS	Altitude (m)	Year of abandonment
YOUNG-1	Joey Van Wyk plot	S 30.28572; E 018.05541	1072	2000
YOUNG-2	Magriet Cloete plot	S 30.29322; E 018.05134	1074	2000
YOUNG-3	Attie Beukes plot	S 30.23697; E 018.06193	1147	2004 – 2007
YOUNG-4	Barend Steve plot	S 30.24727; E 018.05213	1147	2006/2007
OLD-1	Between 2 koppies	S 30.23175; E 018.05374	1131	1980's
OLD-3	Roadside site near Baileysvlakte	S 30.33181; E 018.09058	1377	Mid 1960's
OLD-4	By water pump in Nouriver	S 30.23655; E 018.06138	1147	Early 1970's
RF-PV-1	Wolfhok farm	S 30.38128; E 018.11380	1132	Reference site
RF-PV-2	Koornlandskloof farm	S 30.37470; E 018.13376	1130	Reference site
RF-PV-3	Ezelfontein farm	S 30.04831; E 18.09650	1143	Reference site
RF-COM-1	Xharas	S 30.34972; E 018.09606	1391	Reference site
RF-COM-2	Opposite Ramkamp	S 30.32111; E 018.08455	1357	Reference site
RF-COM-3	Baileysvlakte	S 30.32934; E 018.07508	1357	Reference site
RF-COM-4	Kleikop	S 30.32191; E 018.0555	1362	Reference site

2.2.2 Data collection

To investigate the impact of cultivation and the successional trends of the two vegetation types I compared soil properties, the composition of the standing vegetation, as well as environmental factors (soil depth, cover of plant litter, bare soil and rock cover; as well as temperature and rainfall) on ploughed and unploughed reference sites.

2.2.2.1. Soils

In February 2015, soil samples were collected from old fields and communal reference farms for chemical and physical analysis in Hardeveld and Renosterveld. Soils from communal reference farms were analysed to determine the role that plant patches have in the formation of fertile islands beneath their canopies. Soils from the old fields were analysed to determine the effect of cultivation on soil properties. To determine if pioneer plants on old fields also create fertile islands, soils from the old fields were analysed in order to assess the changes in soil over the longest recovery time period possible and to ascertain whether patches on old fields were functioning similarly to their counterparts on reference farms.

Due to the private reference farms' being located a substantial distance away from the cultivated fields in the communal area, soil was analysed from the communal reference farms only. Thus, differences in the soil between ploughed and reference sites could more accurately be attributed to ploughing and recovery, and not to potential geographical and geological differences in soil.

Three old field sites and three communal reference sites were selected. At each site, three samples were taken from between shrubs (called ‘open’ microsites), as well as three from under the dominant shrubs forming a patch (called ‘under patch’ microsites). Where soil was taken from beneath a patch, the diameter of the relevant clump was measured. Diameter was measured because, as shrubs grow, they increase more in width than in height. Diameter is therefore an indicator of the age of a patch. After removing any surface litter or dung, a soil sample of the top 10 cm of soil was extracted using a soil corer with a diameter of 10 cm. The soil sample from the corer was thoroughly mixed in the field and then stored in a paper bag. The samples were taken to the University of Cape Town and oven-dried in the laboratory at 70 °C for at least 48 hours. Soils were then sieved to 2 mm and split into sub samples via the coning and quartering method, which is used to separate the sample size without creating a systematic bias (Crosby & Patel, 1995). The following traits were evaluated by SGS Laboratories:

Values for pH were determined electrometrically from a paste (10 g soil and 25 ml solution) with deionized water and with 1 M KCL (McLean, 1982). Phosphorus was extracted from the soil using Bray No 1 solution as an extractant. The extracted phosphorus was measured colorimetrically based on the reaction with ammonium molybdate and the development of the "Molybdenum Blue" colour (Bray & Kurtz, 1945). The organic matter fraction was determined from the loss-on-ignition after 8 hours at 375 °C. Soil organic carbon was determined by the Walkley-Black chromic acid wet oxidation method, whereby oxidisable matter in the soil was oxidised by a 1 M K2Cr2O7 solution (Nelson & Sommers, 1982). Extractable cations Na, K, Ca, and Mg (cmol (+)/kg and mg/kg) were determined by placing 5 g of soil and 50 ml of ammonium acetate solution on top and shaking it for 30 minutes, after which it was filtered and analysed with the ICP (Chapman, 1985). Particle size analysis was performed using a long bed particle sizer, Malvern Mastersizer 2000, attached to a Hydro 2000G wet sample dispersion unit, after disaggregating samples on a whirlimixer in a sodium pyrosphosphate solution. Lastly, total nitrogen concentration was determined by the Dumas combustion method, using a Costech 4010 Elemental Analyzer System. Samples are flash combusted under helium in the presence of oxygen, and the resulting gases are separated by gas chromatography and detected quantitatively by a thermal conductivity detector (Sparks, 1996).

Analysis

To determine the role that patches of plants have on various soil properties beneath their canopies in both ploughed and reference sites, soil properties between nine open and nine under planted micro-sites were compared between the two land uses by applying ANOVA and Tukey HSD tests (StatSoft, Inc. 2016). These tests were also used to determine the effect of cultivation on fertile islands in the soil by comparing under patch soil samples from communal reference farms and ploughed fields.

2.2.2.2. Vegetation surveys and environmental factors

Vegetation surveys were undertaken in July 2014 for the Hardeveld sites and in August/September 2014 for the Renosterveld sites. A long-term monitoring system was set up in this area by Nuture Restore Innovate (NRI) to monitor sections of unploughed vegetation by sampling along a 100 m transect, and this method was used as a guideline for this research project. As a result, four 25-m transect-plots were completed at each site, two meters apart, in order to complete sampling of the 100-m transect-plot for that site. The four transects, 25 m apart, were orientated along an east-west axis. The GPS coordinates and the elevation were recorded at the start and end of each transect. With the use of measuring tape, a 25 m line was laid out in the site and the area (transect-plot) 1 m to the north of the tape was sampled. The next transect was shifted exactly 2 m from the starting transect-plot in an approximate northerly direction. This ensured that the subsequent transect-plots were parallel to the starting 25 m transect-plot and that each 25 m transect-plot was independent of one another. Although this method was designed for small remnants of intact land, it was used to sample both ploughed and unploughed sites. In Hardeveld, four young fields, four old fields, four communal reference farms, and four private farms were each sampled with this 100 m transect. In Renosterveld, four young fields, three old fields, four communal reference farms, and three private farms were each sampled with this 100 m transect. See Appendix F 1 – 4 for pictures on the vegetation surveys.

Once the transect line was in place, all perennial species, including numbers of individuals, were recorded on field data sheets, and the length (cover) of each perennial species (excluding annuals and bulbs) was recorded along the measuring tape. Species were assigned to growth form classes, which were later verified with the assistance of literature. Plants were assigned to growth form classes based on the following criteria:

(a) Perennial graminoids: includes perennial grasses and sedges. Examples include *Ehrharta barbinodis, Fingerhuthia africana, Pentameris curvifolia, Restio gossypina*

(b) Perennial herbs: plants with no woody parts above ground. Examples include *Hypertelis salsoloides, Microloma sagittatum, Limeum africanum* and *Pharnaceum confertum.*

(c) Small leaf succulent (SLS) shrubs: plants with succulent leaves that are compact and low growing, are below or roughly equal to 0.3 m in height, and seldom have visible stems. Examples are *Conicosia, Cephalophyllum, Cheirodopsis* and certain *Crassula* species.

(d) Medium leaf-succulent (MLS) shrubs: plants with succulent leaves that are 0.3 – 1 m in height and have woody stems. Examples are *Ruschia, Leipoldtia, Othonna, Zygophyllum, Tetragonia and Aridaria species*

(e) Stem succulent (SS) shrubs: plants with succulent stems. Leaves are often barely present. Examples are *Euphorbia* species, *Sarcocaulon species* and *Quaqua incarnata.*

(f) Small non-leaf succulent (SNLS) shrubs: woody plants that are below 0.5 m in height. Examples are *Hirpicium alienatum, Stoebe* and certain *Pelargonium* species*, Chrysocoma ciliata, Hermannia disermifolia* and *Pentzia incana*

(g) Medium non-leaf succulent (MNLS) shrubs: woody plants that are over 1 m in height. Examples are *Searsia, Calobota, Eriocephalus, Pteronia, Osteospermum, Berkheya, Didelta,* and *Cliffortia ruscifolia* type species.

Finally, the two woody shrubs *Galenia africana* and *Dicerothamnus rhinocerotis*, which were classified as MNLS shrubs, were also analysed as individual species because one of the key focus points of this thesis was to determine their role in ploughed and reference sites.

Where one plant grew under another, and it was covered by the tape measure, the cumulative cover of both plants on the tape was recorded. The abundance and cover of dead shrubs was also recorded. The numbers of plants that existed as part of a patch were recorded, as it is a key indicator of the structure of the community. ‘Patches’ or groups of plants growing together were determined if more than 50% of a plant occurred beneath the canopy of another plant. If the canopies of two plants were more than 25% intertwined, then both plants were recorded as part of a patch. Thereafter the number of plants in each growth form occurring as part of a patch was calculated and expressed as a percentage. Record was also made of the number of individual plants and species that were grazed, and expressed as a percentage of the total number of plants recorded, as an indicator of grazing and degradation.

In sampling other environmental factors, soil depth was recorded at 10 m intervals by hammering a sharpened steel pole into the soil until it encountered bedrock. The length on the tape of the cover of plant litter, bare soil and rock was also recorded. Average temperature and rainfall data for each site was obtained from Schulze (1997, 2010).

Analysis for the vegetation survey

Species accumulation curves, which reflect the cumulative number of species recorded in a particular environment as a function of the cumulative sampling effort, provide a way of estimating the number of additional species that might be discovered with further effort (Ugland *et al*., 2003). This is a useful approach to assess the efficiency and reliability of the sampling design and to predict species richness. Species accumulation curves were computed in R (R Development Core Team, 2010, and the related Vegan package). The results showed that the number of replications for both the vegetation survey and the soil survey was sufficient to capture the plant composition for all the sites.

The following analyses were performed in order to: (1) to assess the impact of cultivation on vegetation composition and (2) to provide a measure of the rate of recovery of vegetation after cultivation. Ordination techniques were used to visually assess the similarities between ploughed and unploughed lands. Two-dimensional ordinations were constructed from the vegetation survey using the abundance of adult plants and the abundance of growth forms. The correlation between the position of plots on an axis and the values of any particular variable is given by the correlation co-efficient (Pearson's r^2, McCune, Grace & Urban, 2002), which could be in any direction across ordination space. Ordinations were not tested as they are simply a means of analysing patterns. Ordinations were conducted using Nonmetric Multidimensional Scaling (NMS) procedures in PC-Ord software (Version 6). This method is advantageous for ecological communities because it is non-parametric and therefore does not assume normality in the distribution of the data. NMS ordinations cope well with sites that are unevenly spaced along an underlying gradient. Also, the approach does not assume linearity in the change of abundances across plots (McCune, Grace & Urban, 2002). A Sorensen (Bray Curtis) distance measure, incorporating a random starting configuration using time of day and 15 runs with real data, was used. The stress test and the Monte Carlo test were used to select the final dimensions for the final ordination (McCune, Grace & Urban, 2002).

For the vegetation survey, measures of plant abundance, species richness, species diversity, evenness and vegetation cover from the 100 m transects from four sites (three sites in Renosterveld old fields and a private reference farm) across the four land uses were compared in ANOVA's and where they were significant, and the assumptions of normality were adequately met, Tukey's (HSD) tests were conducted (StatSoft, Inc. 2016).

Analysis of the growth forms from four sites (with the exception of only three sites for both old fields and private reference farms in Renosterveld) across the four land uses for the vegetation survey were presented graphically and were compared using generalized estimating equations (GEE), to account for random variance due to different sampling seasons, with a negative binomial error structure and log-link function (Liang & Zeger 1986). Wald statistics were used to test the significance of these models. Sites were treated as subjects for correlated responses, and the analyses used an exchangeable correlation matrix structure. The significance of differences among means was assessed using multiple comparisons with sequential Sidâk adjustment of the alpha value (IBM SPSS, 2015).

The Shannon index of general diversity (Odum, 1971) was used to measure the diversity of above-ground vegetation in each of the land use categories. The Shannon index is expressed as:

H = si = 1 pi log pi

Where pi = proportion of individuals in the species, s = total number of species.

The Simpson's diversity index for an infinite population (D) is calculated as:

D = 1 - the sum of (pi*pi)

The evenness of a community can be represented by Pielou's evenness index, whereby Shannon's diversity index H is divided by the natural logarithm of species richness ln (S).

2.3 Results

The results of the soil sampling are presented for Hardeveld and Renosterveld separately. Afterwhich the results of the environmental factors, the vegetation community descriptors and the vegetation survey, consisting of seven growth forms, are presented for each vegetation type.

2.3.1 Soils

2.3.1.1 Hardeveld

Surface soil (0–10 cm) on old fields and communal reference farms was classified as sand, with 0.5% clay, 9.5% silt, and 90% sand. In general, the soils were low in carbon, organic matter, and nitrogen and quite high in potassium, magnesium, and calcium (Tables 2.3 and 2.4). Patches of shrubs on old fields consisted almost exclusively of *Galenia africana*, and on communal reference farms they were dominated by a *Ruschia* species and were very similar in size, 104 and 105 cm.

There was an indication that patch occurrence on old fields significantly influenced the soil quality. Soil pH changed from 5.5 in open microsites to 7.6 under patches. Even though levels of organic matter and carbon were very low on old fields, patches significantly increased their levels. A noteworthy find is that patches had a substantial effect of increasing phosphorus from 18.1 mg/kg in open microsites to 27.1 mg/kg under patches. Patches also had a substantial effect, increasing potassium from 55.6 in open microsites to 273.9 mg/kg under patches. Sodium also increased significantly from open microsites (17.4 ± 21.0 mg/kg) to under patches (36.8 ± 14.5 mg/kg, Table 2.3).

In unploughed intact areas, patch occurrences had a considerable effect on the soil microsites underneath them. Patches significantly increased the organic fraction of the soil, as well as the carbon percentage relative to open areas (Table 2.3). The cation concentrations of potassium, magnesium, and sodium under patches were exceptionally higher, almost three times as much, compared to the open (between shrubs) microsites. Patch occurrence did not have an effect on the pH, nitrogen, or potassium levels of the soil, which were similar across both open and patch microsites (Table 2.3).

Although there is an indication that the patches that form on old fields ceased do create fertile islands, the soil under these patches is still significantly lower in organic matter, carbon, and sodium compared to patches on reference farms. Patches on old fields were also significantly higher in pH, phosphorus, and potassium, compared to patches on reference sites (Table 2.3).

Table 2.3 Chemical (mean ± SD) and physical properties of soil collected from three old field sites and three from communal reference farms Kamiesberg Hardeveld. At each site, three soil samples to a depth of 10 cm were collected with the use of a soil corer from open (between shrub) microsites and three from under patch microsites. Different letters aligned horizontally indicate significant differences among microhabitats (Tukey HSD). Statistical results are listed in Table 2.4

	Land use			
	Old fields		**Communal reference farms**	
Soil property	**Under patch (n=9)**	**Open (n=9)**	**Under patch (n=9)**	**Open (n=9)**
pH (KCl)	7.6 ± 0.5 ^{a}	5.5 ± 0.6 ^{b}	4.5 ± 0.4 ^{c}	4.1 ± 0.8 ^{c}
Organic matter (%)	0.7 ± 0.2 ^{ac}	0.4 ± 0.1 ^{ac}	1.8 ± 1.0 ^{b}	1.1 ± 0.4 ^{bc}
Total Nitrogen (%)	0.2 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}	0.18 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}
Carbon (%)	0.4 ± 0.1 ^{ad}	0.2 ± 0.0 ^{b}	1.1 ± 0.6 ^{c}	0.6 ± 0.2 ^{d}
Phosphorus (mg/kg)	27.1 ± 6.5 ^{a}	18.1 ± 4.3 ^{b}	12.1 ±6.0 ^{bc}	11.7 ± 4.9 ^{bc}
Potassium (mg/kg)	273.9 ± 48.3 ^{a}	55.6 ± 13.6 ^{bd}	171.2 ± 54.8 ^{c}	75.4 ± 44.3 ^{bd}
Calcium (mg/kg)	248.0 ± 59.8 ^{a}	181.2 ± 40.8 ^{b}	185.7 ± 102.4 ^{b}	131.8 ± 75.5 ^{b}
Magnesium (mg/kg)	122.2 ± 24.9 ^{ac}	41.7 ± 12.0 ^{bc}	143.5 ±51.8 ^{ab}	64.0 ± 31.5 ^{abc}
Sodium (mg/kg)	36.8 ± 14.5 ^{ad}	17.4 ± 21.0 ^{bd}	152.9 ± 87. 9 ^{c}	40.3 ± 35.8 ^{d}
Texture	sand	sand	sand	sand

*Table 2.4 Statistical parameters (F and significance levels) for each analysis of variance (ANOVA) performed on soil properties presented in Table 2.4. Significance is indicated *P<0.05, **P<0.005, ***P<0.001, and not significant as NS, df = 1, 32.*

Soil property	Land use	Micro-sites	Interaction of land use & micro-sites
pH (KCl)	132.3***	42.3***	17.5***
Organic matter (%)	22.6***	9.9**	1.4 NS
Total Nitrogen (%)	3.7 NS	0.0 NS	1.6 NS
Carbon (%)	50.2***	20.0***	1.1 NS
Phosphorus (mg/kg)	33.7***	6.5*	5.4*
Potassium (mg/kg)	8.2**	118.5***	18.0***
Calcium (mg/kg)	9.7**	6.8*	0.0 NS
Magnesium (mg/kg)	3.8 NS	51.9***	0.0 NS
Sodium (mg/kg)	25.0***	32.0***	1.0 NS

2.3.1.2 Renosterveld

Surface soil (0–10 cm) on old fields and communal reference farms consisted of 1% clay, 12% silt, and 87% sand, and was classified as sand. There was only one communal reference site where the soil verged on being loamy sand. In general, the soils were low in carbon, organic matter, and nitrogen and quite high in potassium and calcium (Tables 2.5 and 2.6). All patches measured in Renosterveld consisted of renosterbos as the dominant species, and they were very similar in size (old fields: 114 cm in diameter; communal reference farms: 106 cm).

On old fields, patch occurrence did not significantly improve soil quality after ploughing. Potassium was the only compound that occurred at a significantly higher level under a patch than in an open microsite (Table 2.5).

On communal reference farms, patches of plants significantly increased the organic fraction of the soil, as well as carbon (Table 2.5). The cation concentrations of patch soils were significantly higher than the open microsites, especially for potassium and magnesium. Phosphorus and total nitrogen levels were significantly lower in soils under a patch. Patches do not have an effect on the pH or sodium levels of the soil.

As mentioned above, patches on old fields had no influence on soil quality, and there was little to no improvement. Organic matter input under patches was significantly lower on old fields (1.5 + 0.7%) compared to communal reference farms (2.7 ± 0.4%). The same occurred with calcium (234 vs. 391 mg/kg, respectively) and magnesium (79 vs. 130 mg/kg, respectively).

The proportion of carbon under patches on old fields was less than 1%, compared to communal reference farms with 1.5%.

Table 2.5 Chemical (mean ± SD) and physical properties of soil collected from three old field sites and three from communal reference farms Kamiesberg Renosterveld. At each site, three soil samples to a depth of 10 cm were collected with the use of a soil corer from open (between shrub) microsites and three from under patch microsites Different letters aligned horizontally indicate significant differences among microhabitats (Tukey HSD). Statistical results are listed in Table 2.6.

	Land use			
	Old fields		**Communal reference farms**	
Soil property	**Under patch (n=9)**	**Open (n=9)**	**Under patch (n=9)**	**Open (n=9)**
pH (KCl)	4.9 ± 0.3 ^{a}	4.7 ± 0.1 ^{a}	5.1 ± 0.3 ^{a}	5.1 ± 0.2 ^{a}
Organic matter (%)	1.5 ± 0.7 ^{a}	1.1 ± 0.7 ^{a}	2.7 ± 0.4 ^{b}	1.8 ± 0.5 ^{c}
Total Nitrogen (%)	0.2 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}	0.2 ± 0.0 ^{b}
Carbon (%)	0.8 ± 0.4 ^{a}	0.6 ± 0.4 ^{a}	1.5 ± 0.3 ^{c}	1.1 ± 0.3 ^{b}
Phosphorus (mg/kg)	5.7 ± 2.0 ^{a}	6.0 ± 1.8 ^{a}	4.8 ± 1.8 ^{a}	6.7 ± 1.7 ^{b}
Potassium (mg/kg)	118.0 ± 41.1 ^{b}	74.2 ± 14.2 ^{a}	140.1 ± 31.0 ^{a}	94.2 ± 26.5 ^{a}
Calcium (mg/kg)	234.1 ± 73.0 ^{a}	207.5 ± 73.8 ^{a}	391.7 ± 66.8 ^{b}	378.8 ± 84.9 ^{b}
Magnesium (mg/kg)	79.9 ± 29.8 ^{a}	64.1 ± 23.0 ^{a}	130.2 ±34.2 ^{b}	93.6 ± 25.1 ^{ac}
Sodium (mg/kg)	16.2 ± 6.9 ^{a}	10.8 ± 4.2 ^{a}	18.1 ± 7.0 ^{a}	15.4 ± 2.9 ^{a}
Texture	sand	sand	sand	sand

*Table 2.6 Statistical parameters (F and significance levels) for each analysis of variance (ANOVA) performed on soil properties presented in Table 2.4. Significance is indicated *P<0.05, **P<0.005, ***P<0.001, and not significant as NS, df = 1, 32.*

Soil property	**Land use**	**Micro-sites**	**Interaction of land use & micro-sites**
pH (KCl)	1 NS	0 NS	1 NS
Organic matter (%)	10**	7 **	1 NS
Total Nitrogen (%)	5 NS	17 ***	10 **
Carbon (%)	10**	7**	1 NS
Phosphorus (mg/kg)	4*	2 *	1 NS
Potassium (mg/kg)	0 NS	15 ***	0 NS
Calcium (mg/kg)	9**	0 NS	0 NS
Magnesium (mg/kg)	6*	9***	0 NS
Sodium (mg/kg)	4 NS	3 NS	0 NS

2.3.2 Vegetation survey

2.3.2.1 Hardeveld

Environmental factors

All sites were similar to each other in terms of their elevation, average rainfall, average temperature, plant litter cover, rock cover, dead shrub cover, and soil depth. The amount of bare soil was the only factor that had substantial differences. Both ploughed field categories had the same extent of bare soil (61–67%), which was double the extent of bare soil on private reference farm categories (36.3%, $P < 0.05$). Communal reference farms had significantly more bare soil than private farms (55.3%, $P < 0.05$) but did not differ from the proportion of bare soil recorded on old fields. Significantly fewer plants were grazed on private reference farms, and similar proportions of grazed individuals were found on young fields, old fields, and communal reference farms, which are all located in the commonage area (Table 2.7).

Table 2.7 Environmental factors (mean ± SD) from four land uses in Kamiesberg Hardeveld. Mean average rainfall and temperature data were obtained from Schulze (1997, 2010). Elevation was recorded with the use of a hand-held GPS. Soil depth and cover proportions of plant litter, rock, dead shrub and bare soil cover were recorded during the vegetation survey along 100 m transects at each of the four sites on young fields, old fields, and private and communal reference farms. Mean values do not differ significantly if superscripts contain the same letter, for each factor as determined by ANOVA (Tukey HSD). The F value for each ANOVA is indicated *P <0.05, **P<0.005, ***P<0.001 and not significant (NS).

	Land use category				
Environmental factor	**Young fields (n = 4)**	**old fields (n = 4)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 4)**	**F value**
Elevation (m)	671.5 (24.1) ^{a}	640.2 (10.9) ^{a}	648.7 (31.1) ^{a}	586.5 (214.7) ^{a}	0.5 NS
Rainfall (mm)	214.2 (11.9) ^{a}	223.7 (5.2) ^{a}	221.7 (9.9) ^{a}	215.7 (4.6) ^{a}	1.1 NS
Temperature (°C)	18.1 (0.1) ^{a}	18.0 (0.1) ^{a}	18.6 (0.7) ^{a}	18.0 (0.2) ^{a}	2.1 NS
Plant litter cover (%)	3.0 (1.4) ^{a}	4.04 (3.7) ^{a}	4.9 (4.7) ^{a}	8.7 (3.8) ^{b}	14.2**
Rock cover (%)	0.0 (0.0) ^{a}	0.3 (0.1) ^{a}	3.0 (3.4) ^{a}	1.9 (3.2) ^{a}	1.6 NS
Dead shrub cover (%)	4.2 (2.8) ^{a}	5.6 (1.6) ^{a}	3.4 (1.7) ^{a}	6.3 (4.6) ^{a}	1.3 NS
Bare soil cover (%)	67.1 (5.4) ^{a}	64.4 (11.3) ^{ab}	55.3 (1.2) ^{b}	36.3 (5.3) ^{c}	15.4 ***
Grazed individuals (%)	18.6 (20.9) ^{a}	24.6 (19.94) ^{a}	27.8 (12.08) ^{a}	11.8 (6.96) ^{b}	14.1 **
Soil Depth (cm)	43.7 (8.52) ^{a}	47.1 (9.61) ^{a}	31.0 (11.99) ^{a}	36.6 (11.91) ^{a}	1.7 NS

Vegetation community descriptors

The vegetation community attributes of the reference farms were similar to each other, and the only difference found between communal and private reference farms was vegetation cover (35.6% and 53.0%, respectively). Plant diversity indices, plant abundance, species richness, and vegetation cover were all significantly lower for ploughed fields compared to both communal and private reference farms (Table 2.8). Species richness and plant abundance decreased by more than half post-ploughing. A similar trend was found with vegetation cover, which was substantially lower, from 35–53% on reference farms to around 24% found on ploughed fields. The proportion of individuals in a patch decreased by at least half, from 40–63% in a patch on reference farms to 20–26% in a patch on ploughed fields. There was no significant improvement or recovery in the plant community with time, i.e., from young to old fields, in any of the community descriptors measured in Table 2.8.

Table 2.8 Vegetation community descriptors (mean ± SD) recorded across four land uses in Kamiesberg Hardeveld. Each land use, young fields, old fields, communal reference farms and private reference farms, had four sites that were surveyed with a 100 m transect. Mean abundances do not differ significantly if superscripts contain the same letter as determined by ANOVA (Tukey HSD). The F value for each ANOVA is indicated *P <0.05, **P<0.005, ***P<0.001 and not significant (NS)

	Land use				
Vegetation descriptor	**Young fields (n = 4)**	**Old fields (n = 4)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 4)**	**F value**
Shannon –Wiener Diversity (H) index	1.3 (0.1)^{a}	1.1(0.2)^{a}	2.3 (0.1)^{b}	2.0 (0.1)^{b}	19 ***
Simpsons Index of Diversity (1 – D)	0.6 (0.0)^{a}	0.5 (0.1)^{a}	0.8 (0.0)^{b}	0.7 (0.0)^{b}	30 ***
Species richness	7.9 (0.6)^{a}	6.3 (0.6)^{a}	18.4 (0.8)^{b}	16.4 (1.2)^{b}	70 ***
Evenness (Pielou's J' evenness)	0.6 (0.0)^{ac}	0.6 (0.0)^{a}	0.8 (0.0)^{b}	0.7 (0.03)^{bc}	29 ***
Plant abundance	265.0 (116.5)^{a}	249.0 (139.0)^{a}	450.0 (123.8)^{ab}	624.0 (117.1)^{b}	9 ***
Vegetation cover (%)	23.7 (1.7) ^{a}	23.9 (8.7) ^{a}	35.5 (3.7)^{b}	53.2 (2.8) ^{c}	30 ***
Individuals part of a patch (%)	26.71 (17.2) ^{a}	20.68 (11.28) ^{a}	40.60 (18.42) ^{b}	63 (17.57) ^{b}	8**

Ordinations of species

The ordination of all species showed a clear distinction between ploughed and unploughed land in terms of abundance values (Figure 2.2.a). The ploughed fields of both age classes were tightly clumped together, with the samples from the old fields occupying the least ordination space, indicating little difference in floristic composition over time. The samples from both reference farms were more scattered and when combined occupy a larger ordination space than the ploughed sites. This suggests a greater floristic heterogeneity within reference farms than within areas that had been ploughed previously. The axes were significantly related to the abundance of *Galenia africana* (r^2 = 0.68), *Euphorbia mauritanica* (r^2 = 0.54,) *Eriocephalus* sp. (r^2 = 0.43), *Leipoldtia* sp. (r^2 = 0.77), *Searsia undulata* (r^2 = 0.55) and *Pharnaceum confertum* ($r^{2\,=}$0.50).

Ordinations of the growth forms revealed very similar trends. The abundance of species within various growth forms showed a clear distinction between ploughed and reference farms (Figure 2.2.b) and can largely be attributed to the correlation of leaf succulent shrubs with the axes (r^2 = 0.65)). Figure 2.2 (b) shows that young and old fields overlapped each other, suggesting that few changes in growth form composition have occurred over time post ploughing. Reference farms were also very similar to each other.

Growth forms

Vegetation transects across the four land use categories (Apendix F.2 and F.3) in Hardeveld recorded 77 perennial species from 18 families, in seven growth forms, see Appendix A1.

The vegetation recorded in the survey was dominated by both medium sized, leaf succulents (MLS) and non-leaf succulents (MNLS) with 28% each. Graminoids and herbs each contributed equally with around 15%. This was followed by small leaf succulent (SLS) and stem succulent (SS) shrubs with 4% each, and small non-succulent (SNLS) shrubs with 2%. Of all the plant individuals recorded in the survey, *Galenia africana* individuals contributed 13%.

The generalized estimating equations (GEE) indicated no significant differences between ploughed fields and reference farms for perennial graminoids (Figure 2.3 a). Although the numbers were similar across the ploughed fields and reference farms, graminoids grew in different areas. On ploughed fields, less than 10% of recorded individuals grew as part of a patch. The majority of graminoids grew in the open (between shrubs) area or as solitary plants

(Figure 2.3.a) this is very different from reference farms where the majority of grasses grow in patches, especially in the case of private reference farms (99%).

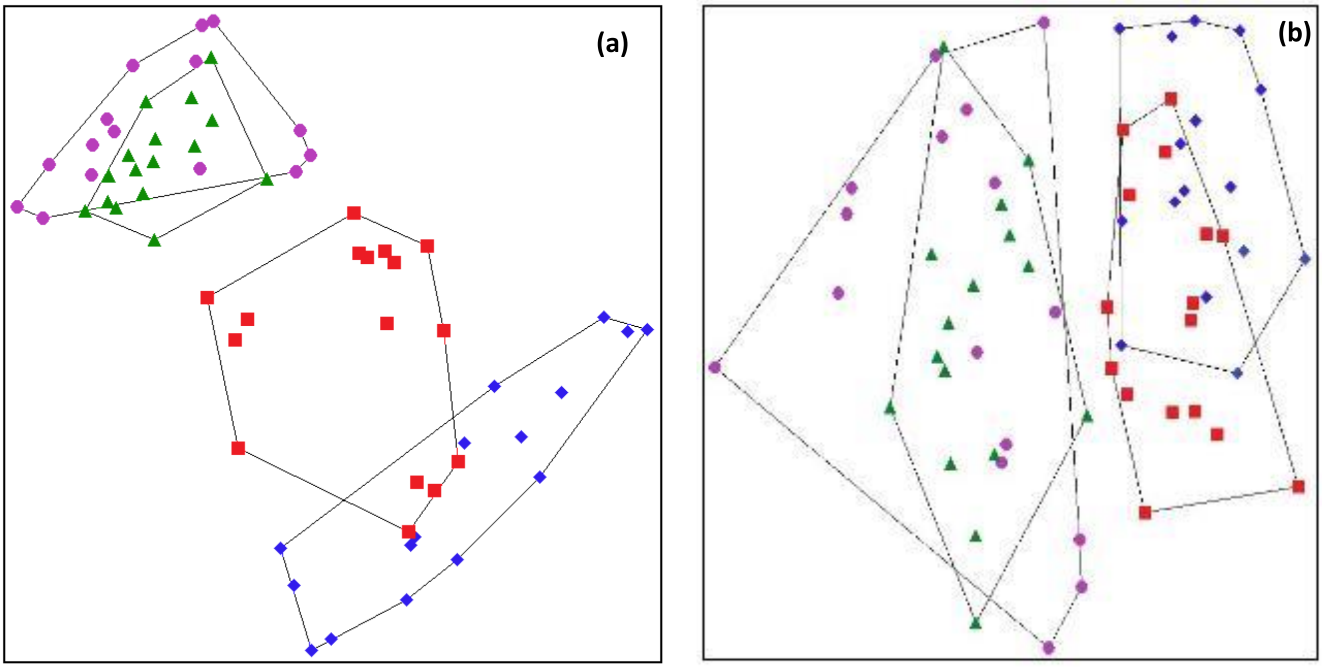


Figure 2.2 Two-dimensional plots of ordinations (NMS) of (a) abundance of all species and (b) abundance within growth form types from Kamiesberg Hardeveld as denoted by: purple circles = young fields, Green Triangles = old fields, red Squares = communal reference farms and blue Diamonds = private reference farms. (Ordination distances in the original, n-dimension, show that the ordinations are fairly well preserved in the two-dimensional plots; with cumulative correlation coefficients (a) = 0.69 and (b) = 0. 69.

After cultivation, perennial herbs on ploughed fields increased significantly to a mean of 105 individuals per transect (χ^2 (3) = 16.3, P < 0.001, Figure 2.3.b) compared to reference farms where the means were below 27 individuals per transect. There was no difference between young and old ploughed fields where only 12 - 23% of perennial herbs grew in a patch. Although the abundance of herbs on reference farms was significantly lower than on ploughed fields, 43 – 59% of those present were found to grow in patches.

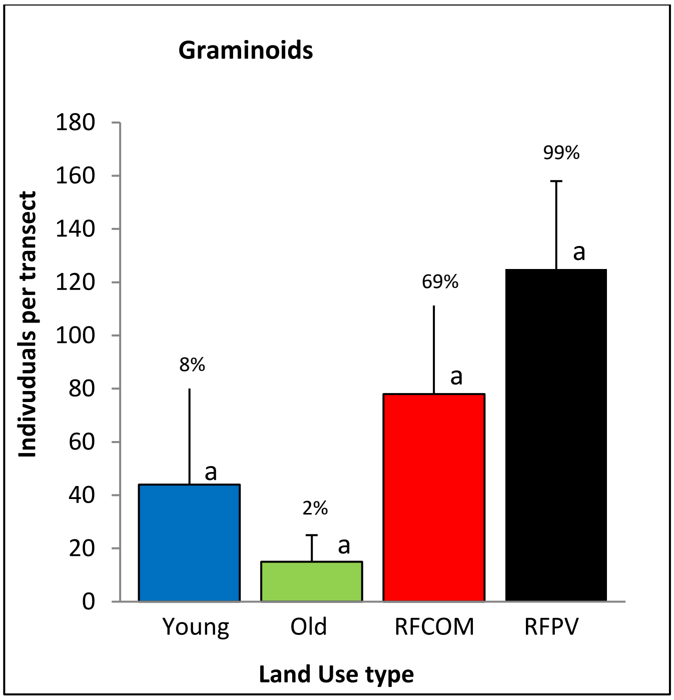
After cultivation, there was a dramatic and significant decline of all succulent growth forms, whereby there was never more than 5 individuals per transect of each growth form present in a transect, and there was no change over time post abandonment. The abundance of succulents on both reference farms was very similar.

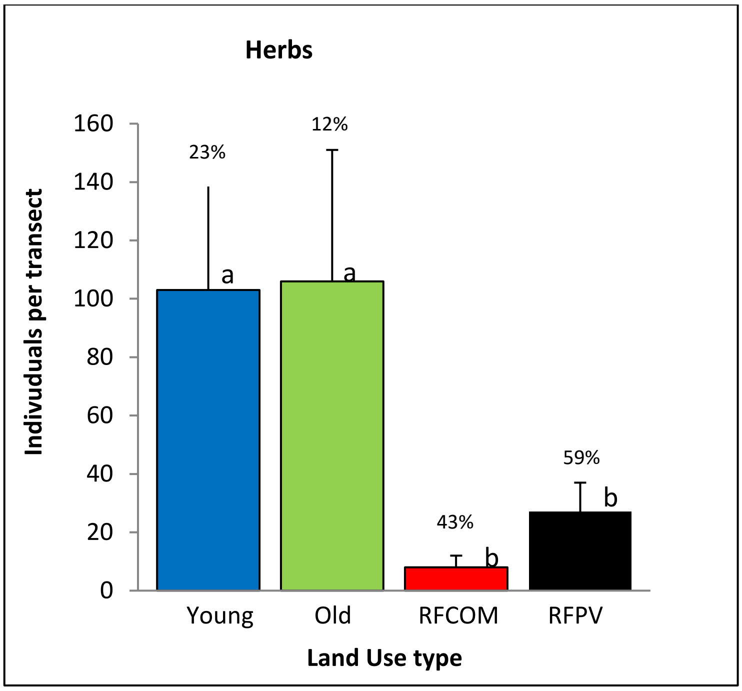
SLS shrubs were highest on communal reference farms (54 ± 16.1 individuals per transect) and differed significantly (χ^2 (3) = 80, P<0.0001, Figure 2.3.c) to the ploughed fields. However, the private reference farms (23 ± 13.3) did not differ significantly from the fields (Figure 2.3.c).

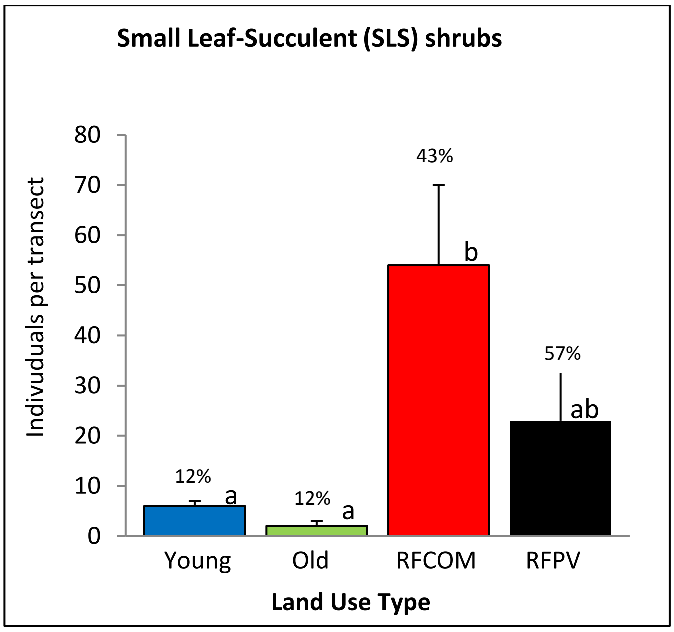
MLS shrubs were the most abundant group. MLS shrubs on the ploughed fields had on average 5 individuals per transect, which contrasts significantly ($\chi^2(3) = 124$, $P<0.0001$, Figure 2.3.d) with both communal (177 ± 40 individuals per transect) and private (262 + 30 individuals per transect) reference farms. SS shrubs occurred on reference farms, ranging from an average of 24 (± 5) individuals per transect on communal farms to 34 (± 18) on private farms (Figure 2.3.e), but were largely absent from any of the ploughed fields surveyed (χ^2 (3) = 15, $P < 0.005$, Figure 2.3.e). On fields, SLS shrubs and MLS shrubs grew as part of a patch 12 – 16%, whilst stem succulent shrubs never grew as part of a patch. On reference farms, the proportion of succulents growing in a patch varied greatly (30 – 69 %).

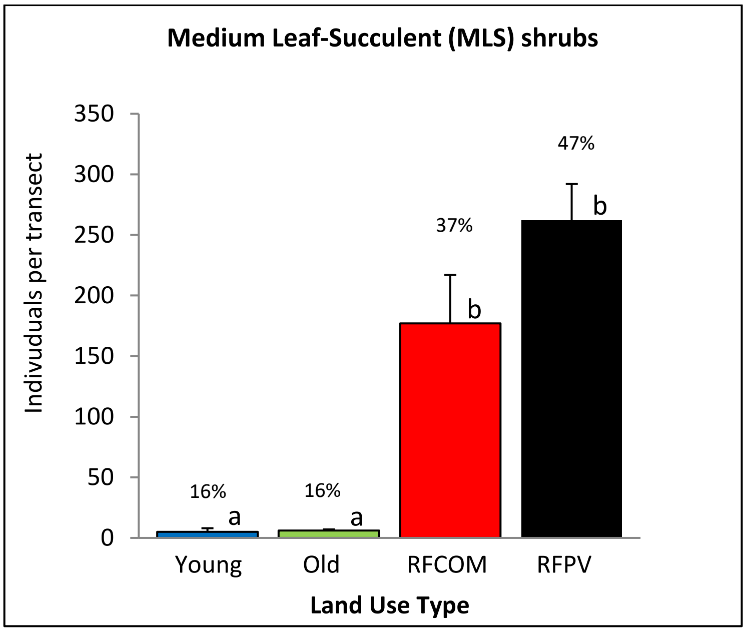
The SNLS shrubs declined significantly (χ^2 (3) = 14.3, $P < 0.005$, Figure 2.3.f) after cultivation had ceased and remained at consistent numbers (3 – 5 individuals per transect) over time. Across the land uses SNLS shrubs, barely part of a patch. The reference farms had the same mean abundance of 16 individuals. For MNLS shrubs, there were no differences in abundance between ploughed fields and reference farms, but there was a marked difference in where the MNLS shrubs grew, as after cultivation, only 30 % grew as part of a patch (Figure 2.3g).

The analysis of *G. africana* indicated that its numbers increased dramatically after ploughing (χ^2 (3) = 54.4, $P < 0.0001$, Figure 2.3.h), from averages of 4 - 10 individuals per transect on reference farms, to an average of 95 individuals per transect on ploughed fields. Again, there were no changes over time post abandonment. It was also clear that once *G. africana* established on young fields, neither the abundance nor the proportion of this plant in a patch changed over time post ploughing (Figure 2.3h).


Graminoids
Indivuduals per transect
0
20
40
60
80
100
120
140
160
180
8%
a
2%
a
69%
a
99%
a
Young
Old
RFCOM
RFPV
Land Use type


Herbs
Indivuduals per transect
0
20
40
60
80
100
120
140
160
23%
a
12%
a
43%
b
59%
b
Young
Old
RFCOM
RFPV
Land Use type


Small Leaf-Succulent (SLS) shrubs
Indivuduals per transect
0
10
20
30
40
50
60
70
80
12%
a
12%
a
43%
b
57%
ab
Young
Old
RFCOM
RFPV
Land Use Type


Medium Leaf-Succulent (MLS) shrubs
Indivuduals per transect
0
50
100
150
200
250
300
350
16%
a
16%
a
37%
b
47%
b
Young
Old
RFCOM
RFPV
Land Use Type

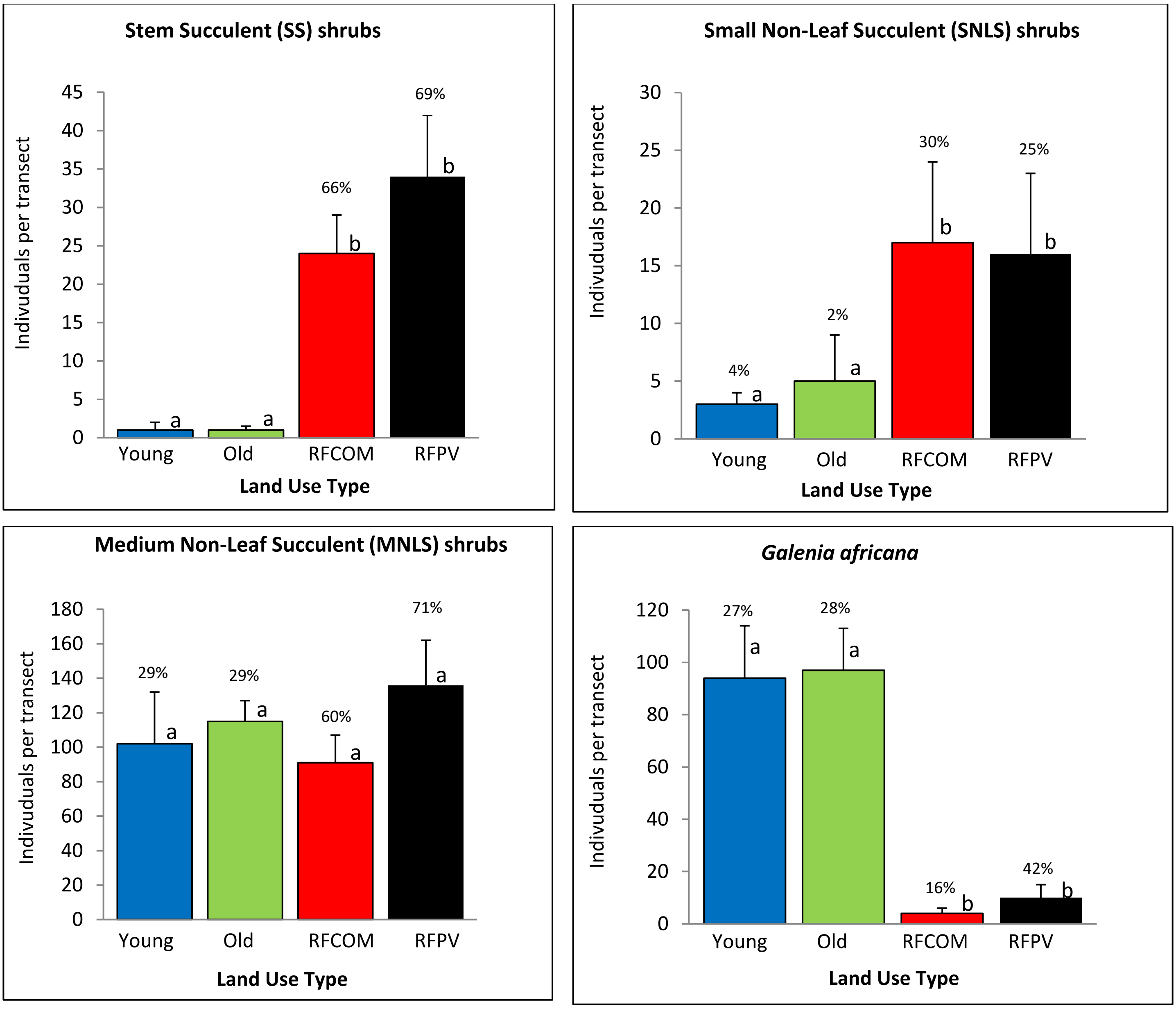


Figure 2.3 Perennial plant abundance (mean + SE) of various growth forms recorded in vegetation surveys across land use types in Kamiesberg Hardeveld. Each site was surveyed with a 100 m transect. Growth forms are plotted as: (a) perennial graminoids, (b) perennial herbs, (c) small leaf succulent (SLS) shrubs, (d) medium leaf-succulent shrubs, (e) stem succulent (SS) shrubs, (f) small non-leaf succulent shrubs, (g) medium non-leaf succulent shrubs, and (h) only Galenia africana. Numbers (percentage) displayed above each bar indicate the percentage of individuals for that growth form found to be part of a patch. Where no number is displayed, the percentage was zero. Mean abundances do not differ significantly if superscripts contain the same letter as determined by GEE and Sidak analyses (P<0.05).

2.3.2.2 Renosterveld

Environmental factors

Ploughed fields and reference farms were similar to each other with regard to their soil depth, rock cover, dead shrub cover, and mean annual temperature. However, they differed in their elevation and rainfall. Communal reference sites were at a significantly higher altitude (1367 m) than private reference sites and young fields. Communal reference sites also had a significantly higher mean rainfall average than young fields. The proportion of bare soil on communal and private reference sites was very similar at 23–24% and increased significantly after ploughing to 46–53%, where it stayed at a consistent level over time post abandonment (Table 2.9).

Plant litter was highest on private reference farms but was similar between the two reference farms. Plant litter decreased after ploughing and stayed consistent on fields with no difference over time. Private reference farms had significantly more litter present than the ploughed fields. The young fields, old fields, and communal reference farms (all located in the commonage area) were similar.

There was no difference in grazing impact between the private and communal reference farms. The proportion of grazed plants on young fields, old fields, and communal reference farms (all located in the commonage area) was similar. Private reference farms had significantly lower grazing impacts than the ploughed fields.

Vegetation community descriptors

The vegetation community attributes of the reference farms were quite different from each other. Communal reference farms were significantly higher in species richness, vegetation cover, and abundance of plants than private reference farms (Table 2.10). Private reference farms had the lowest mean abundance of 403 individuals and differed significantly from communal reference farms, which had a mean abundance of 853 individuals per 100 m transect.

The diversity indices, species diversity, species richness, and evenness were significantly lower for ploughed fields compared to both communal and private reference farms (Table 2.10) and decreased by around half. Vegetation cover was significantly reduced after ploughing (43%–45%) compared to reference sites (65–82%), particularly communal reference farms. The proportion of plants growing in a patch was quite low and similar across the land categories, ranging from 20–24% on ploughed fields to 35–36% on reference farms. Plant abundance was similar between the communal reference farms and the ploughed fields, and was significantly higher than the private reference farms.

Table 2.9 Environmental factors (mean ± SD) from four land uses in Kamiesberg Renosterveld. Mean average rainfall and temperature data were obtained from Schulze (1997, 2010). Elevation was recorded with the use of a hand held GPS. Soil depth, and cover proportions of plant litter, rock, dead shrub and bare soil cover were recorded during the vegetation survey along 100 m transects at each site on young fields, old fields, communal reference farms and private reference farms. Mean values do not differ significantly if superscripts contain the same letter, for each factor as determined by ANOVA (Tukey HSD). The F value for each ANOVA is indicated *P <0.05, **P<0.005, ***P<0.001 and not significant (NS)

	Land use				
Environmental factor	**Young fields (n = 4)**	**Old fields (n = 3)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 3)**	**F value**
Elevation (m)	1110.0 (42.7)^{a}	1218.8 (137.5)^{ab}	1366.7 (16.3)^{b}	1135.0 (7.0)^{a}	10 *
Rainfall (mm)	289.2 (20.6)^{a}	297 (51.1)^{ab}	343.2 (21.3)^{b}	257.6 (64.0)^{ab}	7 *
Temperature (°C)	15.7 (0.1)^{a}	15.5 (0.8)^{a}	14.9 (0.8)^{a}	15.6 (1.5)^{a}	1 NS
Plant litter cover (%)	8.4 (1.9)^{a}	9.5 (5.2)^{a}	12 (7.5)^{ab}	16.5 (5.8)^{b}	8 *
Bare soil cover (%)	53.0 (7.3)^{a}	46.7 (16.1)^{a}	23.0 (6.3)^{b}	24.6 (2.1)^{b}	7 ***
Dead shrub cover (%)	3.4 (4.1)^{a}	3.2 (2.1)^{a}	4.1 (3.3)^{a}	4.5 (4.9)^{a}	1 NS
Grazed (%)	22.6 (13.2)^{a}	15.9 (9.7)^{a}	12.3 (6.6)^{ab}	9.6 (5.4)^{b}	9 *
Rock cover (%)	0.17 (0.15)^{a}	0.03 (0.05)^{a}	0.5 (1.83)^{a}	0.70 (0.46)^{a}	1 NS
Soil Depth (cm)	39.85 (11.86)^{a}	39.29 (13.02)^{a}	29.21 (12.95)^{a}	20.40 (0.70)^{a}	1 NS

Table 2.10 Vegetation community descriptors (mean ± SD) across four land uses in Kamiesberg Renosterveld. Young fields and communal reference farms had four sites each that were surveyed and old fields and private reference farms had three sites each that were surveyed. Each site was surveyed with a 100 m transect. Mean abundances do not differ significantly if superscripts contain the same letter as determined by ANOVA (Tukey HSD). The F value for each ANOVA is indicated *P <0.05, **P<0.005, ***P<0.001 and not significant (NS)

	Land use				
Vegetation descriptor	**Young fields (n = 4)**	**Old fields (n = 3)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 3)**	**F Value**
Shannon Diversity (H) index	1.4 (0.2) ^{a}	1.7 (0.4) ^{a}	2.3 (0.6) ^{b}	2.2 (0.1) ^{b}	19 *
Simpsons Index of Diversity (1 – D)	0.4 (0.1) ^{a}	0.7 (0.1) ^{a}	0.3 (0.2) ^{b}	0.5 (0.0) ^{b}	30 *
Species richness	10.0 (1.4) ^{a}	11.1 (2.39) ^{a}	21.2 (3.1) ^{b}	14.1 (2.3) ^{c}	70 ***
Evenness	0.1 (0.1) ^{a}	0.7 (0.1) ^{b}	0.1 (0.1) ^{c}	0.3 (0.0) ^{c}	29 *
Plant abundance	856 (254) ^{a}	658 (184) ^{ab}	853 (258) ^{a}	403 (74.0) ^{b}	11 *
Vegetation cover (%)	43.7(9.2) ^{a}	45.2 (12.3) ^{a}	81.6 (15.2) ^{b}	61.1 (5.3) ^{a}	7 ***
Individuals part of a patch (%)	24.1 (11.9) ^{a}	20.0 (10.5) ^{a}	35.0 (10.1) ^{b}	36.8 (5.2) ^{b}	8**

Ordinations of species

The ordination of species composition showed a clear distinction between ploughed and unploughed land in terms of abundance values (Figure 2.4). The ploughed fields of all age structures were fairly tightly grouped together indicating similarity. However, there was a slight increase in floristic heterogeneity with time post abandonment, The samples from both reference farms, however, were more scattered and when combined occupy a larger ordination space than the ploughed sites. This suggests a greater floristic heterogeneity within reference sites than within previously ploughed areas. The axes were significantly related to the abundance of *Eriocephalus africanus* (r^2 = 0.54), *Helichrysum hamulosum* (r^2 = -0.53), *Pentameris curvifolia* (r^2 = 0.53), *Pentzia incana* (r^2 = 0.41), *Chrysocoma ciliata* (r^2 = 0.36) and *Drosanthemum hispidum* (r^2 = 0.35). Ordinations of growth form abundance (Figure 2.4.b) did not reveal the same trends as above and there was a large degree of overlap between the ploughed fields and reference farms.

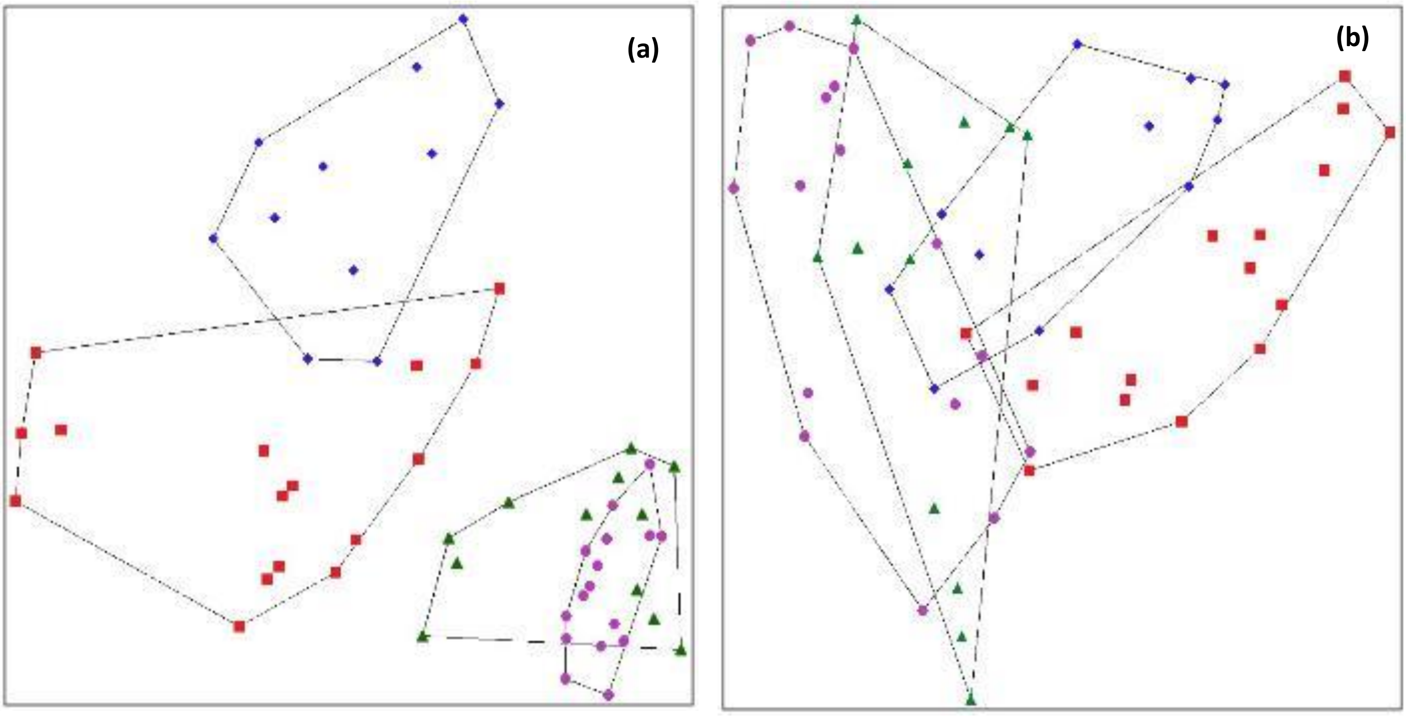


Figure 2.4 Two-dimensional plots of ordinations (NMS) of (a) abundance of all species, and (b) abundance within growth form types, from four different land use categories in Kamiesberg Renosterveld, as denoted by: purple circles = young fields, green Triangles = old fields, red Squares = communal reference farms and blue Diamonds = private reference farms. (Ordination distances in the original, n-dimension, show that the ordinations are well preserved in the two dimensional plots; cumulative correlation coefficients (a) = 0.82, and (b) = 0. 94)

Growth forms

Vegetation transects across the four land use categories in Renosterveld (Appendix F.1 and F.4) recorded 59 perennial species from 22 families in five growth forms, see Appendix A2. Overall, perennial graminoids contributed the most (47%) to the total plant abundance found in the vegetation survey. Perennial herbs were the next highest (25%), followed by SNLS shrubs (16%) and perennial herbs (11%). Leaf succulent shrubs contributed less than 1%. Of all the plant individuals recorded in the survey, renosterbos individuals contributed 12%. In general, there was a large degree of similarity between the ploughed and unploughed lands.

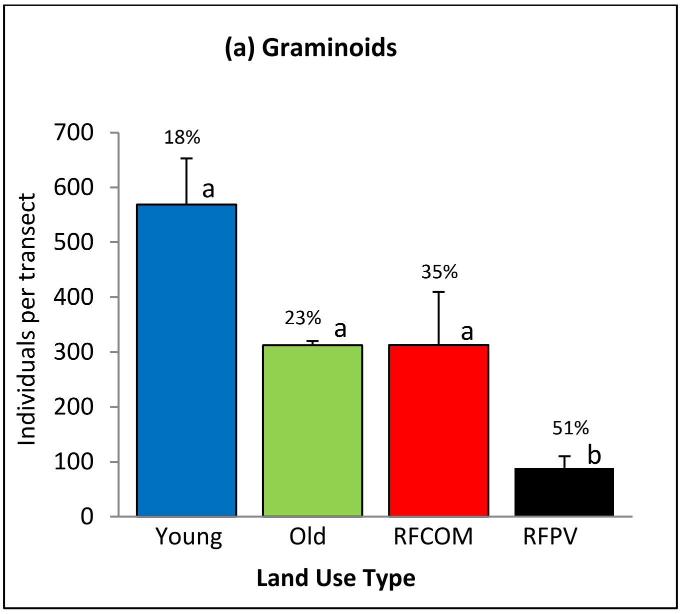
Within the first 20 years after cultivation ceased, perennial graminoids increased significantly (χ^2 (3) = 48.72, P 0.001, Figure 2.5.a) compared to private reference farms, which had the lowest abundance (89 + 21 individuals per transect), but not to communal reference farms. Young fields had the highest mean graminoid abundance (569 + 84.0 individuals per transect). Over time, perennial graminoid abundance did decline, but not substantially so, where abundance was reflected by perennial graminoids on communal reference farms. On reference farms, 35–51% of graminoids grew as part of a patch, whereas on all ploughed fields, less than 25% grew as part of a patch (Figure 2.5.a).

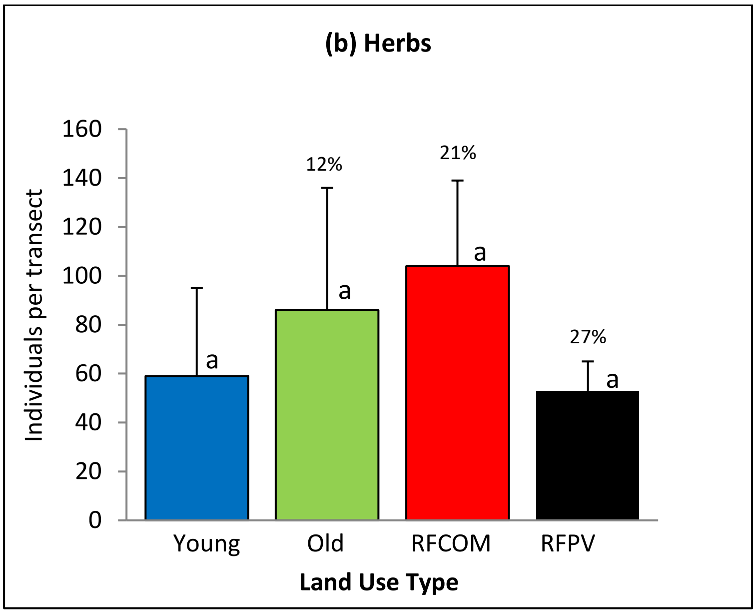
There were no significant differences between ploughed and reference sites for the perennial herb growth form. Although the numbers were similar across the land categories, on ploughed fields, less than 12% of recorded individuals grew as part of a patch, whereas on reference farms, 21–27% of herbs grew as part of a patch (Figure 2.5.b).

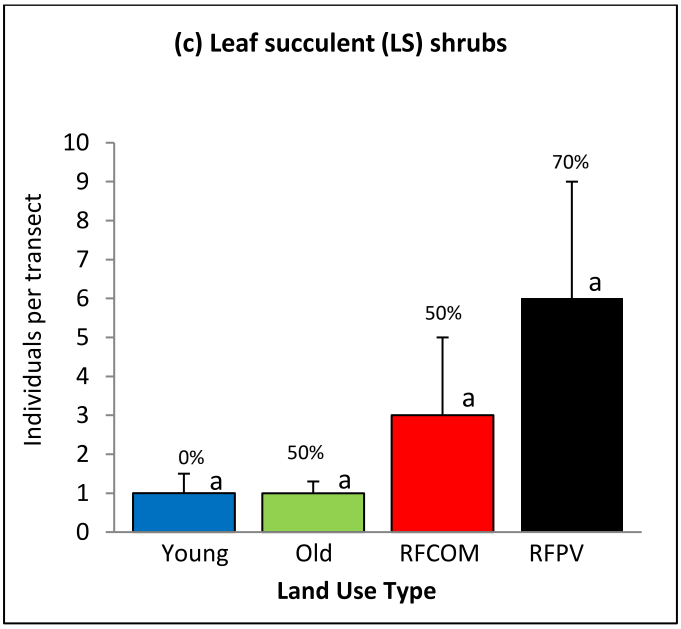
In Renosterveld, succulent shrubs are less abundant than in Hardeveld. Therefore, numbers were too low to form two growth form types (small and medium) and only one leaf (LS) succulent shrub class was created. The mean abundance of LS shrubs was very low, and ranged between 1–6 individuals per transect, and there was no difference between ploughed and reference sites (Figure 2.5.c). On young fields, the singular succulent to occur was *Conicosia elongata*, which did not grow as part of a patch. On old fields and both reference farms, 50–70% of other succulent species become part of a patch.

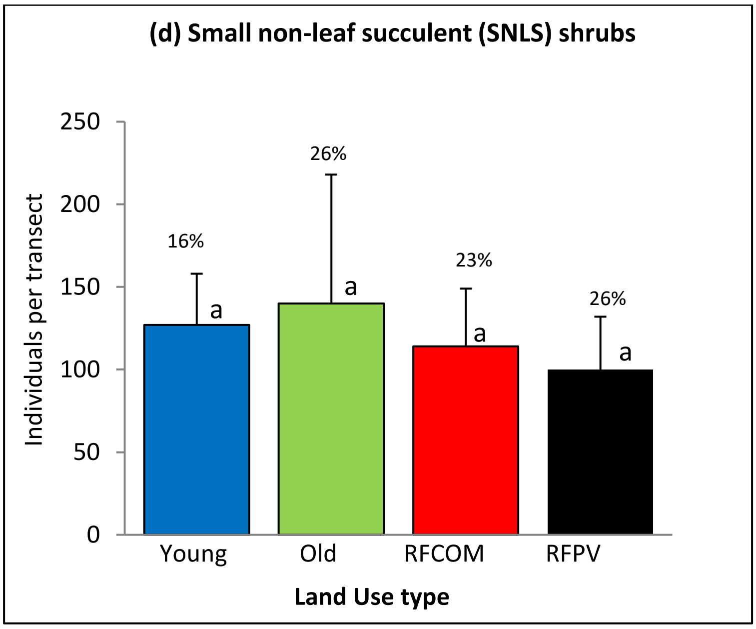
The abundance of SNLS shrubs was consistent across ploughed and reference sites, with means ranging from 100–140 individuals per transect, and no significant differences were found between ploughed and reference sites (Figure 2.5.d). On young fields, 16% grew as part of a patch and this increased over time to 26%, which is the same as the proportions found on reference sites.

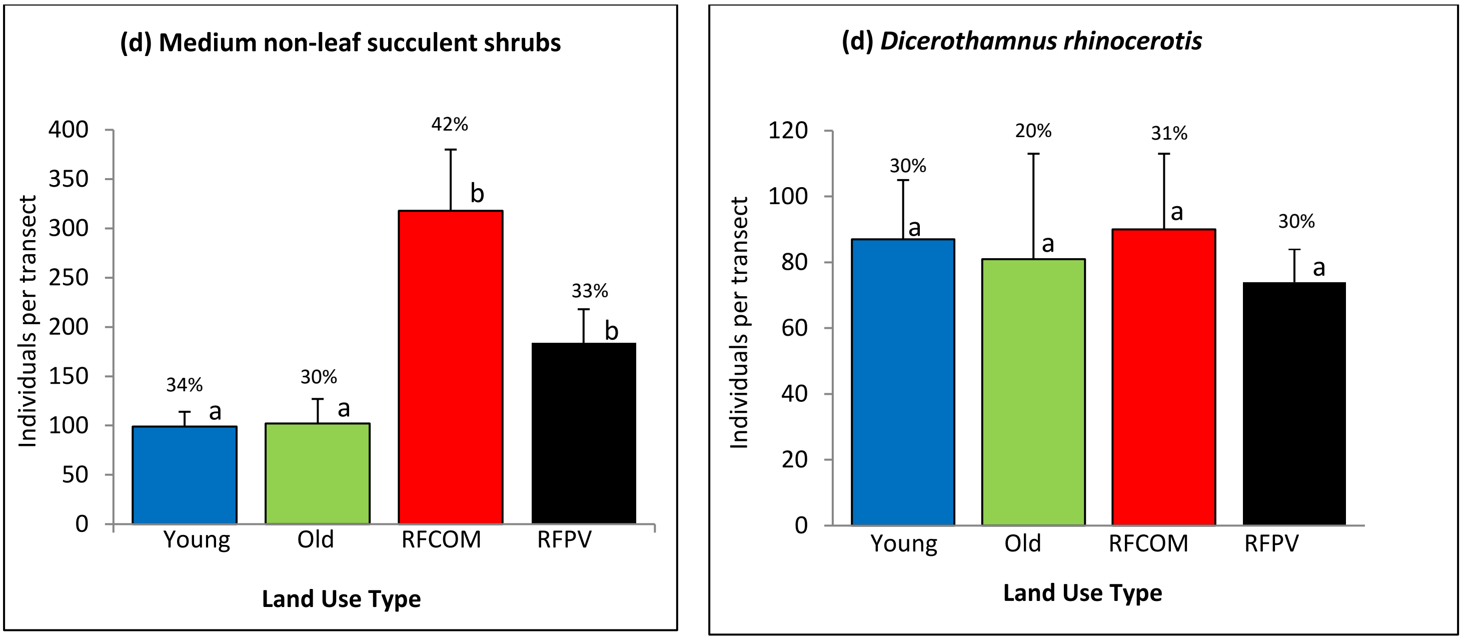
After cultivation ceased, MNLS shrub abundance declined and stayed consistent over time at around 100 individuals per transect (Figure 2.5.e). Communal reference sites had the highest abundance of 318 (± 62) individuals per transect and differed significantly from both fields (χ^2 (3) = 48.72, P 0.01, Figure _e) but not from private reference farms with 184 (± 34) individuals per transect. Between 30 and 40% of MNLS shrubs grew in a patch across the land use. Renosterbos abundance was consistent across ploughed and reference sites. It also consistently grew by 20–30% as part of a patch (Figure 2.5.f).


(a) Graminoids


(b) Herbs


(c) Leaf succulent (LS) shrubs


(d) Small non-leaf succulent (SNLS) shrubs



(d) Medium non-leaf succulent shrubs

(d) *Dicerothamnus rhinocerotis*

Figure 2.5 Perennial plant abundance (mean + SE) of various growth forms recorded in a vegetation survey across four land use types in Kamiesberg Renosterveld. Each site was surveyed with a 100 m transect. Growth forms are plotted as: (a) perennial graminoid, (b) perennial herbs, (c) leaf succulent (LS) shrubs, (d) small non-leaf succulent shrubs, (e) medium non-leaf succulent shrubs and (f) the shrub D. rhinocerotis. Numbers (percentage) displayed above each bar indicate the percentage of individuals for that growth form found to be part of a patch. Where no number is displayed, the percentage was zero. Mean abundances do not differ significantly if superscripts contain the same letter as determined by GEE and Sidak analyses (P<0.05)

2.4. Discussion

Ploughing is an immediate, intense, and unnatural disturbance, resulting in the complete removal of the standing vegetation as well as having below-ground impacts. It has a different impact from that of grazing or fire and causes a different successional pathway. This study revealed that passive recovery after cultivation does not occur primarily because of the removal of perennial vegetation, a decline in soil condition, and a disruption of the fertile islands associated with long-lived plants.

2.4.1 Soils

2.4.1.1 The effect of cultivation on the physical and chemical properties of the soil

Soils in this area are underlain by granite gneiss, which has weathered to a structureless, sandy, and yellow-brown to brown loamy sand. Like those of other semi-arid areas, the sandy, colluvial soils around Leliefontein and Tweerivier are poor in nitrogen and organic matter (Garcia-Moya & McKell, 1970; Allsopp, 1999; Watkeys, 1999; Carrick, 2001). Cultivation has an impact on the soil that is significant and long-lasting (Allsopp, 1999), and it negatively affects the functioning and formation of the fertile islands. Despite nearly seven decades having elapsed since cultivation, there are significantly lower levels of organic matter and nutrients on the old fields. This is due to crops removing nutrients from the soil, as well as the removal of vegetation, which creates large areas of bare soil that are vulnerable to wind and water erosion. In the Mediterranean Basin, where widespread fertilisation occurs (Römermann *et al*., 2005), abandoned fields are often enriched with nutrients, which can enhance the establishment of alien species, particularly grasses (Heelemann, 2010; Sharma *et al*., 2010). My study did not indicate any kind of nutrient enrichment. In fact, in both vegetation types, nutrients decreased after ploughing. This is very likely due to the farming methods used by communal farmers in this area, who do not have access to expensive broad-spectrum commercial fertilizers and do not farm as intensively as large-scale commercial farmers.

The long-term effect of cultivation on the soil was different for the two study areas. In Hardeveld, only the organic matter fraction, sodium and carbon proportion decreased, while pH and phosphorus increased on old fields. This is in line with other studies for semi-arid environments, where the loss of shrubs leads to a significant decrease in carbon mineralization rates (Vinton & Burke, 1995) and a loss in organic matter (Allsopp, 1999). This also mirrors the results found for pH, which were recorded as being significantly higher in a kraalbos dominated community, (therefore similar to the ploughed fields in this study), than in a *Ruschia* dominated (therefore similar to the reference farms used in this study) community (Carrick, 2001). In Renosterveld, all the measured soil variables in my study were negatively affected by ploughing. This differs from Heelemann (2010) and Walt (2006), who found that pH and phosphorus increased significantly on old fields in Renosterveld. In these two studies, the increase in phosphorus was attributed to the addition of fertilizer to old fields.

2.4.1.2 The role of patch dynamics on soil

In this study I show that shrubs are responsible for changing soil in their immediate environment, instead of simply selecting more nutrient-rich microsites for establishment. In unploughed vegetation communities in both Hardeveld and Renosterveld areas, patches of plants growing together influence the quality of the soil, by increasing the organic matter fraction, carbon, sodium and nutrients such as potassium and magnesium. This is a noteworthy finding that supports the concept of fertile islands under patches, and how high productivity is ensured in patches.

This accumulation of nutrients, organic matter and biotic activity under shrubs is likely to influence ecosystem functioning (Milton, 1995b). Plant debris from the plants within the patch contributes to surface organic matter and consequently nitrogen accumulation (Garcia-Moya & McKell, 1970)*. This has been recorded in other semi-arid ecosystems.* Schlesinger *et al*. (1996) found that in North America extractable phosphate and potassium are concentrated under patches of shrubs. Similarly, Rostagno *et al*. (1991) found that exchangeable potassium, magnesium and sodium were concentrated under shrubs in South America. In South Africa, higher pH, organic matter and nitrogen values have been found under shrubs in the Karoo (Carrick, 2001; Stock *et al*., 1999). In Hardeveld Carrick (2001) found that patches of succulent plants increased nitrogen in the soil. This trend has also been recorded in Renosterveld by Mills and Fey (2004), who found that soil carbon and nitrogen was significantly greater under renosterbos than in open sites.

2.4.1.3 Role of pioneer plants on patch dynamics

It is important to know if fertile islands reform after cultivation has ceased. Despite the reduction of nutrients on old fields, patterns of concentrating nutrients under shrubs could ensure higher productivity in a rather barren landscape and be essential for improving ecosystem processes (Allsopp, 1999; Tongway, 1990; Tongway & Ludwig, 1991). Hardeveld and Renosterveld vegetation had very different results in this regard. Both kraalbos (*Galenia africana*) and renosterbos *(Dicerothamnus rhinocerotis)* function as pioneer plants. Results from this study suggest that kraalbos can improve soil fertility by increasing organic matter, carbon and all nutrients except nitrogen under its canopy, as compared to the surrounding soil. These findings are similar to those from nearby Paulshoek (Allsopp, 1999; Carrick, 2001). Its most significant impact is that kraalbos significantly increases soil pH (Allsopp, 1999; Carrick, 2001). Even though soils that have been ploughed in this area already have a higher pH than those which have not been cultivated, the soil underneath kraalbos is now relatively alkaline (pH 7.6), whereas under patches in intact vegetation the soil is relatively acidic (pH 4.5). The same trend was found for potassium, sodium and phosphorus concentrations. This supports findings from Allsopp (1999) where phosphorus doubled under the canopy of kraalbos and from Carrick (2001) with regard to sodium. I theorise that although kraalbos does create a fertile island which could facilitate the re-establishment of the original community, it has created a more basic or alkaline soil environment, which the original vegetation cannot tolerate. This change could contribute to the success of kraalbos itself, whereby nutrients become more available for individuals of this species (Allsopp, 1999). Kraalbos patch size was also positively correlated with increases in carbon and organic matter. This coincides with Allsopp's (1999) findings for kraalbos, indicating that these shrubs created fertile islands and did not simply establish on patches of existing increased fertility.

In Renosterveld, renosterbos occurred on both ploughed and unploughed reference sites. The results indicated that in unploughed, intact vegetation renosterbos creates a fertile island with improved levels of carbon, organic matter, nitrogen, and minerals. It therefore follows that soil properties under renosterbos in old fields should be similar. However, in old fields that have lain fallow for decades and which have been colonised by renosterbos it does not appear that this species has had any discernible influence on soil fertility, other than increasing potassium slightly. This poses an interesting question about what is contributing to the formation of the fertile islands under renosterbos in unploughed, intact areas. It is possible that other species need to be present under the canopies of mature renosterbos individuals in order to enrich the soil in renosterbos patches. This is an area that requires further research.

2.4.2 Vegetation

2.4.2.1 The impact of cultivation on the vegetation

Cultivation has led to a reduction in vegetation cover in both the lowland and upland areas of the Leliefontein commonage (Anderson & Hoffman, 2007). The removal of shrubs leads to the establishment of renosterbos and kraalbos, with few other species, and an increase in the cover of bare soil that persists for decades. The loss of the diversity and abundance of perennial shrubs is compensated by an increase in annual herbs and grasses (Chapter 3) during the wetter months and in high rainfall years (Todd & Hoffman, 1999). As in other areas of Namaqualand, this was evident in Hardeveld, but was not as evident in Renosterveld.

Current land-use practices have an important influence on natural recovery processes on abandoned fields in the Kamiesberg region (Kellerman & van Rooyen, 2009). Most fields in the communal areas are subjected to continuous grazing. Therefore, the vegetation struggles to recover irrespective of the length of time elapsed since abandonment. My study did not assess recovery on fields on commercial farmland. However, Kellerman & van Rooyen (2009) found that plant diversity was generally higher on old fields on commercial farmland than on communal land. It has also led to species such as renosterbos and kraalbos, two disturbance-tolerant species (Hongslo, Rohde & Hoffman, 2009), forming almost mono-specific, dense stands. This trend was already recorded in the early 1990's (Van der Merwe & Van Rooyen, 2011). Models of succession assume that colonising species are able to germinate in disturbed environments, have high seed production, and rapid growth (Connell & Slatyer, 1977). Such traits are present in both renosterbos and kraalbos. These ideas are explored further in Chapter 3.

The impact of cultivation on the Hardeveld vegetation community is pronounced. Species richness, vegetation cover, and numbers of plant individuals were only about half of those of the unploughed community and did not increase with time since cultivation. Diversity was also considerably reduced. Studies from Namaqua National Park (NNP) which is also located on Namaqualand Klipkoppe Shrubland, indicated that total plant species richness steadily increased with recovery time (Schmiedel *et al*., 2010), which may in part be due to it being inside a reserve/protected area, unlike the sites in my study that are exposed to continuous grazing. It is also evident that little to no autogenous recovery of the vegetation occurs over time. After ploughing in Hardeveld, bare soil cover is 60% and does not decrease with time. Whilst on private reference lands bare soil cover is 36%.

There is a shift in Hardeveld vegetation composition and structure, from a state dominated by succulent plants before cultivation to one dominated by woody and non-succulent shrubs and herbs. Perennial herb plants, such as *Pharnaceum confertum* and *Leysera gnaphalodes*, are the first pioneer herb species to establish rapidly after cultivation and maintain consistent numbers over time. They contribute close to half the plant abundance on old fields but are barely present on unploughed, reference lands. The diversity of succulent plants did not return after cultivation, with only a scattered few individuals of leaf succulents. Hardly any small non-leaf succulent (SNLS) shrubs returned after cultivation. Unlike small shrubs, there was no impact on the medium non-leaf succulent (MNLS) shrub group, which was the most dominant growth form recorded in the study. Nine common species occurred on all land types, in differing densities, suggesting that successional processes within this growth form have started on old fields. Three of these species are pioneers affiliated with disturbed communities, namely *Pentzia incana*, *Calobota sericea*, and *Eriocephalus* sp. (Beukes & Cowling, 2003; Hoffman and Rohde, 2007; Kellerman & van Rooyen, 2009). Even though there was a small overlap of common species, it is worth noting that after cultivation, roughly 22 shrub species do not return to fields. Continual subjection to grazing means these fields remain barren and dominated by unpalatable shrubs (Hoffman & Rohde, 2007). Perennial grasses as a group are not affected by cultivation.

Kraalbos is a pioneer plant that is aggressive in establishing on disturbed land and can survive for several years. They have undesirable characteristics in that they are unpalatable, difficult to control, and can be toxic to livestock (Todd & Hoffman, 1999; Krug & Krug, 2007). Allsopp (1999) notes that Kraalbos is able to tolerate poor quality soils and build up resources under its canopy, which contributes to its success in establishing on old lands. This is reflected in my study, with kraalbos establishing rapidly and prolifically in the first few years, with consistent numbers over time. These results clearly indicate that abandoned fields undergo little recovery of any form of the original vegetation community.

The findings from Renosterveld differed from those for Hardeveld. The results could indicate that the fields are undergoing some form of recovery from the original community, but only in terms of the vegetation structure. This is because the growth forms that occurred in the intact vegetation re-occurred in similar proportions to those on ploughed fields. This trend is reflected in other studies where there was a reduction in diversity, abundance, and changes in species composition following abandonment, but no changes in vegetation structure (Walton, 2006; Krug & Krug, 2007; Anderson, Hoffman & O’Farrell, 2010; Cowan & Anderson, 2019). In my study, there was a significant negative impact on species diversity, richness, and vegetation cover, which decreased by half on cultivated fields. There was also no improvement in these variables over time. Plant abundance was similar between communal reference lands and ploughed fields. However, bare soil cover was around 50% after ploughing, and stayed consistent over time. Two other studies have mentioned the problem of slow succession in abandoned fields in Renosterveld (Saayman & Botha, 2008; Horn *et al*., 2011). In line with similar studies conducted in other mediterranean-type ecosystems (Krug & Krug, 2007), studies on Renosterveld ecosystems in South Africa reveal some of the reasons for the slow recovery of abandoned fields, including dominance of competitive alien species, nutrient enrichment, and a depleted indigenous soil seed bank (Heelemann *et al*., 2013). It was found that annuals and small woody shrubs were abundant throughout the various stages of succession In Roggeveld Mountain Renosterveld (Van der Merwe & Van Rooyen, 2011) and in Overberg Lowland Renosterveld (Cowan & Anderson, 2019).

Although there was little difference after cultivation in growth forms, there were differences in species composition in Renosterveld. The perennial grass *Pentameris curvifolia,* which is ecologically important in protecting trampled and disturbed rangelands from soil erosion (Gibbs-Russell *et al*., 1999), and the SNLS shrub *Chrysocoma ciliata* (short lived with a weedy life strategy), were both rarely present on reference sites*,* but were the first pioneer species to establish and dominate the cultivated fields over time. This has been noted by other restoration studies in the area (Simons, 2017). Heelemann *et al*. (2013) similarly recorded poor re-establishment of indigenous species in degraded habitats, even after a long period of rest. After cultivation it is typical for fallow fields in Renosterveld to be colonised by ruderal species and grasses (Cowan & Anderson, 2019; Walton, 2006). Renosterbos itself returns to fields soon after ploughing, and rapidly increases over a short time frame to abundances found prior to cultivation. Renosterbos develops a deep tap root and can withstand a variety of temperature and water fluctuations, contributing towards its successful dominance (Scott & van Breda, 1937; Walton, 2006). It was also unexpected that perennial grasses were so abundant in cultivated fields, as it is normally annuals that first colonise disturbed areas. Considering the strong prevalence of grass on old fields, competition from grass could have a strong effect on the establishment of shrubs (Midoko-Iponga *et al*., 2005).

2.4.2.2 The impact of cultivation on patch dynamics

In the Hardeveld vegetation community, the theory that unploughed, intact vegetation grows together as part of a patch is well supported. About 40 – 63 % of all plants recorded did so, with all grasses, most herbs, and half the succulent and non-succulent shrub species following this trend. Larger shrubs protect understorey vegetation, such as grasses and forbs, from the effects of high temperature (Garcia-Moya & McKell, 1970). Almost half of the dead shrubs occurred within a patch, together with other plants, and could play a function in protecting seedlings, by creating microsites (Esler & Cowling, 1993).

After ploughing, however, the vegetation growing on these fields does not follow the original community trend of multiple plants growing together in patches. Fewer than 20 % of all plants were recorded as growing together as part of a patch. Grasses, herbs, SNLS shrubs and succulent plants grow mostly in the open spaces or on their own. Patches consist primarily of multiple kraalbos plants, with a handful of other species that tend to decrease over time, even though soil conditions under its canopy are more fertile than in the open sites. I theorise that the lack of indigenous plant establishment under kraalbos is due to changes that kraalbos has caused in the soil, via increased pH levels and phosphorous, which is likely beyond concentrations that other species can tolerate.

In Renosterveld the proportion of plants growing in a patch on all land uses was not as prominent as it is in Hardeveld, and it is therefore difficult to interpret the impact and rate of recovery. Patch dynamics is not a concept that has been studied in detail in Renosterveld, although it has been reported that renosterbos has a facilitatory role as a ‘nurse’ site for geophytes, herbs, dwarf shrubs, and perennial grasses (Walton, 2006). As renosterbos is one of the most dominant plants on all land types it follows that other plants would grow in a patch with it. However, in my study it was only perennial grasses that grew in a patch to any significant extent, and this was only seen on private reference farms. Leaf succulents also had a preference for growing together in a patch, but their numbers were very low across the study. Renosterbos seedlings appear intolerant of shading and therefore germinate in open spaces (Levyns, 1927). This was evident in my study with only 20 – 30 % of renosterbos seedlings forming part of a patch across all land types.

2.4.2.3 Effect of different grazing pressures on the vegetation in reference lands

The reference farms were chosen in order to obtain a more complete understanding of the functioning and composition of intact, unploughed vegetation, under different grazing pressures that occur in communal and privately-owned lands (Anderson & Hoffman, 2007; Todd & Hoffman, 2000). It should also be noted that ploughed fields and communal reference farms had similar grazing values, which is to be expected, as both land types can be exposed to regular grazing in the commonage.

In Hardeveld all the sites across the land uses were similar in terms environmental factors such as elevation, average rainfall, average temperature, plant litter, rock cover and soil depth.

The private and communal reference sites were comparable to each other in environmental factors and vegetation community structure. The intact community is very diverse and abundant in succulent species, with *Leipoldtia schultzei, Ruschia* sp.*, Lampranthus* sp. and *Cephalophyllum* sp. dominating the community. Other perennial plants constituting a major part of the community are the shrub *Eriocephalus ericoides* and the grass *Ehrharta barbinodis.* There are very few kraalbos in the community. Differences due to grazing pressure were observed in the proportion of grazed individuals, as there is a significantly higher proportion of grazed individuals on communal reference farms compared to private reference farms, supporting the theory of a higher grazing pressure on communal farms. Grazing could also account for the significantly lower vegetation cover of 35 % compared to 53 % on private land. As a consequence of higher grazing and trampling activity, communal sites had significantly more bare soil than private farms. Higher grazing pressures in communal areas is further supported by the results, where communal farms had similar proportion of bare soil cover as old fields, and similar proportions of grazed individuals were found on young fields, old fields and communal reference farms, which are all located in the commonage area.

In Renosterveld the communal and private farms were similar to each in terms of soil depth, rock cover and temperature. They differed in terms of elevation, rainfall, species diversity, vegetation cover and abundance, with communal reference lands having higher recordings of each. An unusual result was that private reference lands had the lowest plant abundance across the study yet had the same grazing impact and plant litter values as communal lands. The communal farms were more vegetated and contained higher numbers of individuals across the growth forms. This difference between the reference lands could be due to private landowners not providing an accurate grazing history, and thus the vegetation is exposed to a higher grazing pressure than was anticipated. However, considering three different private farms and their landowners were involved in the study, it unlikely that all of them were not specific in the information provided. The difference in vegetation between the private and communal farms is more likely attributed to the difference in altitude and rainfall. Private reference farms consistently had the lowest plant abundance, as well as the lowest mean rainfall of all four land uses. In rainfall restricted dry environments, a difference of 40 – 80 mm could have significant implications for vegetation, as well as challenging the findings for understanding intact vegetation. Perennial grass was the only growth form to substantially differ between the reference lands, where the abundance on private lands was very low. The restioid species *Restio gossypina* and the sedge *Ficinia* sp were not present on the private lands. In Renosterveld the reference farms were dominated by the shrubs renosterbos*, Helichrysum hamulosum* and *Euryops lateriflorus,* the grass *Tribolium hispidum* and the herb *Pharnaceum confertum*.

2.5 Conclusion

In this study, I confirmed the theory that patches of plants in unploughed, intact vegetation do exhibit improved soil fertility beneath their canopies in both Hardeveld and Renosterveld vegetation. In Hardeveld, there is a clear preference for plants to grow in patches, which was not as clear in Renosterveld.

Cultivation has resulted in the removal of much of the original vegetation and has negatively impacted the condition of the soil. Even though previously cultivated fields have been left to rest for decades, albeit with continued grazing pressure, passive recovery is extremely slow or non-existent. Fallow fields appear to be locked in an alternative state, characterized by a change in species composition and a loss of cover. Only in Renosterveld did the alternative community resemble the original in terms of structure, but not in terms of composition.

The pioneer plants that colonise old fields are either not re-creating fertile islands over time (renosterbos) or have created fertile islands but have altered soil conditions to such an extent that the original vegetation community may struggle to survive in such conditions (kraalbos). In both Hardeveld and Renosterveld, these results indicate a vital aspect of patch functioning that is lacking on fallow fields and is a significant barrier to the establishment of other species. There is also an indication that pioneer plants are not providing a patch-like environment for other species to grow in, which limits the number of locations within which seedlings can be established.

Chapter 3 Seed bank dynamics and post-cultivation succession in two arid vegetation types in the Kamiesberg, South Africa

3.1 Introduction

This chapter describes the impact that cultivation and fallowing have had on the composition and dynamics of the soil seed bank in two vegetation communities in the uplands and lowlands of the Leliefontein commonage in Namaqualand.

3.1.1 Cultivation and grazing

Large parts of the world's arid and semi-arid regions have been transformed by agriculture Hobbs & Walker, 2007). In Namaqualand, the area cultivated for cereal crops had declined significantly by the mid-1990s due to economic and social constraints (Hongslo *et al*., 2009). This has resulted in many abandoned croplands lying scattered throughout the Namaqualand landscape (Schmiedel *et al*., 2010). Long-term ploughing strips an area of the natural vegetation, depletes the soil of the natural seed bank and possibly also buries seeds too deeply in the soil (Hobbs & Walker, 2007). The soil seed bank is comprised of all viable, un-germinated seeds in the soil (Baskin & Baskin, 1998; De Villiers, Van Rooyen & Theron, 2003) and enables the long-term survival and coexistence of many species (Grime, 1974; Donnell, Fryirs & Leishman, 2014). The abundance of species and the quantity of seed produced in the growing season by the established vegetation primarily determines the composition of the seed bank (Connor & Pickett, 1992). The presence of a soil-stored seed bank also increases the resilience of plant communities to disturbance (Donnell, Fryirs & Leishman, 2014).

Grazing by goats and sheep has also contributed towards degradation and is likely to hinder recovery of the vegetation. Intense browsing of flowers and fruit on shrubs reduces seed production (Milton, 1994), and therefore reduces seed input into the soil. Reduction in flower and seed production has been recorded in Paulshoek (Todd & Hoffman, 1999) and the Karoo in general (Milton, 1995b). As a result of grazing, the flowers and seeds of palatable species are reduced which leads to changes in plant species composition is over time (Anderson & Hoffman, 2007). The intensity of grazing pressure can influence seed bank composition, and in the study area livestock farming methods differ greatly between communal agricultural land (which is browsed continuously throughout the year by multiple farmers) and private commercial farms (which is browsed on a rotational basis with periods of rest).

3.1.2 Succession

There are many factors that delay or hinder the recovery of old fields after abandonment. Removing the source of the disturbance may not always result in improvement (Whisenant *et al*., 1995), particularly in arid areas where water is a limiting factor to re-vegetation (Von Hase *et al*., 2003). Other factors that affect the rate of vegetation recovery in these old fields are due to seed limitations (Hobbs & Walker, 2007; van Oudtshoorn & Van Rooyen, 1999). This includes a limited quantity of perennial seeds in the soil as a result of limited seed dispersal, competition from dominant herbaceous plants and herbivory by ungulates (Midoko-Iponga *et al*., 2005). It is also affected by the proximity of the disturbed area to intact, unploughed vegetation, from where seeds can disperse and from where the colonisation of degraded areas can begin. The loss of vegetation is well documented, but the role of seed limitation as a driving force for retaining habitats in a degraded state is not (Suding & Hobbs, 2009).

Holl *et al.* (2000) indicated that the initial step in studying the recovery of a vegetation community is to determine whether propagules are present in the disturbed area. The availability of seeds is an important step towards the onset of recovery, as the composition of the vegetation on these degraded lands will depend on fresh seed rain. Soil seed banks play a crucial role in rebuilding biodiversity after disturbance and can be destroyed by extreme events (Suding & Hobbs, 2009). After degradation, the seed bank composition usually consists of plants that colonise the degraded area.

3.1.3. Soil seed banks

Studies of soil seed banks are important in plant population ecology, conservation, restoration, and management of plant communities and have only recently considered the importance of dispersal in the establishment of ‘target’ communities. The knowledge of dispersal syndromes present in different vegetation types is essential for conservation, management, and restoration of indigenous vegetation communities (Chambers, 2000). Seed dispersal was the most important factor in the second phase of restoration, after activating the seed bank in dry grasslands and Succulent Karoo vegetation (Bakker *et al*., 2013; De Villiers *et al*., 1994; K. Thompson *et al*., 1993).

In the Succulent Karoo, seed bank studies are quite extensive and have been conducted in a number of areas in Namaqualand, along the coast in Strandveld (De Villiers *et al*., 2002, 2003), in Goegap and Skilpad Reserves (Van Rooyen, 1999), and around Paulshoek (Carrick, 2001;

Simons & Allsopp, 2007). Recovery after cultivation on Namaqualand's shrublands is slower than on grasslands, due to the relatively short-lived seed bank and the poor seed dispersal properties of the dominant succulent shrub species (Hongslo *et al*., 2009; van Rooyen, 2002). In Renosterveld, seeds of indigenous shrub species are absent in old-field soil and succession appears to take many decades (Midoko-Iponga *et al*., 2005; Saayman & Botha, 2008; Shiponeni, 2003) with poor re-establishment of indigenous species, even after a long period of rest (Heelemann *et al*., 2013; Kemper *et al*., 1999).

Soil seed bank studies of old fields and adjacent native vegetation in Mediterranean biomes have received some attention (Krug & Krug, 2007), but only a few studies have been done in South Africa's Renosterveld ecosystems (Heelemann *et al*., 2013; Saayman & Botha, 2008; Shiponeni, 2003). The Renosterveld, which borders the Succulent Karoo lacks important information on ecological processes (Cowan & Anderson, 2019; Curtis, 2013). There is a vital need for studies into the biological attributes (such as seed dispersal and seed banks) of key species in Renosterveld which are required for future restoration projects. Studies on vegetation recovery and seed banks after cultivation in the Renosterveld have been centred on shale derived Renosterveld remnants in Cape Town, with little research on the mountainous, and in particular, the Kamiesberg, granite-derived Renosterveld. In Coastal Renosterveld, seeds of indigenous shrub species are absent in old-field soil (Midoko-Iponga *et al*., 2005; Saayman & Botha, 2008; Shiponeni, 2003), with poor re-establishment of indigenous species, even after a long period of rest (Heelemann *et al*., 2013; Kemper *et al*., 1999). This is in contrast to seed bank studies conducted in Renosterveld which analysed soil under alien trees, particularly pines, where the desirable seed bank is well preserved and present (Cowan & Anderson, 2014; Heelemann *et al*., 2013). Thus, it is concluded that the activities of agriculture that have negatively impacted the seed bank.

In this study, I compared the seed bank of unploughed vegetation remnants to fallow fields ranging in age from 7 to 60 years since abandonment, in two previously unstudied vegetation types, in order to ascertain the following:

1. The effect of cultivation on the composition of the soil seed bank and the process of autogenic recovery over time in relation to intact, uncultivated land.
2. The effect of different grazing pressures on the composition of the soil seed bank in intact, uncultivated land.

3.2 Methods

The soil samples collected to study the seed bank in ploughed fields and reference lands were located on the same sites as those used in the vegetation surveys in Chapter 2. In Chapter 2, Tables 2.1 and 2.2 provide information regarding the GPS co-ordinates, location, land-use history, and elevation of all the sites used in the study, and a map of the sampling sites is shown in Figure 2.1.

The collection of soil used in the seed bank study took place in the dry month of March 2014, before the first winter rains fell and before germination could commence. A rectangular strip of soil, roughly 30 cm long by 10 cm wide, directly under the 'skirt' (the outer edge of leaves or branches of a plant, or clump of plants, which overhangs the ground) around the plant of the most dominant adult species at a site was marked out. If the 'skirt' of the plant touched the ground, it was carefully lifted to be able to access the soil. After removing surface litter and dung, the top 5 cm of soil from the strip was collected. It was assumed that this was where the majority of seeds would be concentrated and that the number of seeds would generally decrease with depth (Donnell *et al*., 2014). This soil sample was thoroughly mixed, bagged and moved to the greenhouse at the University of Cape Town for the germination experiments. At each sampling site, soil collection took place in the same area as the vegetation surveys were conducted. This was done by moving through the transect-sampled area and randomly selecting 12 shrubs under which soil was collected. Thus, for each land use category of young fields, old fields, communal reference farms, and private reference farms, each category had three to four sampling sites, where 12 soil samples were taken, therefore 48 samples for each land use.

The number of seeds of each species in a seed bank can be determined by either separating the seeds from the soil or allowing them to germinate. Allowing seeds to germinate in the soil eliminates the problem of deciding whether collected seeds are viable and if they would have lived until the time of the natural germination season in the habitat (Gross, 1990). The 48 soil samples from each land use were taken to the greenhouse (Appendix F.5), where 600 g of each soil sample was placed in a punnet (15 x 20 cm) for germination and spread to 3cm deep. The soil was sieved to remove roots and plant material and spread over a 3 cm deep, rich organic mix (of approximately neutral pH) in punnets that had been layered at the base with shade netting to contain the soil and allow water drainage. A thin layer of acid-washed sand was spread over the soil to limit desiccation. The punnets were kept continuously moist by twice-daily watering and were periodically treated with a fungicide. In order to limit the differences in lighting/ shading, and airflow effects within the greenhouse, punnets were rotated around the greenhouse every week. The punnets were inspected every week for the first seven weeks and then fortnightly thereafter. At each inspection, newly emerged seedlings were identified (with the aid of plant identification books and the assistance of the Bolus Herbarium curator), assigned to one of six growth form classes, marked (to avoid being re-counted in subsequent recordings), counted, and then carefully removed, by clipping the above-ground portion of the plant, thereby leaving the soil intact. Plants were marked with coloured paperclips, to avoid being re-counted if the plant grew from the undisturbed roots. The experiment ran for 4.25 months (17 weeks in total), at which point less than three new individual seedlings per punnet had germinated in the preceding fortnight and the experiment was terminated. Plants were assigned to growth form classes based on the following criteria:

(a) Annual herbs: plants without woody parts above ground that complete their lifecycle in one year. Examples include *Adenogramma glomerata, Felicia australis,* and various *Wahlenbergia* species.

(b) Annual graminoids: include grasses and sedges that also complete their life cycle in one year. Examples include *Aristida* sp.*, Bromus pectinatus* (an alien grass species) and *Pentameris airoides.*

(c) Perennial graminoids: include grasses and sedges that live for more than two years. Examples include *Ehrharta calycina, Digitaria argyrograpta,* and *Pentameris curvifolia.*

(d) Leaf succulent (LS) shrubs: woody plants with succulent leaves. As the number of germinating individuals was so low, this group was not divided into small and medium LS shrubs. Examples include *Drosanthemum* sp., *Crassula muscosa*, *Leipoldtia* sp. and *Ruschia* sp.

(e) Non-leaf succulent (NLS) shrub: all woody plants with non-succulent leaves. As the number of germinating individuals was so low, this group was not divided into small and medium NLS shrubs. Examples include *Euryops lateriflorus, Hermannia* sp.*,* and *Wiborgia* spp.

(f) Geophytes: plants with an underground storage organ. Examples include *Oxalis* and *Moraea* sp.

As with the vegetation survey (chapter 2), seed numbers of *Galenia africana* (kraalbos) and *Dicerothamnus rhinocerotis* (renosterbos) were analysed separately.

To control for the potential contamination of alien seeds in the greenhouse, six punnets were filled with the organic mix and sand and randomly located in the greenhouse amongst the experimental punnets. Only one plant species, a common garden weed found around the premises of the greenhouse, was recorded in the control punnets and in a handful of seed bank punnets. At the end of the trial, this species was removed from the data prior to analysis.

Over this period, the temperature in the greenhouse ranged between 13 °C and 42 °C and the relative humidity between 16% and 92%.

3.2.1. Analysis

Species accumulation curves were computed in R (see Chapter 2). The results showed that the number of replications for the seed bank study was sufficient to capture the plant composition for all the sites.

The following analyses were performed to assess the impact of cultivation on seed bank composition and to provide a measure of the rate of recovery of the seed bank after cultivation. Ordination techniques (the same as used in Chapter 2) were used to visually assess the similarities between ploughed and unploughed lands. For the seed bank, ordinations were constructed using the abundance of all seedlings and growth forms. For both Hardeveld and Renosterveld vegetation, useful ordinations of growth forms from the seed bank couldn't be made due to high stress, so each growth form was graphed separately.

Measures of plant abundance, species richness, species diversity, and evenness from the 12 punnets from the four sites (other than in Renosterveld, where it was three sites for old fields and private reference farms) across the four land uses were also compared with ANOVA’s and Tukey’s HSD. Analysis of the growth forms for the seed bank study from four sites (other than in Renosterveld, where it was three sites for old fields and private reference farms) across the four land uses was also compared using generalized estimating equations (GEE) with multiple comparisons with sequential Sidâk adjustment of the alpha value (IBM SPSS, 2015). The Shannon index of general diversity (Odum, 1971) was used to measure the diversity of seed banks using the same approach as outlined in Chapter 2.

3.3 Results

The results of the seed bank trial are presented for Hardeveld and Renosterveld separately. For each vegetation type, the vegetation community descriptor results are presented first, followed by the results of the five growth forms.

3.3.1 Hardeveld

During the 17-week period of the greenhouse experiment, a total of 3557 individual seedlings of 53 species, from 18 families, in six growth forms were counted from soils collected in Hardeveld vegetation (Appendix A3).

Vegetation community descriptors

The reference sites were very similar to each other for all descriptors except for the two diversity indices which were significantly lower for the communal reference farms. Ploughing had little consistent effect on the abundance, richness, evenness and diversity of species in the soil. There were no differences between young and old fields for any of the community descriptors listed in Table 3.1.

Table 3.1 Vegetation community descriptors (mean ± SD) of the soil seed bank across four land uses in Kamiesberg Hardeveld, germinated from 48 x 600 g replicate soil collections along the skirt of the dominant shrub in each land use. Mean abundances do not differ significantly if superscripts contain the same letter as determined by ANOVA (Tukey HSD). The F value of for each ANOVA is indicated *P <0.05, **P<0.005, ***P<0.001 and not significant (NS)

	Sites				
	Young fields (n = 48)	**Old fields (n = 48)**	**Communal reference farms (n = 48)**	**Private reference farms (n = 48)**	**F value**
Shannon –Wiener Diversity (H) index	1.5 (0.6)^{a}	1.4 (0.8)^{a}	1.1 (1.2)^{b}	1.4 (1.2)^{a}	12.1 *
Simpsons Index of Diversity (1 – D)	0.7 (0.1)^{a}	0.7 (0.1)^{a}	0.5 (0.2)^{b}	0.7 (0.1)^{a}	7.0 *
Species richness	5.3 (2.0)^{a}	5.0 (1.6)^{a}	4.6 (1.9)^{a}	5.5 (1.7)^{a}	1.0 NS
Evenness (Pielou's J' evenness)	0.6 (0.1)^{a}	0.4 (0.1)^{ab}	0.7 (0.3)^{b}	0.8 (0.1)^{ab}	8.0 *
Number of individuals	14.8 (1.6)^{a}	22.7 (4.5)^{a}	18.3 (2.6)^{a}	18.1 (1.9)^{a}	1.1 NS

Ordinations of species

The ordination of all species (Figure 3.1.a) indicated a high degree of overlap and similarity between ploughed and reference sites. Samples from the old fields occupy the least ordination space, indicating little floristic heterogeneity. The axes were significantly related to the abundance of *Crassula glomerata* ($r^2 = 0.53$), *Ficinia* sp. ($r^2 = 0.59$), *Felicia australis* ($r^2 = 0.48$) and *Helichrysum leontonyx* ($r^2 = 0.33$).

No reliable ordination plot of all growth forms could be produced, but when the growth forms were split into annual and perennial plant species, patterns did emerge. The ordination plot of perennial species (Figure 3.1b) suggests that the reference farms and ploughed fields are floristically different from each other. Reference farms were more diverse in their composition of perennial species, than the ploughed fields. The most abundant perennial species, *Ficinia* species, was correlated ($r^2 = 0.72$) with the vertical axis. The only other species that was significantly correlated with the vertical axis at the $r^2 > 0.3$ level, was a species of *Ruschia* ($r^2 = 0.58$).

However, the ordination of annual species indicated that ploughed and reference sites occupy the same ordination space and thus do not appear to differ in their composition of annual species (Figure 3.1c). *Felicia australis* (r2 = - 0.437), *Pentameris airoides* ($r^2 = - 0.494$)*,* and *Conyza bonariensis* ($r^2 = + 0.411$) were correlated with the horizontal axis. No species were correlated with the vertical axis at the $r^2 > 0.3$ level).

Growth forms

Overall, annual herb seedlings contributed the most (53%) to the total count of individuals in the greenhouse trial. Annual graminoid seedlings (which included grasses and sedges) were the next highest (20%) and were followed by perennial graminoids (16%). Perennial shrubs, of both non-succulent and succulent species combined, contributed about 10%, while geophytes contributed less than 1% to the total number of seedlings counted in the greenhouse trial. The shrub kraalbos on its own contributed 3% to the overall count of seedlings.

Old fields differed significantly from communal reference farms in terms of herb seedling numbers ($\chi^2_{(3)} = 15.75$, $P < 0.001$, Figure 3.2a). There was no significant difference in the number of herb seedling numbers between private reference farms (8.5 ± 1.3) and communal reference farms (5.2 ± 0.7).

The reference farms seedling numbers were very similar to each other and had low numbers of annual graminoid seedlings (mean of 3 individuals per punnet). Graminoid seed numbers were similar on ploughed and reference sites, However, these seedlings increased significantly ($\chi^2_{(3)} = 11.87$, $P < 0.01$, Figure 3.2b) over time, from young fields of 2 individuals per punnet to old fields of 5.9 individuals per punnet. The abundance of perennial geophyte seedlings was extremely low across all land use categories, with no significant difference between them (Figure 3.2c).

Reference farms ranged between 2 and 9 seedlings of perennial graminoids per punnet, with communal farms having the highest number of 9 individuals. There was a significant decline in reference sites relative to ploughed sites ($\chi^2_{(3)} = 49.77$, $P < 0.001$, Figure 3.2d). Very low numbers, <1 seedling per punnet, of perennial graminoid seedlings emerged from soil collected from ploughed fields, and this did not differ between young and old fields.

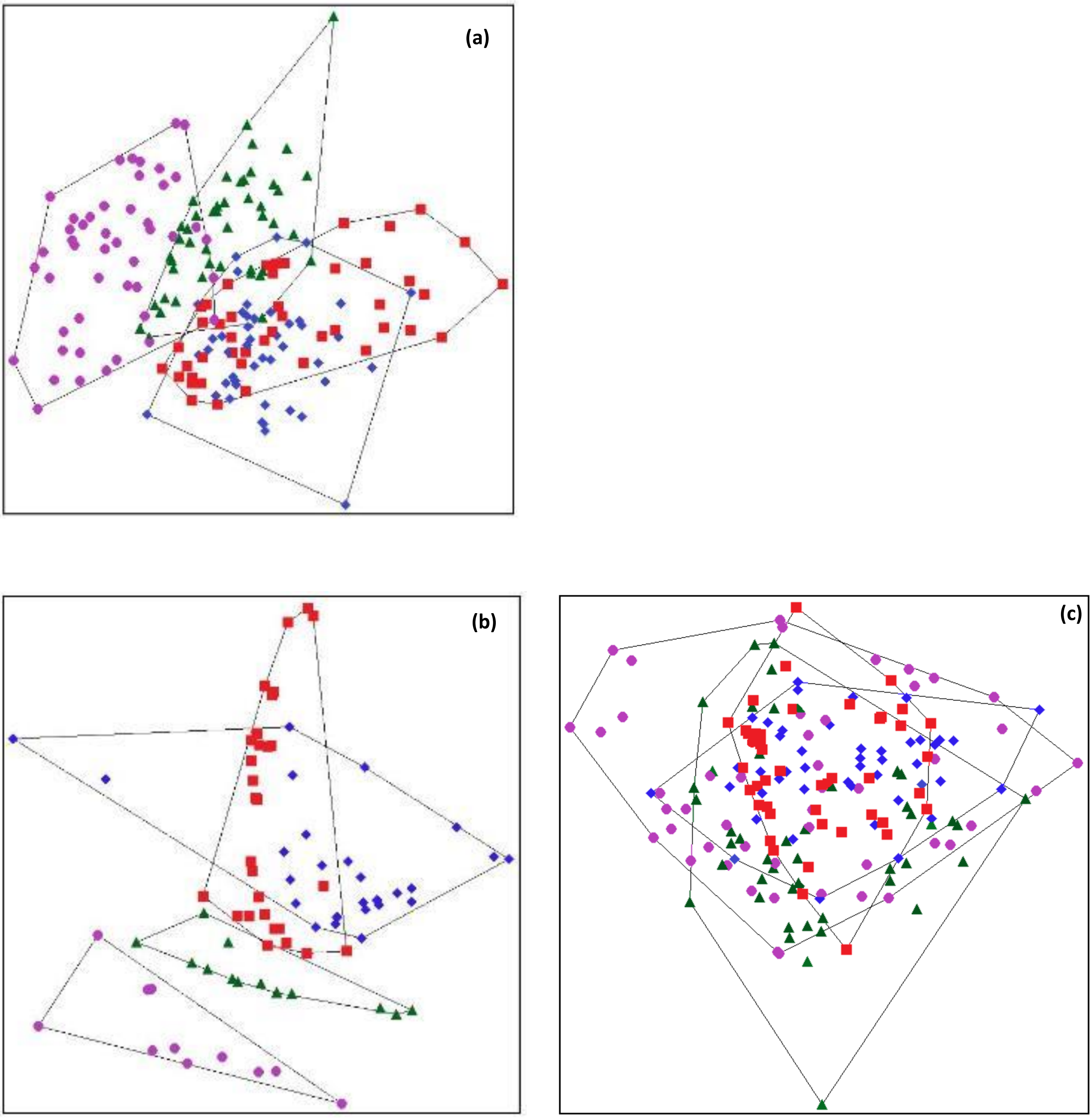
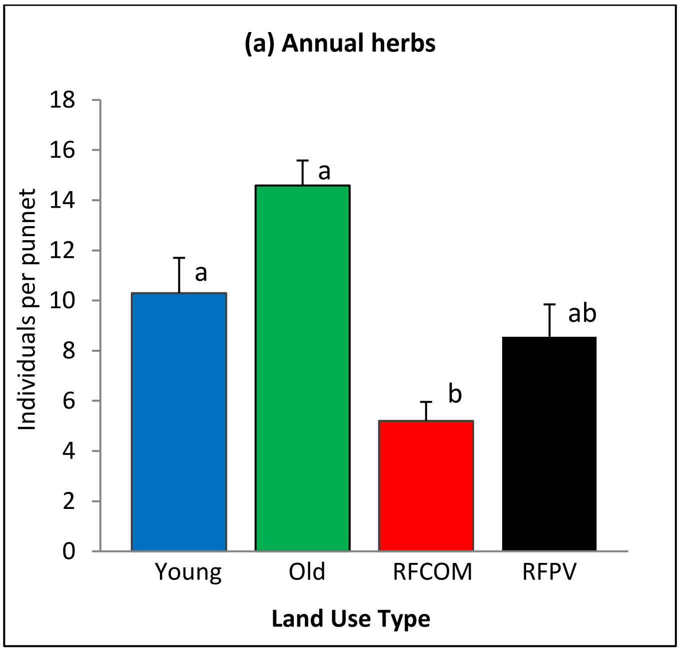
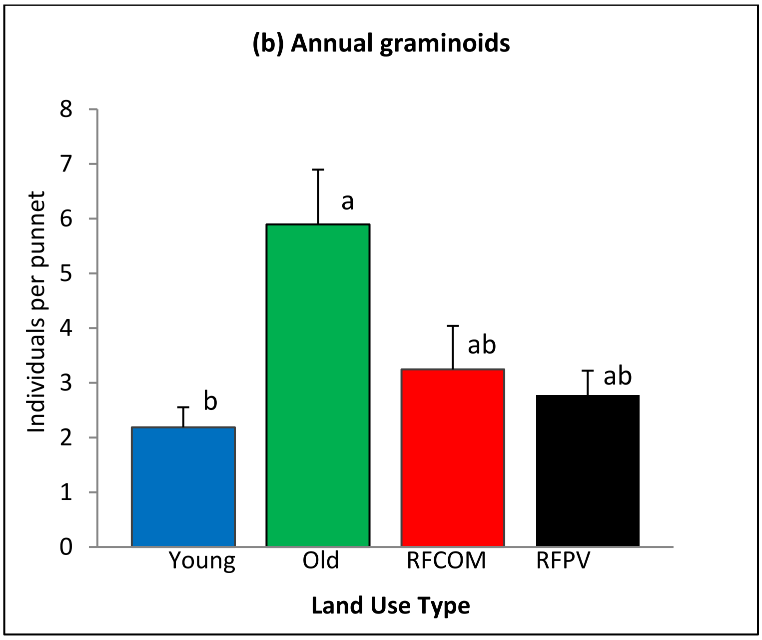


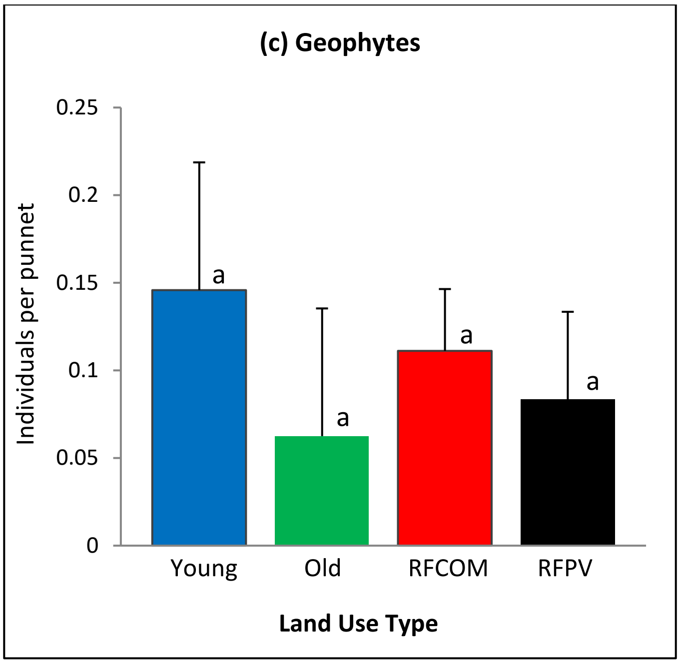
Figure 3.1Two-dimensional plots of ordinations (NMS) of the abundance of (a) all species, (b) all perennials, and (c) all annuals germinated from the seed bank in Kamiesberg Hardeveld germinated from 48 x 600 g replicate soil collections along the skirt of the dominant shrub in land use, as denoted by: purple Circles = young fields, green Triangles = old fields, red Squares = communal reference farms and blue Diamonds = private reference farms. (The cumulative correlation coefficient for (a) = 0.72; (b) = 0. 54 and (c) = 0.59.

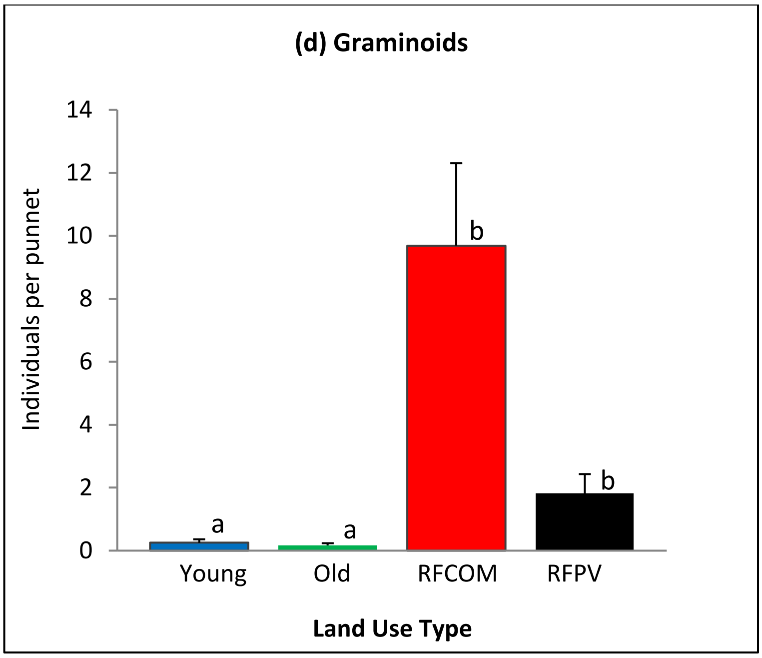
Reference farms contrasted ($\chi^{22}_{(3)}$ = 407, $P < 0.001$, Figure 3.2e) with each other in terms of the number of leaf succulent (LS) shrub seedlings. Communal farms had a mean of 0.33 (± 0.11) while private farms had a mean of 3.56 (± 1.14). Most noticeably, no recorded LS seedlings were found on any of the ploughed fields (Figure 3.2.e).

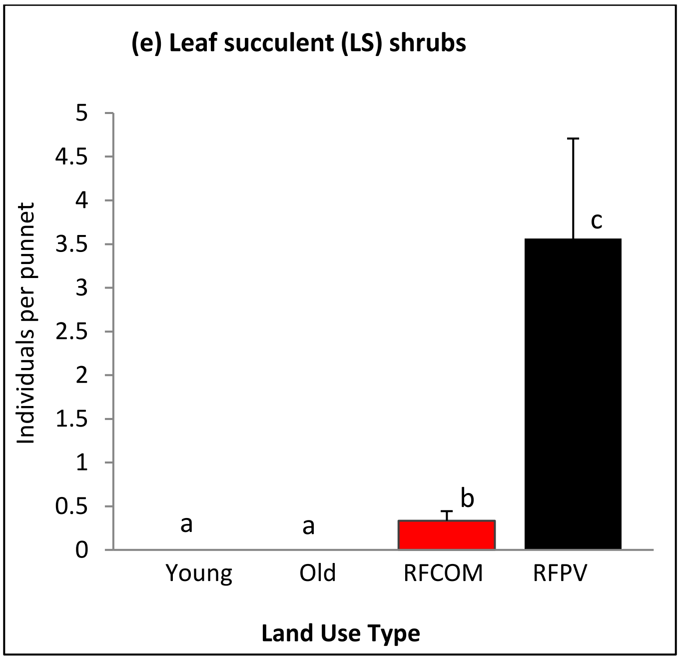
The numbers of non-leaf succulent shrubs did not change after cultivation, but numbers were significantly higher on the old, ploughed fields ($\chi^{2}_{(3)}$ = 22.22, $P < 0.001$, Figure 3.2.f) than on the reference farms. Kraalbos was hardly present on reference farms but was consistently present on all ploughed fields (Figure 3.2.g).

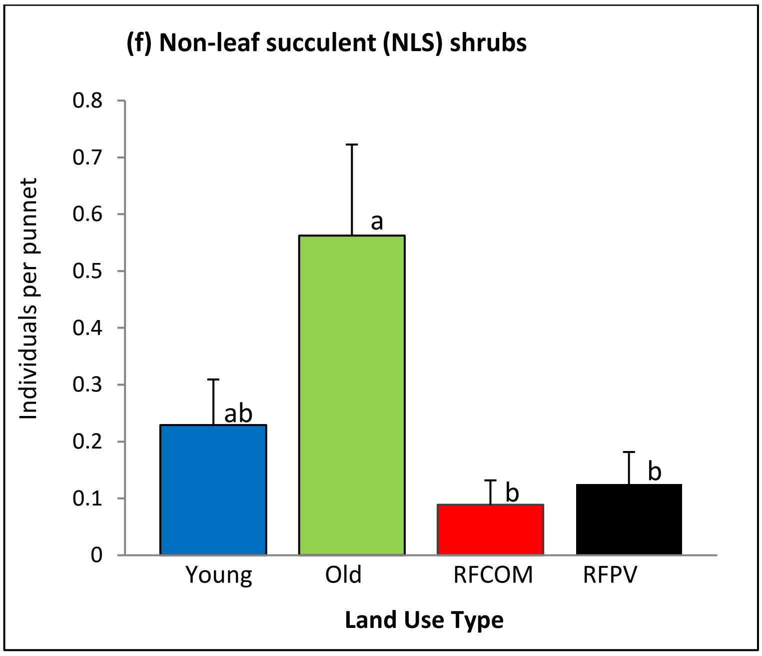





(c) Geophytes
Individuals per punnet
0.25
0.2
0.15
0.1
0.05
0
a
a
a
a
Young
Old
RFCOM
RFPV
Land Use Type


(d) Graminoids
Individuals per punnet
14
12
10
8
6
4
2
0
a
a
b
b
Young
Old
RFCOM
RFPV
Land Use Type


(e) Leaf succulent (LS) shrubs
Individuals per punnet
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
a
a
b
c
Young
Old
RFCOM
RFPV
Land Use Type


(f) Non-leaf succulent (NLS) shrubs
Individuals per punnet
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
ab
a
b
b
Young
Old
RFCOM
RFPV
Land Use Type

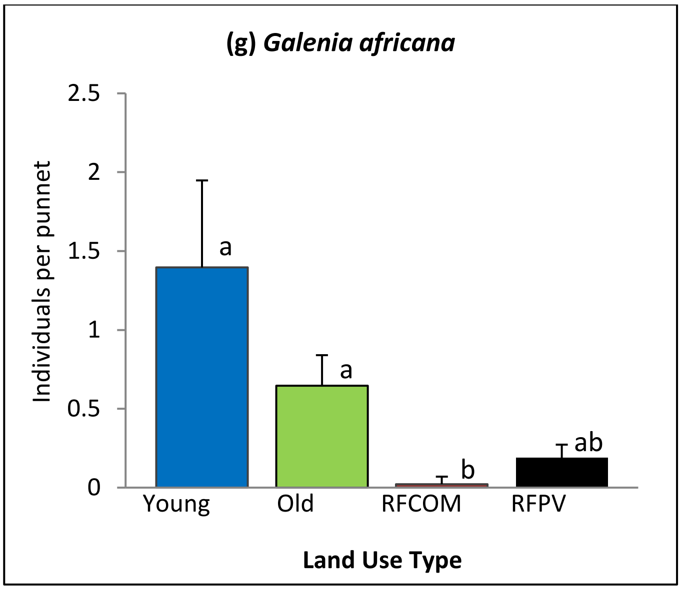


Figure 3.2Seedling abundance (mean ± SE) of various growth forms from four land uses in Kamiesberg Hardeveld, germinated from 48 x 600 g replicate soil collections along the skirt of the dominant shrub in each and type. Growth forms are plotted as: (a) Annual herbs, (b) Annual graminoids, (c) Perennial Geophytes, (d) Perennial graminoids, (e) Perennial leaf succulent (LS) shrubs, (f) Perennial non-leaf succulent (NLS) shrubs, and (g) Galenia africana (Kraalbos). Mean abundances do not differ significantly if superscripts contain the same letter as determined by GEE and Sidak analyses (P<0.05).

3.3.2 Renosterveld

Vegetation community descriptors

The reference sites were very similar to each other for all descriptors (Table 3.2). Species diversity and evenness decreased significantly after ploughing, where it was lowest on young fields, and improved with time post abandonment. Plant abundance increased significantly soon after abandonment and decreased by around half this amount on old fields. Species richness was the only factor that was similar across the land use categories.

Table 3.2 Vegetation community descriptors (mean ± SD) of the soil seed bank across four land uses in Kamiesberg Renosterveld, germinated from 48 x 600 g replicate soil collections along the skirt of the dominant shrub in each land use. Mean abundances do not differ significantly if superscripts contain the same letter as determined by ANOVA (Tukey HSD). Asterisks indicate degree of significance, where: *P <0.05, **P<0.005 and ***P<0.001.

Diversity measures	**Land use**				
	Young fields (n = 48)	**Old fields (n = 36)**	**Communal reference farms (n = 48)**	**Private reference farms (n = 36)**	**F Value**
Shannon –Wiener Diversity (H) index	0.9 (0.4)^{a}	1.9 (0.4)^{b}	1.1 (0.4)^{ab}	1.3 (0.1)^{b}	7.9 *
Simpsons Index of Diversity (1 – D)	0.4 (0.2)^{a}	0.5 (0.2)^{b}	0.6 (0.2)^{b}	0.6 (0.2)^{b}	30.1 **
Species richness	4.9 (1.5)^{a}	5.1 (1.9)^{a}	4.2 (1.9)^{a}	5.2 (2.1)^{a}	1.0 NS
Evenness (Pielou’s J’ evenness)	0.5 (0.2)^{a}	0.7 (0.2)^{b}	0.8 (0.1)^{c}	0.7 (0.2)^{bc}	34.2 ***
Plant abundance	39.8 (26.3)^{a}	21.2 (12.0)^{b}	12.6 (11.8)^{b}	20.2 (12.6)^{b}	15.0 ***

Ordinations of species

The ordination of all species (Figure 3.3a) indicates no distinction in ordination space between seed banks from ploughed fields and reference farms. Young fields occupy the most ordination space, indicating high floristic heterogeneity at the sampling site scale. The most abundant species, an *Aristida* species (r^2 = + 0.38) and the third most abundant, the alien grass *Bromus pectinatus* (r^2 = + 0.37), were correlated with the horizontal axis. *Pentameris curvifolia* (r^2 = - 0.79) correlated with the vertical axis.

The ordination of perennial species (Figure 3.3.b), indicates that young fields are substantially different in their perennial floristic composition relative to reference sites, but old fields share some similarities with the reference sites. Again, young fields occupy the most ordination space, indicating high floristic heterogeneity across the sites. Reference farms completely overlap and occupy a relatively small area of ordination space, indicating that they are alike and are less floristically diverse. The two most abundant perennial species, *Pentameris curvifolia* (r^2 = + 0.44) and renosterbos (r^2 = + 0.96), were correlated with the axes. *Pentameris curvifolia* (r^2 = + 0.755) and *Cyperus* sp. (r^2 = + 0.548) were also correlated with the axes.

The ordination of annual species was similar to that produced for all species (Figure 3.3c), with a complete overlap of ploughed and reference sites, indicating no differences in the seed bank composition. *Limeum africanum* (r^2 = + 0.705) and *Adenogramma glomerata* (r^2 = + 0.555) were correlated with the horizontal axis, while *Bromus pectinatus* (r^2 = + 0.333) and *Wahlenbergia annularis* (r^2 = + 0.541) were correlated with the vertical axis.

Growth forms

During the 17-week period of the greenhouse experiment, a total of 4371 individual seedlings of 48 species, from 16 families and seven growth form types, were counted from soils collected in Renosterveld vegetation (Appendix A4). Overall, annual graminoids dominated (62%) the total count of seedlings in the greenhouse trial. Annual herb seedlings were the next highest (25%) and were followed by perennial graminoids (9%). Non-leaf succulent shrub (NLS) and leaf succulent (LS) shrub growth forms combined contributed about 4%, while geophytes contributed less than 1% to the total number of seedlings counted in the greenhouse trial. The shrub renosterbos on its own contributed 3% to the total number of seedlings recorded.

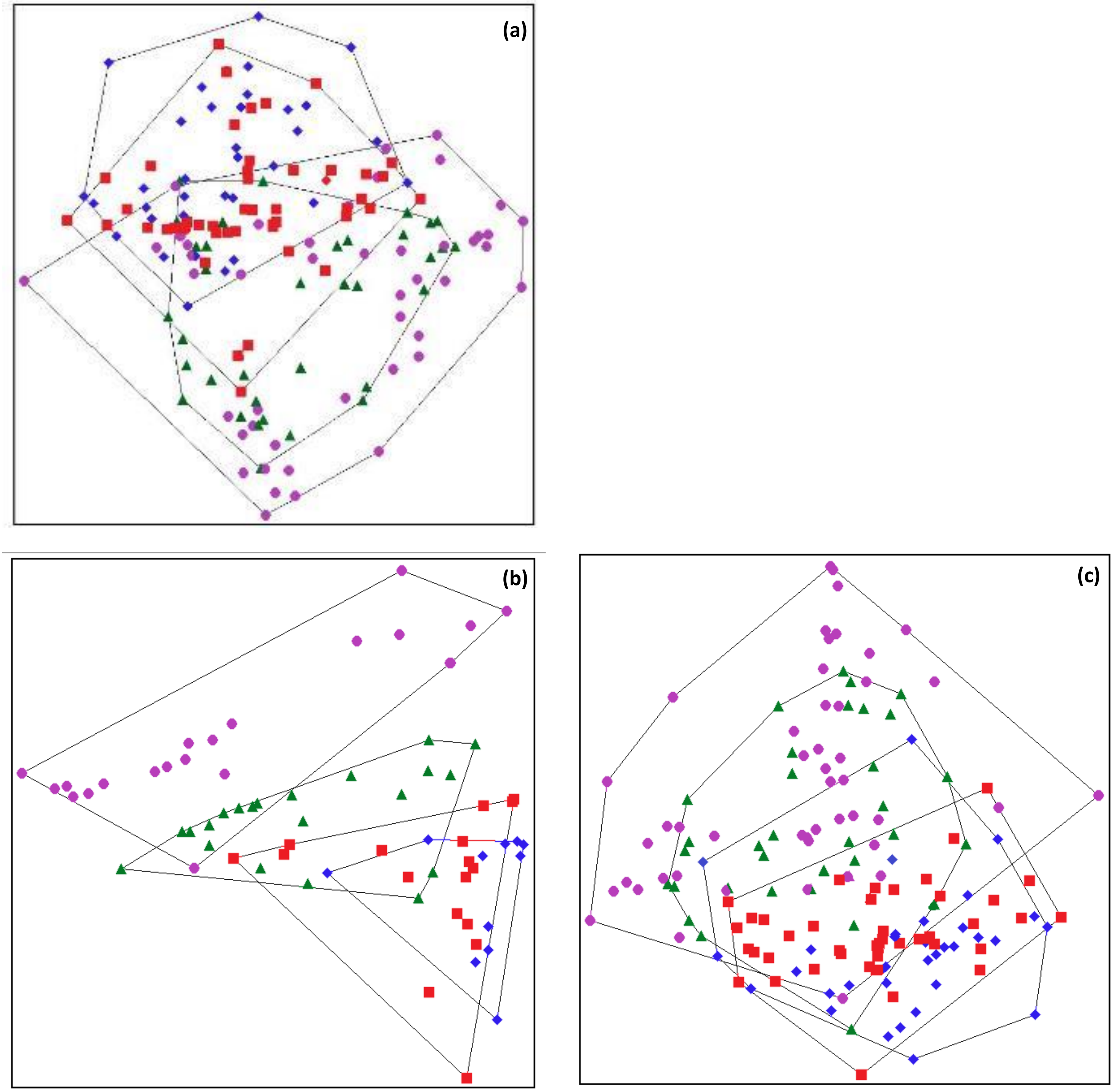


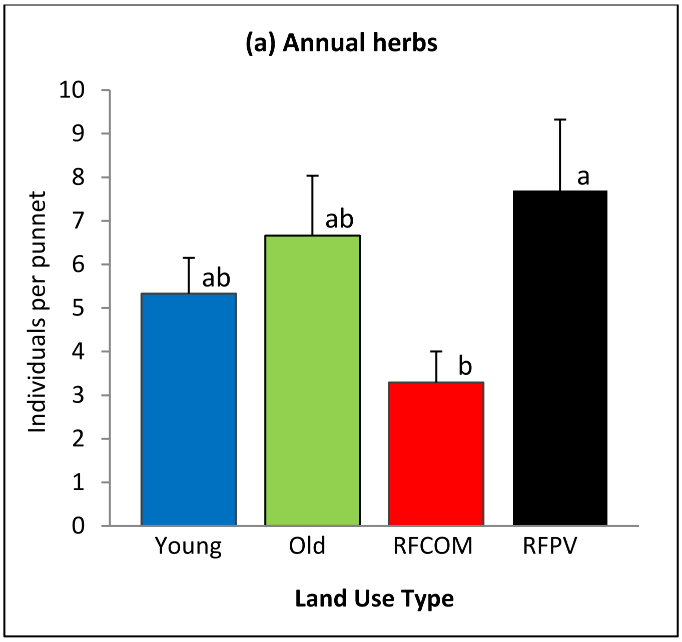
Figure 3.3 Two-dimensional plots of ordinations (NMS) of the abundance of (a) all species, (b) all perennials, (c) all annuals, germinated from the seed bank in Kamiesberg Renosterveld, germinated from 600 g replicate soil collections along the skirt of the dominant shrub in each land use as denoted by purple Circles = young fields (n = 48),green Triangles = Old fields (n = 36), red Squares = communal reference farms (n = 48) and blue Diamonds = private reference farms (n = 36). The cumulative correlation coefficients for (a) = 0.54, (b) = 0.87, and (c) = 0.82

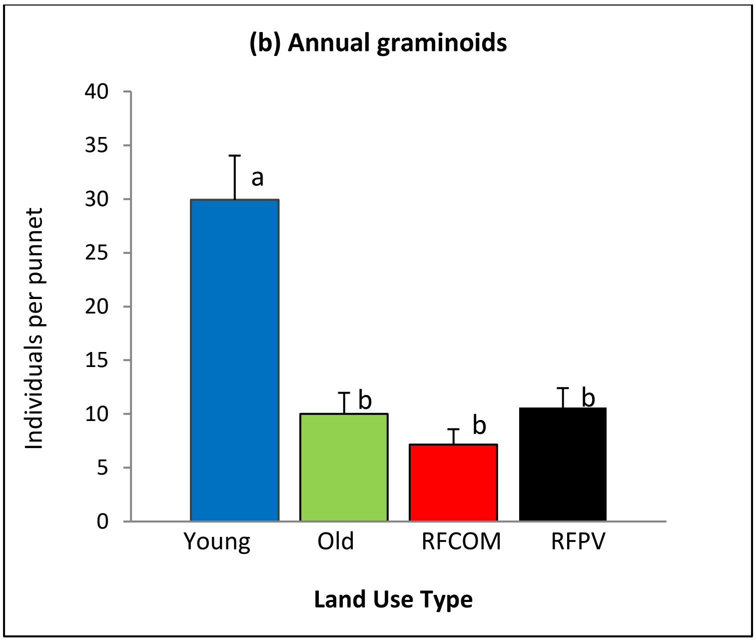
The reference farms contrasted with each other in terms of the number of annual herb seedlings that emerged in the punnets ($\chi^2_{(3)}$ = 12.07, P < 0.001, Figure 3.4.a). Private reference farms had a mean of 7.7 (± 1.6) seedlings, while communal reference farms had a mean of 3.3 (± 0.7). There were no differences in the annual herb seed bank between the young and old fields.

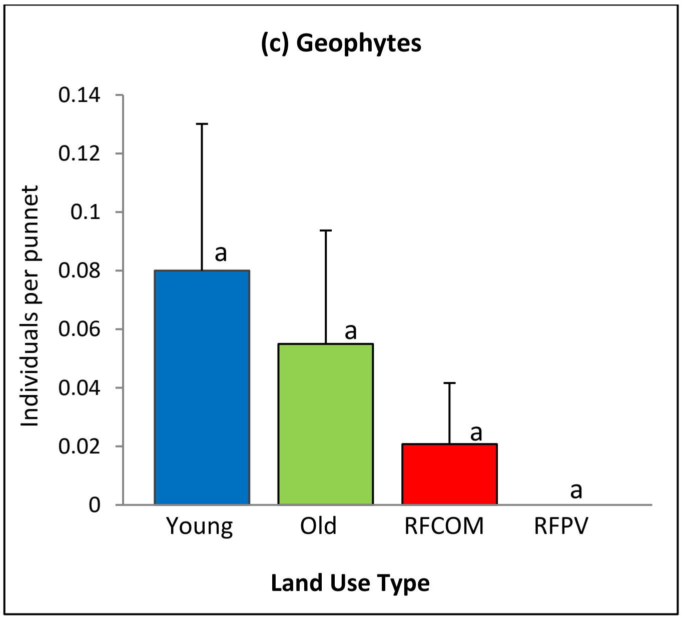
There was no difference between the reference farms for annual grass seedlings. There was a significant decline ($\chi^2_{(3)}$ = 15.0, P < 0.001, Figure 3.4.b) in annual grass seedlings after cultivation, and this decline in seedling numbers continued over time, from young fields of 29 individuals per punnet to old fields with 10 individuals per punnet. The mean abundance of perennial geophyte seedlings was extremely low (less than 1 individual per punnet), across ploughed and reference farms, with no significant difference between them (Figure 3.4.c).

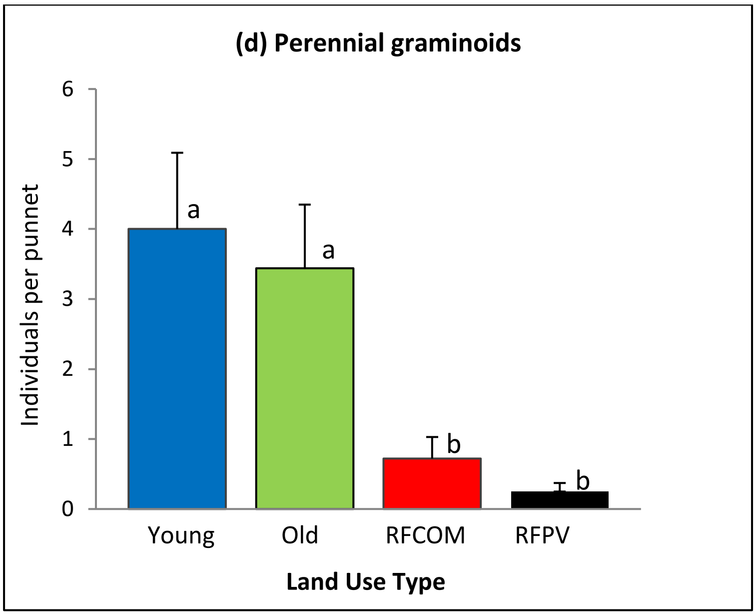
There was no difference between the reference farms, but after cultivation, the number of perennial grass seedlings increased significantly ($\chi^2_{(3)}$ = 42.26, P < 0.001, Figure 3.4.d), and maintained consistent numbers over time, with a mean of 3-4 seedlings per punnet in young and old fields. LS shrub seeds were hardly found in the soil, and it was only in soil collected from private reference farms that a handful of LS shrub seedlings were present (Figure 3.4.e).

There were no discernible differences between land uses for the NLS shrubs (Figure 3.4.f), whose seedling numbers were very low. Renosterbos seedling abundance was similar on both reference farms but declined significantly ($\chi^2_{(3)}$ = 17.13, P < 0.001, Figure 3.4.g) after cultivation. Renosterbos seedling numbers remained consistent over time, with no differences between young and old fields.


(a) Annual herbs


(b) Annual graminoids


(c) Geophytes


(d) Perennial graminoids

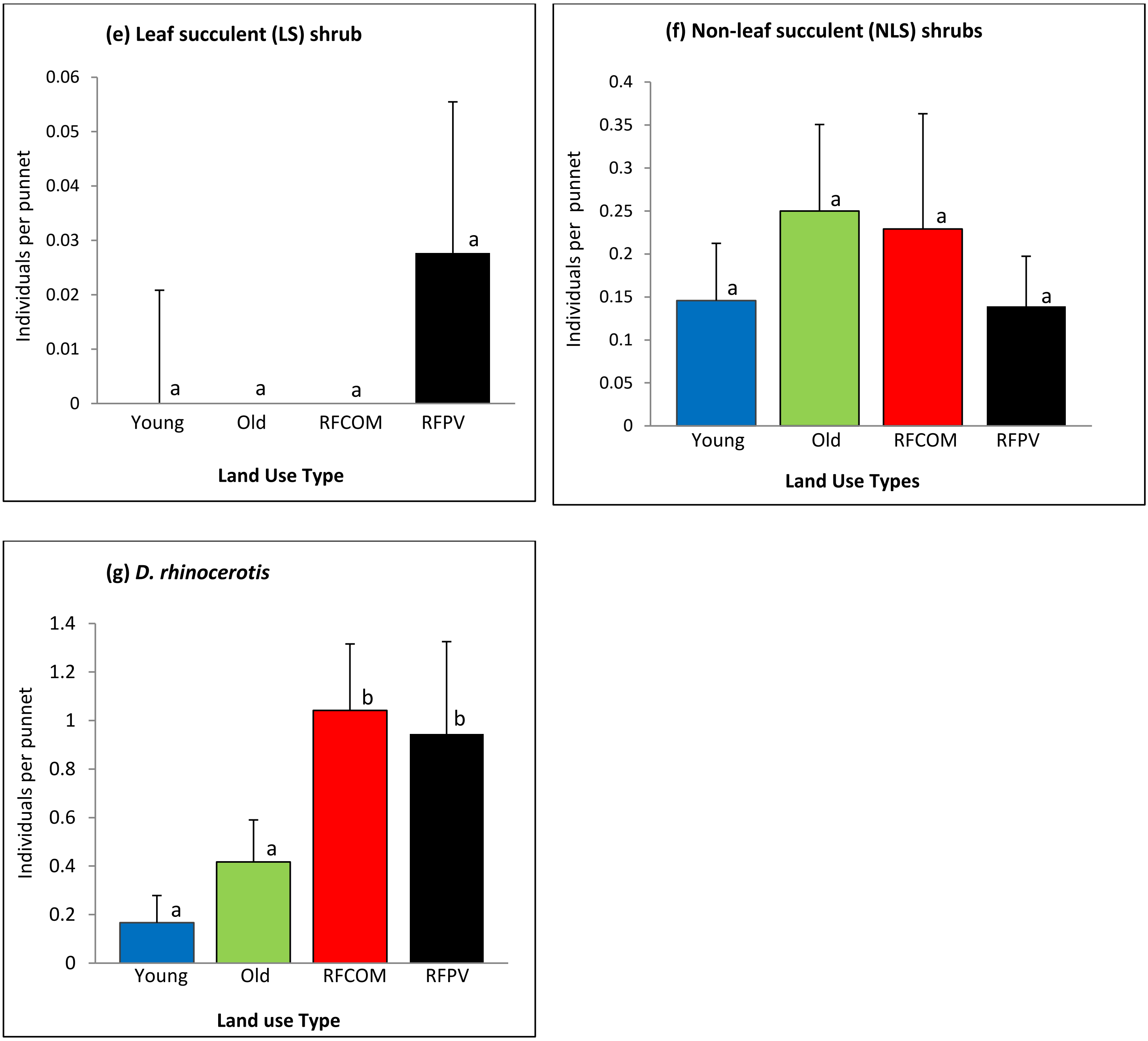


***Figure 3.4** Seedling abundance (mean ± SE) of various growth forms from four land uses in Kamiesberg Renosterveld germinated from 600 g replicate soil collections along the skirt of the dominant shrub in each and type. Growth forms are plotted as: (a) Annual herbs, (b) Annual graminoids, (c) Perennial Geophytes, (d) Perennial graminoids, (e) Perennial leaf succulent (LS) shrubs, (f) Perennial non-leaf succulent (NLS) shrubs, and (g) D. rhinocerotis (renosterbos). Mean abundances do not differ significantly if superscripts contain the same letter as determined by GEE and Sidak analyses (P<0.05).*

3.4 Discussion

3.4.1. The impact of cultivation on the seedbank

Cultivation involves ripping the soil to deal with compaction and weeds. In the process, seeds that remain near the soil surface get buried too deep and the seed bank is often destroyed (Colbach *et al*., 2014; Hobbs & Walker, 2007). Other seeds are often introduced into the soil (Hobbs & Walker, 2007). After decades of ploughing, seeds of the original vegetation have been removed, or are not viable anymore (Heelemann *et al*., 2013). Although disturbance and physical stress, such as ploughing and grazing (Milton *et al*., 1994), hinder the formation of a dense community of perennials, it is the reduction in the number of seeds produced that is a major cause of vegetation change and the reason for the slow recovery of abandoned fields. This has been recorded in the Southern Karoo (Milton, 1994; Milton & Dean, 1990) and near Paulshoek (Carrick, 2001), as well as in studies from other Mediterranean-type ecosystems (Hobbs & Walker, 2007; Heelemann *et al*., 2013).

The results from this study assessed the ‘germinable seed bank’, and may not fully capture the dormant seeds or those requiring other stimulants, such as heat, smoke, acid treatment that I have not provided. The results discussed should not generalise the entire seed bank. My study indicates that cultivation in both Hardeveld and Renosterveld vegetation had significant impacts on seed bank dynamics. The impact is clearly seen with the loss of seeds from perennial plants, which did not improve significantly over time. Interestingly, the ploughed fields in Hardeveld and Renosterveld had the same species richness as the reference sites, but their species composition differed. In Hardeveld, the seed bank diversity and abundance of seeds did not change after cultivation, which is largely due to the similarity of annual seeds across the land types. There was also no change in species richness and diversity over time from the young to the old fields. In comparison, further west in the Skilpad Wildflower Reserve, total species richness increased with time after cultivation has ceased (Van Rooyen, 1999). In Renosterveld, once ploughing activities have ceased, the abundance of propagules in the soil is high, but the diversity is very low. Over time the abundance declines whilst the diversity improves.

Annuals

Across both vegetation types, annuals constituted the majority (over 80%) of emerged seedlings in the seed bank trial. This reiterates findings from semi-arid Colorado (Coffin &

Lauenroth, 1989) and Western Australia, where immediately after abandonment, annual herbs and grass establish (Hobbs & Walker, 2007). The annual floral displays in spring that Namaqualand is well known for occur predominantly on old fields and degraded land. This has led to a common misconception that annuals occur only on degraded land, and would disappear if the vegetation condition improved, which is not the case. In Goegap, a comparison of disturbed versus unploughed vegetation indicated that although annuals were more conspicuous in the disturbed vegetation, no significant differences were found between the sites (Van Rooyen, 1999). The results presented here largely follow a similar trend. The seed bank in both Hardeveld and Renosterveld was dominated by annuals, with hardly any significant differences between ploughed and intact land.

Thompson and Grime (1979) defined seed banks as either persistent (in which some seeds remain viable for longer than one year) or transient (in which no seeds remain viable for more than one year). Annuals are well suited to colonising a field after abandonment. Most annuals are small, light, round, smooth-coated seeds that are easily wind dispersed from surrounding vegetation and are more likely to persist in the soil for more than one year in a short-term persistent seed bank. Annuals, typically found in arid regions, are important in early succession as they survive harsh conditions as seeds. They have a rapid lifecycle to avoid being grazed by livestock and to take advantage of seasonally moist soils, whereas perennials use morphological and biochemical mechanisms of defence. Their rapid life cycle allows annuals to germinate in autumn and be well established by the end of the winter after which they contribute again to what is often a persistent seed bank (Hobbs & Walker, 2007). These seeds can also have different kinds of germination strategies, known as heterodiaspory, which occurs when ‘two or more types of diaspores are produced above ground and differ in ecological functions of dispersal and dormancy’ (Baskin & Baskin, 2014). This greatly enhances their ability to establish under favourable conditions and reduces the chances of local extinction (Berger, 1985; De Villiers *et al*., 2002; Dreber *et al*., 2011). This includes genera such as *Cotula, Senecio,* and *Wahlenbergia.* Thus, these annuals form a major contribution towards the re-vegetation of an area, which was reflected in my results. In Hardeveld, reference lands had low numbers of annual grass seeds. However, after abandonment, the soil on young fields was dominated by annual herbs and continued to increase with time since last cultivation. Annual grasses such as *Pentameris airoides* and *Aristida* sp. have also increased over time.

In Renosterveld, annual grasses dominated the seed bank in this trial, particularly on ploughed fields. These results have been noted by other studies in Mediterranean shrublands (Holmes & Richardson, 1999). In Roggeveld Mountain Renosterveld it was found that annuals were abundant throughout the various stages of succession (Van Der Merwe & Van Rooyen, 2011b). However, in other Renosterveld types, the seed bank is dominated by alien, not indigenous, grass seeds. In this study, only two of five annual grasses, *Vulpia myuros* and *Bromus pectinatus,* were alien grasses, but they were found in very low numbers. It was only on young fields that *Bromus pectinatus* was prominent, but their number decreased significantly over time post abandonment. This is an interesting result and does not conform to other Renosterveld areas where much effort and research has been directed towards dealing with unwanted, competitive alien grasses. In Coastal and Swartland Renosterveld, abandoned agricultural fields adjacent to Renosterveld remnants are dominated by alien grasses. This is a major hindrance to recovery, because competition with alien grasses reduces the establishment and productivity of indigenous vegetation (De Villiers *et al*., 2003; Heelemann *et al*., 2013; Midoko-Iponga *et al*., 2005; Muhl, 2008; P. Waller, 2013). Another interesting finding from my study, annual grass seedling numbers in Renosterveld declined significantly with time post abandonment, to density levels that were similar to reference lands. This could be due to increased competition from annual herbs or perennial shrubs, which increased in density over time. The results recorded here regarding annual grass dynamics have important implications for future management of this Renosterveld type and how it differs from other Renosterveld types.

Perennials

Seedlings of perennial species contributed low numbers (less than 26%) to this study in both Hardeveld and Renosterveld vegetation, which is normal in seed bank studies. This is due largely to the transient nature of their seed banks and short dispersal distances of many species within the Aizoaceae. Intact vegetation can be located many kilometres from ploughed fields that cover large distances. De Villiers, Van Rooyen and Theron (2002) adapted the seed bank classification key developed by Grime and Hillier (1981) to classify the seed bank in Namaqualand's Strandveld vegetation type. They recorded that all perennial species had transient seed bank strategies, and no long term dormancy (Esler & Rundel, 1999; Milton *et al*., 1997). Long term dormancy is not a feature of Karoo perennials (Carrick, 2001; Esler, 1999; Milton *et al*., 1997). In semi-arid Colorado, most species have a transient seed bank (Coffin & Lauenroth, 1989) which suggests that this might be a common feature of perennials in arid and semi-arid environments.

After cultivation, the seed bank on ploughed fields in Hardeveld lacked perennial plants. This did not change with time since cultivation. Perennial grass and leaf succulent shrub species, which constitute a major portion of the vegetation in pre-disturbed Hardeveld communities, are not present in the seed bank on fallow fields, which is a major hindrance to the recovery of the lands to their former state. The Renosterveld seed bank in this study hardly contained any perennial plant species. The perennial grass *Tribolium hispidium* was only found on reference lands, and not on soil collected from old fields, likely due to its short dispersal distance (Shiponeni, 2003). In Coastal Renosterveld, seeds of indigenous shrub species are absent in old-field soil (Midoko-Iponga *et al*., 2005; Saayman & Botha, 2008; Shiponeni, 2003), with poor re-establishment of indigenous species, even after a long period of rest (Heelemann *et al*., 2013; Kemper *et al*., 1999). Perennial seed numbers were very low and showed no significant differences between reference lands and ploughed fields, which is consistent with Shiponeni (2003).

A puzzling result was that the number of perennial grass seedlings were higher on soil collected from ploughed fields compared to soil taken from reference lands. This was almost entirely due to high numbers of *Pentameris curvifolia* seeds in the punnets. This was also seen in the vegetation survey (Chapter 2). Similar results were also found at Elandsberg Nature Reserve, where *P. curvifolia* is well established on fields abandoned 10 years earlier but not on fields abandoned 20 years earlier (Memiaghe, 2008). Linder and Ellis (1990) recorded that *P. curvifolia* is present in the natural vegetation, but in a weak vegetative state. It survives periods between fires as persistent and almost dormant plants, and after fire they coppice from the base (Linder & Ellis, 1990). Although the fire history for my sites could not be collected, it was noted that fields are sometimes ‘felled and burned.’ This could partly explain why *P. curvifolia* functions as a pioneer plant, establishing well after disturbance and burning.

3.4.2. Effect of different grazing pressures on the seedbank in reference lands

The seed bank in soil from reference lands in Hardeveld contained a diversity of perennial seed species of, succulent shrubs and high numbers of perennial grass seeds. Reference lands were the only locations where succulent shrub seeds contributed substantially to the seed bank. This result was expected given the dominance of succulent shrubs in the standing vegetation (chapter 2). However, soil taken from private reference lands contained ten times the seed numbers than soil from the communal lands, even though succulents were found in similar densities in the standing vegetation on both reference lands. In fact none of the small succulent shrub species recorded in the standing vegetation of communal lands were recorded in the seed bank. This suggests that a substantial portion of the canopy seed bank, held in the hygrochastic capsules of most Aizoaceae, forms part of the seed bank on private farms but not on communal rangelands. This is likely due to the more intense browsing of flowers and fruit on shrubs in communal areas, which greatly reduces seed production (Milton, 1994). In Paulshoek, communal rangelands had reduced flower production and seedling recruitment than those on private rangeland (Todd & Hoffman, 1999). Milton (1995) found that sheep browsing of *Pteronia empetrifolia,* even at the relatively low stocking densities found on privately owned farms, reduced flowering by 80 – 90%.

In Renosterveld, seed diversity was similar in heavily grazed communal and lightly grazed privately owned sites. This is similar to the findings of others (Heelemann *et al*., 2013; Shiponeni, 2003). However, the reference lands differed in their annual and perennial seed composition. Soils from communal reference sites were the only soils which contained substantial amounts of seed from two perennial species (*P. curvifolia* and renosterbos) while the private farms contained mostly annual grasses. Leaf succulent seed numbers were extremely low across all land types in Renosterveld. This is not surprising as succulents only made up around 1% of the plants recorded in the vegetation survey (Chapter 2).

3.4.3. Seed dispersal strategies

The soil seed bank is influenced by interactions of seed dispersal, dormancy, and germination (Esler, 1999). The knowledge of dispersal syndromes present in different vegetation types and plant families is essential to understanding seed bank dynamics, as well as for conservation and restoration of indigenous vegetation communities. Geophytes were hardly present in the seed bank in this study. Geophyte seeds are relatively large and only disperse over short distances (Kemper *et al*., 1999). In Renosterveld vegetation of the Roggeveld escarpment, geophytes were severely depleted by ploughing and it took over 20 years for them to slowly start returning (Van Der Merwe & Van Rooyen, 2011b). Perennial grass colonisation was also extremely slow (D’Angela *et al*., 1988).

A number of Karoo shrubs have large seeds (>5 mm) adapted for wind dispersal (Esler, 1999), which should allow them to be carried to degraded areas from adjacent sites with intact vegetation. However, they are rarely transported more than 20–30 m before being trapped by other shrubs (Wiegand & Milton, 1996). Natural dispersal is therefore slow and unreliable (Van der Valk & Pederson, 1989). Perennial shrubs in the Karoo and arid grasslands appear not to produce a persistent seed bank, even though seeds are located on plants near the soil surface (Coffin & Lauenroth, 1989; De Villiers *et al*., 2003). Large seeds sometimes have uneven shapes and projections on the coat (Baskin & Baskin, 1998; Thompson *et al*., 1993) that restrict seed burial by rain, animals, or gravity. Large seeds experience high levels of predation on the soil surface. Seeds of perennial shrubs are not abundant in the seed back even though in the standing vegetation their parent plants are plentiful (Chapter 2). For example, species with large seeds, such as *Pteronia divaricata, Tetragonia fruticosa, Eriocephalus* species, *Pteronia incana,* and *Zygophyllum morgsana* were recorded in the vegetation survey (Chapter 2) but not in the seed bank.

Seeds of perennial shrubs barely entered the seed bank on ploughed fields, but both kraalbos and renosterbos formed a considerable component of the seed bank and both continued to increase with time post abandonment. This is due to various characteristics that provide them with competitive advantages. In the case of kraalbos*,* this species can reproduce after only one year of growth, and seed availability is relatively unaffected by livestock grazing, as compared to more palatable species (Todd, 2000). Although kraalbos seedlings are poor competitors, the reduced cover of other perennial species in degraded land enhances kraalbos seedling survival (Carrick, 2001). Renosterbos was one of the few perennial species that established rapidly and successfully on degraded land, as also recorded by Shiponeni (2003) in Coastal Renosterveld. This establishment success is due to adult Renosterbos bushes producing large quantities of seed that are well suited for wind dispersal (Cowling *et al*., 1986) that disperse over 30 m. The seeds have an initial period of seed dormancy, which spreads germination out over several years (Levyns, 1927). Shade severely inhibits the germination of renosterbos*,* and even in a moderately closed community, the shade provided by an adult bush prevents germination. It has been noted that abandoned fields are sometimes burnt by the local communities, to encourage grass growth. However, renosterbos seed germination is highly stimulated by fire (Cowling *et al*. 1986). Therefore, in disturbed and open vegetation such as abandoned fields, where shade is not a limiting factor, seed production is high and seedlings establish themselves rapidly (Levyns, 1956). These features enable renosterbos to be a successful pioneer of disturbed vegetation.

The reappearance of a plant species after disturbance is the result of its persistence in the soil seed bank, and if it does not occur in the seed bank, then it must be transported to the degraded site by some vector of wind, water, animals, or humans. Environmental conditions encountered in arid ecosystems differ vastly from those in more mesic ecosystems and seed dispersal strategies in arid environments reflect these differences (Fotouo Makouate *et al*., 2012). Renosterveld is bordered by Fynbos and Succulent Karoo, two vegetation types that are well researched, but there is little information on ecological processes of Renosterveld (Cowan & Anderson, 2019; Curtis, 2013), and few studies focusing on seed bank dynamics. Seed dispersal syndromes have been intensely researched in Fynbos (Cowling *et al*., 1997; Le Maitre & Midgley, 1992) and in the Karoo (Esler, 1999; Milton & Dean, 2001; van Oudtshoorn & Van Rooyen, 1999; Van Rooyen, 1999), but not in the Renosterveld that borders them. In Fynbos, seed dispersal is predominantly by ants (myrmecochory) and serotiny is common. Serotinous species store their seeds in the canopy where they are dispersed after a fire. However, Renosterveld, which is also classed as a fire-prone ecosystem, lacks canopy seed banks and myrmecochory (Cowling *et al*., 1997; Slingsby & Bond, 1981). In Renosterveld, most plant species are thought to re-sprout after fire (Kemper *et al*., 1999) or to be wind-dispersed (Kemper *et al*., 2000).

Wind is an important factor in these environments, and most seeds are adapted for wind dispersal. In Namaqualand, 66.3% of all species are dispersed by wind (Van Rooyen, 1999). However, seeds of most species do not disperse over large distances from natural vegetation in the Succulent Karoo (Esler & Rundel, 1999; van Oudtshoorn & Van Rooyen, 1999) or Renosterveld (Krug & Krug, 2007; Shiponeni, 2003), a feature repeatedly observed in arid and semiarid habitats (Ellner & Shmida, 1981; van Oudtshoorn & Van Rooyen, 1999). The proportion of species with short-distance dispersal syndromes in semi-arid environments has been recorded as 50 - 75% in Israel, 21% in Namaqualand (Ellner & Shmida, 1981; van Oudtshoorn & Van Rooyen, 1999) and 80% in Spain (García-Fayos *et al*., 2013). In Renosterveld around 41% of species is dispersed by wind (Krug & Krug, 2007).

Succulent species belonging to the Aizoaceae, have seeds in capsules that are water-dispersed via a rain ballistic seed dispersal mechanism. Not all the seeds are dispersed from the capsule at the same time, and a seed bank is held in the plant's canopy (De Villiers *et al*., 2002; van Oudtshoorn & Van Rooyen, 1999). The mean distance of seed expulsion from a capsule varies between 7 and 65 cm, with a maximum of 164 cm (Parolin, 2001). These small (approximately 0.1 mg) seeds often colonise open sites, from 1.65 m – 5 m away from the parent plant (Milton *et al*., 1997).

Several of the abundant plant species in Namaqualand display myxospermy, a phenomenon where the epidermis of the seed contains mucilaginous cells, which swell and become sticky when wet, adhering the seed to the soil. This action restricts it from being carried away by the wind (Ellner & Shmida, 1981; Gutterman, 1993; van Oudtshoorn & Van Rooyen, 1999). The ecological importance of myxospermy in the vegetation of Namaqualand has been shown in several studies (Fotouo Makouate *et al*., 2012; Rosch, 1977; van Oudtshoorn & Van Rooyen, 1999).

Species could also be dispersed through the dung of domestic livestock (endozoochory). It has been found that a high abundance of seedlings emerge from dung in the Knersvlakte (Haarmeyer *et al*., 2010). Domestic animals could carry seeds to around 20 km away (Samuels *et al*., 2007) and promote long-distance dispersal in succulent plants. Milton and Dean (2001) also found that succulent plants constituted a large portion of the individuals emerging from dung and could aid the primarily short-distance dispersed seeds in occasionally dispersing across long distances. In Hardeveld, succulents were not found in the seed banks of ploughed fields, but were recorded in low numbers in the standing vegetation (Chapter 2). This indicates that some seeds have successfully germinated in fallow fields but are not contributing to the seed bank. Given the vast distances between ploughed and reference sites, the occurrence of succulent plants on ploughed fields could possibly be due to dispersal by livestock moving through the area regularly and depositing dung. This is an hypothesis that requires further study. Renosterveld has very fertile soils that supported large herds of game in the past (Rebelo, 1996), so dispersal by animals may have played an important role (Shiponeni, 2003). Shiponeni and Milton (2006) concluded that endozoochory works well for grasses and species that have no specific dispersal mechanism. Whilst birds disperse seeds of 26-46% of shrub species (Le Maitre & Midgley, 1992), due to the lack of perches and nest sites on old fields, seeds of these shrubs are not likely to colonise fields.

3.4.4. The role of patch dynamics in the seedbank

In an arid environment, seeds have a better chance of survival close to the parent or “nurse” plant (Esler, 1999; Wiegand & Milton, 1996). Seeds accumulating in plant litter result in increased seed germination because of a more favourable moisture environment (Esler, 1999), which is lacking in cultivated fields. In the southern Karoo, there were more than three times the numbers of seeds found under shrubs than in the open spaces (Esler & Cowling, 1993). Early opinions were that whilst the benefit of long-distance seed dispersal is to spread genetic material in space, others argued that in resource-restricted environments, the occupation of the few favourable sites that do exist could be a superior adaptive strategy for plants (Cohen & Levin, 1991). This is called the “mother-site theory”, as an adult plant’s strategy is to keep as many seeds as possible within their own environment, which is considered favourable compared to the open and barren matrix surrounding the plant (Ellner & Shmida, 1981). Seed survival in arid ecosystems is also strongly impacted by soil erosion, which can bury seeds. A global review of arid grasslands found trends that seeds do not disperse far and cluster around the mother plant (Hopfensperger, 2007). As mentioned above, myxospermy restricts seeds from being carried away by the wind and has evolved as a way for the seed to remain close to the mother site.

To conclude, the short-distance seed dispersal mechanisms that are favoured over long-distance mechanisms and contribute to the origins and maintenance of patches in semi-arid vegetation, highlights the importance of the role of patch dynamics (Chapter 1) in the functioning of vegetation in the arid Karoo.

3.5 Conclusion

A seed bank trial is a useful experiment to assess the restoration potential of the vegetation of an area and to understand species dynamics and reproduction efficiency. This study yielded results that are of significance to semi-arid environments. The impact of cultivation in the Kamiesberg is severe and long-lasting. In both vegetation systems, the seed bank is largely destroyed by cultivation. The fields in the Hardeveld respond to cultivation in much the same way as most of the area does to any form of degradation. Annual grasses and herbs colonise fields together with individuals of the perennial shrub, kraalbos. Due to seed mechanics and short dispersal distances, seeds of perennial species do not enter the persistent seed bank of fields. This is especially true of succulent plants within the Aizoaceae a key component of Karoo vegetation.

The fields in Kamiesberg Renosterveld do not respond to the impacts of agriculture in the same manner as Swartland and West Coast Renosterveld fields do. Alien grasses are considered a major hindrance to restoration efforts of other Renosterveld types, and the lack of alien grasses in my study area has positive implications for the restoration of the

Kamiesberg Renosterveld. Similarities in the vegetation structure of old fields to reference sites over time indicate signs of recovery, but at a very slow trajectory.

Results from this study suggest that the recovery of cultivated fields in the Hardeveld does not occur largely because the seed bank of perennial species has been depleted. This is due to the low seed production of perennials as well as their short dispersal mechanisms and short lifespan of the seeds. Furthermore, because seeds of the natural vegetation are designed to disperse across a short distance to a suitable safe site within a patch under a nurse plant, recovery on open fields does not occur.

In both ecosystems, the seed bank alone will not be sufficient to re-vegetate abandoned fields because many of the species that dominate the aboveground vegetation do not produce persistent seed banks. The lack of diversity of perennial seeds in the soil seed bank continues to restrict recovery. The absence of perennial seeds keeps old fields locked in an alternative state, which without some form of management intervention, will likely never fully return to its original state.

Chapter 4 Restoration of post cultivated fields in two arid vegetation types in the Kamiesberg, South Africa

4.1 Introduction

This chapter explores the idea of using under-canopy patches created by the pioneer shrubs *Galenia africana* and *Dicerothamnus rhinocerotis* as suitable micro-site locations to enhance plant establishment in active restoration experiments of fallow fields. The experimental study was undertaken in the two vegetation communities in the uplands and lowlands of the Leliefontein commonage in Namaqualand.

4.1.1 The extent and impact of cultivation on dryland environments

Large parts of the world's arid and semi-arid regions have been transformed by cultivation Hobbs & Walker, 2007). Land abandonment after cultivation is a common practice as a consequence of environmental and socio-economic changes (Hobbs & Walker, 2007; Scott & Morgan, 2012). This trend has occurred in the Succulent Karoo and Fynbos biomes as well, particularly in low lying areas that were used for cropping in the previous century. In the winter rainfall region of Namaqualand, cultivation declined substantially due to economic, social, climatic, and ecological factors. Once government subsidies to farmers were terminated, cropping was no longer economically viable (Taljaard, 2008), and many abandoned croplands are evident across the region (Hoffman & Ashwell, 2001; Schmiedel *et al*., 2010; Van Der Merwe & Van Rooyen, 2011b).

The numerous ecosystem services that these once productive natural lands provided are reduced when the functional integrity of the ecosystem is transformed by cultivation (Madsen *et al*., 2012). After cultivation, the biodiverse plant communities of the Succulent Karoo and Renosterveld undergo a shift towards a novel or alternative stable ecosystem which is unlikely to return to its pre-disturbed state (Bosco *et al*., 2018; Hobbs *et al*., 2013) and as recorded in chapters 2 & 3. In Namaqualand, the vegetation composition changes from diverse communities dominated by palatable shrubs to a community shaped by unpalatable pioneer perennial shrubs that are low in diversity and agricultural value (Van Der Merwe & Van Rooyen, 2011b). Species such as *Galenia africana* (kraalbos) dominate old lands in the Karoo areas and *Dicerothamnus rhinocerotis* (renosterbos) in the Renosterveld areas. Annual species are usually common in old fields (Allsopp, 1999; Helme & Desmet, 2006; Simons &

Allsopp, 2007). Most of these former croplands in Namaqualand are now used solely for grazing. Herbivory can inhibit the natural recovery process as animals selectively consume palatable plants and their reproductive structures, thereby reducing seed input into the soil (Jones & Esler, 2004).

4.1.2 Passive and active restoration

In arid environments, passive recovery by resting the vegetation is ineffective due to environmental constraints on plant establishment and limited seed dispersal (Scott & Morgan, 2012). Colonisation from natural areas is very slow and cannot be relied on (Esler, 1999; Holmes & Richardson, 1999), as also recorded in chapter 3. Recovery of the vegetation through the establishment of vegetation is also reliant on the existence of suitable germination microsites, which are often not available (Bosco *et al*., 2018; Carrick & Kruger, 2007; Esler, 1999; van den Berg & Kellner, 2005). These trends have been recorded in both the Succulent Karoo and Renosterveld (Allsopp, 1999; Van Der Merwe & Van Rooyen, 2011b; van Rooyen, 2002; Walton, 2006), and have been discussed in detail in chapters 2 and 3. The seed bank and standing vegetation are dominated by unpalatable pioneer species, such as renosterbos and kraalbos, as well as annual grasses and herbs. Seed banks play little importance in the recovery of old fields (Milton, 1995b). The original perennial species richness, cover, and diversity are lost and do not return, even after decades. Fallow fields are kept in this state unless some management intervention overcomes the barriers to germination and establishment.

The restoration of degraded rangelands is encouraged to build resilience in ecosystems, restore biodiversity and ecological functioning, as well as provide forage for wildlife and domestic animals (Gabriels *et al*., 2003; Huber-Sannwald & Pyke, 2005; Roberts *et al*., 2012; Schmiedel *et al*., 2010; Simons & Allsopp, 2007). However, restoring this diverse ecosystem is difficult, time consuming, labour-intensive and challenging with current tools and knowledge (Bourne *et al*., 2017). Returning foundation plant species is critical in semi-arid and arid areas and relies on the reintroduction of palatable, indigenous species (Jones & Esler, 2004; Saayman *et al*., 2017; Seymour *et al*., 2010). Sowing seeds of herbaceous species will be necessary for successful revegetation, also in parts of Namaqualand (De Villiers *et al*., 2002). Shrub re-establishment on abandoned fields is vital, because shrubs provide important ecosystem services and functions (Porensky *et al*., 2014). However, restoration methods that have focused on sowing seeds to improve rangeland productivity have often been disappointing, because of failed germination or poor seedling establishment (De Malach *et al*., 2014; Hanke *et al*., 2011; Merino-Martín *et al*., 2017; Saayman *et al*., 2017; Swart, 2019). This approach is also costly and labour- intensive. Prioritizing where these intensive methods are applied may improve efficiency (Davies *et al*., 2020; Swart, 2019).

There are a number of factors that can cause poor seedling establishment, such as insufficient rainfall, incorrect timing of seed sowing in relation to rainfall, seed predation, competition from pioneer plants, or poor seed quality (Milton, 1995b; Porensky *et al*., 2014; Saayman *et al*., 2017). In situ conditions also pose challenges, as seeds and seedlings are usually exposed and vulnerable to desiccation, wind erosion, temperature fluctuations, and predation. This poses a major constraint for plant regeneration in the landscape (Bertiller & Carrera, 2015), and for restoration specialists. However, if suitable microsites are provided, seedling survival increases (Saaed *et al*., 2018; Saayman *et al*., 2017; Simons & Allsopp, 2007) and active intervention may be needed to create suitable sites. Activities such as sowing large volumes of seeds, reducing undesirable standing vegetation, and loosening the soil are often required (Saayman *et al*., 2017). Providing a form of shelter via brush packing also significantly increases success rates in Namaqualand studies (Bourne *et al*., 2017; Simons & Allsopp, 2007), in the Karoo (Hanke *et al*., 2011; Schmiedel *et al*., 2010) as well as in other semi-arid studies (Coetzee, 2005; Tongway & Ludwig, 1991).

4.1.3 Patch dynamics and its use in restoration practice

In undisturbed arid and semi-arid areas, there are two major ecological theories that drive vegetation structure, namely patch dynamics and facilitation. Patch dynamics is the process where woody vegetation canopies accrue soil nutrients, moisture, trap seeds and provide protection for seedlings within the patch (Aguiar & Sala, 1999; Schlesinger *et al*., 1996). These ‘resource islands’, contribute towards a high productivity and diversity of plants. The soil beneath the patch is called an ‘island of fertility’, due to the increased organic matter, nutrient levels, and increased microbial activity (Camargo-Ricalde & Dhillion, 2003; Stock *et al*., 1999). Woody plants are often referred to as ‘nurse plants’ because they provide protection from harsh elements and from herbivory by animals (Aguiar & Sala, 1999; Callaway, 1995; Saayman *et al*., 2017). This facilitates the mutual growth and survival of plants. Wind dispersed seeds are more easily trapped by patches and therefore germinate in a more suitable micro-climate (Milton & Dean, 1990; Saayman & Botha, 2010). However, there may be negative interactions between seedlings and their nurse plants due to the competition for resources, or shading of seedlings, which can reduce their growth. Interactions between plants can either be negative (competition) or positive (facilitation), but due to widespread occurrence of multi-species patches in Namaqualand, facilitation likely plays a bigger role (Eccles *et al*., 1999).

Although patch dynamics is a fairly well known concept, it has not been applied to active restoration measures as a means assess the impact on seedling establishment. Understanding the processes of multi-species clump formation in Namaqualand is important, but it is still largely hypothetical, partly due to a shortage of research into restoration ecology in this ecosystem (Kruger, 2010). Classic restoration plans called for the removal of unwanted woody shrubs, followed by seeding of other species (Huber-Sannwald & Pyke, 2005). Established vegetation such as kraalbos and renosterbos, although undesirable, could provide favourable germination microsites, as opposed to sowing seeds in barren, vegetation free areas (Carrick, 2003; Merino-Martín *et al*., 2017; Simons & Allsopp, 2007). These shrubs can create resource islands under their canopies that might remain after their removal, and be available to seedlings (Davies *et al*., 2020). This could facilitate the re-establishment of the original community without the need for expensive soil intervention.

The success of plant survival in different microsites may differ among plants with different functional traits because of their different seed dispersal characteristics. Wind-dispersed seeds likely get trapped in branches of shrubs and therefore germinate within a patch (van Oudtshoorn & Van Rooyen, 1999), while water dispersed seeds may be more suited to establishing in inter-patch areas as they move with water (Esler, 1999). Understanding the microsite scale together with the needs of different plant traits is important (Bertiller & Carrera, 2015; Bosco *et al*., 2018), as researchers improve the efficiency and effectiveness of dryland restoration techniques (Bourne *et al*., 2017; Carrick & Kruger, 2007; Erickson, 2015; Erickson *et al*., 2016; Madsen *et al*., 2012; Turner *et al*., 2013). By artificially creating safe sites with a variety of shelters, that trap resources and provide protection without competing with the seedlings for resources as a nurse plant would, one may be able to assist in the formation of fertile patches that facilitate the establishment of seedlings.

This study aims to inform restoration efforts in the rangelands of the Hardeveld and Renosterveld areas of the Kamiesberg. In this chapter, I explore the effects of different abiotic environments and microhabitats as well as the addition of nutrients on the seedling establishment of different plant growth forms in areas previously denuded by cultivation.

The different abiotic environments include open locations with no perennial plants present and locations where the above-ground perennial plants *Galenia africana* (kraalbos) in Hardeveld and *Dicerothamnus rhinocerotis* (Renosterbos) in Renosterveld were present and had been removed with the roots left intact below the soil surface, which tests the impact of the possible underground fertile island on seedlings. Here I hypothesized that pioneer plants create a fertile island that could improve seedling establishment success. Several microhabitats, or treatments, were created in old fields in Hardeveld and Renosterveld vegetation to test their influence on seedling establishment. Treatments include micro-depressions in the soil surface, brush packs, box shelters and the addition of nutrients (see sections 4.2.4 and 4.2.5). The response of seedlings to different treatments, which were designed to mimic different aspects of patch formation, was examined to test how theoretical concepts of vegetation dynamics in semi-arid environments could be used in restoration practice. The treatments tested the hypotheses that adding fertilizer to treatments and adding shelters would increase seedling establishment. Seed was also sown in two subsequent years to investigate the difference that climatic conditions have on the germination, establishment, and growth of different growth forms.

4.2 Methods

4.2.1 Location of study sites

For this study, six abandoned fields, three in Hardeveld and three in Renosterveld, were chosen for a seeding trial to test the key objectives and hypotheses. A map of the sites, in relation to the villages, is found in Figure 4.1, while Table 4.1 provides information regarding the GPS co-ordinates, location, land-use history, and elevation of the sites in the study.

In Hardeveld, the three sites were dominated by open ground with kraalbos cover of between 27 – 38 %. Site HV-1 was the most southerly site and was closest to Tweeriver village (Figure 4.1). This site was situated on a slight west-facing slope, and apart from kraalbos, there were scatterings of *Pteronia divaricata, Hypertelis salsoloides and Pharnaceum confertum.* Site HV-2 was located on flatter ground where *Pteronia divaricata, Pharnaceum confertum,* and a species of *Ruschia* were well established. HV-3 was the most northerly site on a very gentle south-west facing slope. This site was rockier than the other two sites and other than *Galenia africana*, only *Manochlamys albicans* was present.

In Renosterveld, sites RV-1 and RV-2 were dominated by open ground, with renosterbos cover at 29 %, and well established *Chrysocoma ciliata* and *Wiborgia* sp. individuals also present.

At site RV-3, *D. rhinocerotis* cover was 46 %, and *Chrysocoma ciliata* and *Helichrysum hamulosum* were well established. RV-1 was the most southerly site and was located on flat ground. RV-2 was the most northerly site (Figure 4.1) and was waterlogged in winter, with standing water and muddy conditions in part of the enclosure. RV-3 was located west of Leliefontein village at the base of Kleikop Mountain.

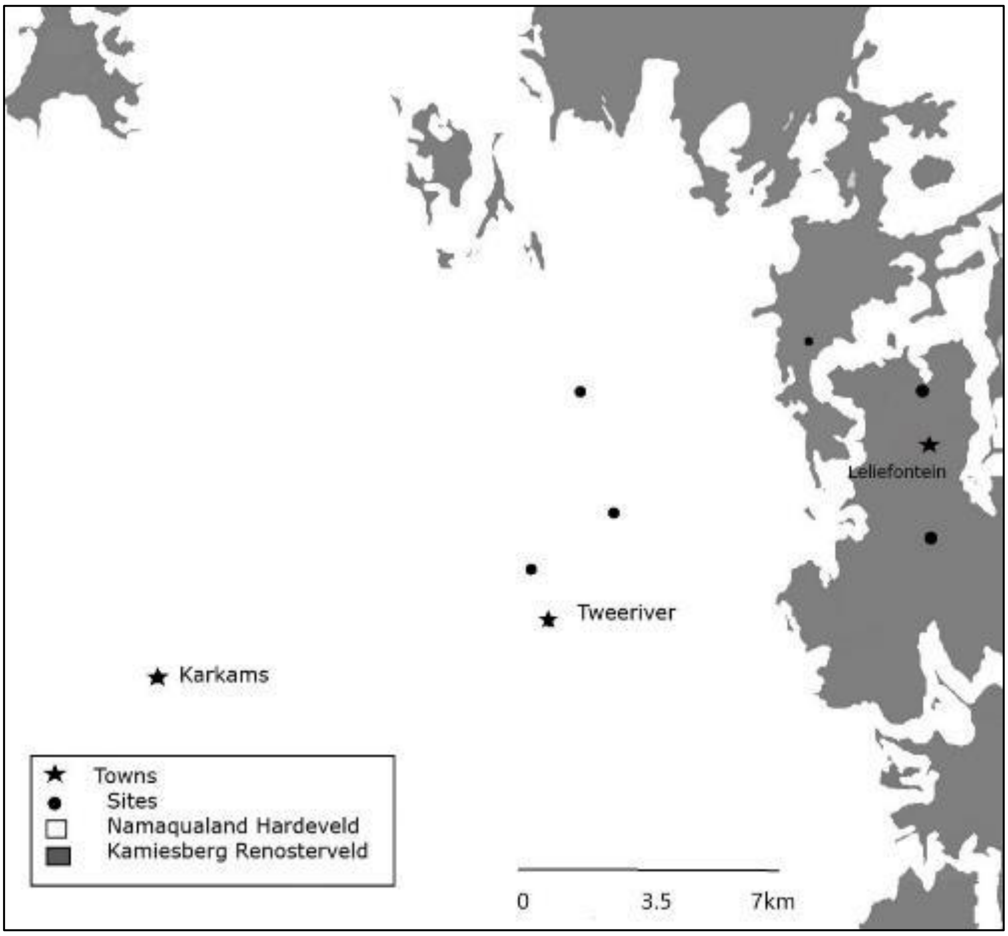


Figure 4.1. Map of the six experimental restoration trials within the two vegetation types of Hardeveld and Renosterveld, in relation to the settlements of Tweerivier and Leliefontein

Table 4.1 Location and name of the six restoration experimental exclosures, together with their relevant GPS co-ordinates, elevation and year when ploughing ceased.

Site	Location	GPS	Altitude (m)	Year of abandonment
HV-1	Hardeveld 1 – Municipal ground	S 30.34200 E 17.9848	660	Unknown but before 1978
HV-2	Hardeveld 2 – East of Dam	S 30.32947 E 18.00606	631	Mid 1970's
HV-3	Hardeveld 3 – Valley	S 30.30258 E 17.99743	680	Unknown but before 1978
RV-1	Renosterveld 1 – Baileysvlakte Peter Links	S 30.33504 E 18.08763	1358	1990s
RV-2	Renosterveld 2 - Langvlei	S 30.29143 E 18.05620	1074	2000
RV-3	Renosterveld 3 - Kleikop	S 30.30242 E 18.08545	1345	Before 1997

Climate

Temperature and rainfall data for Tweeriver and Leliefontein was collected between 2013 – 2015 from Conservation South Africa (CSA) and the Agricultural Research Council (ARC) weather stations respectively (Figures 4.4 and 4.5). The station in Tweeriver was only erected in mid-August 2013, thus data from the next nearest village of Kharkams (14 km away) was sourced from the South African Weather Service. Unfortunately, only rainfall data were available from this station. Therefore, temperature recordings for Tweeriver only start in August 2013 (Figure 4.5).

During the three-year study period, the total rainfall for the village of Leliefontein declined slightly from 2013 (543 mm) to 2014 (527 mm), and was considerably lower in 2015 (343 mm) (Figure 4.2). This trend was also recorded in Tweeriver, where rainfall was 289 mm in 2013 and 213 mm in 2014. In 2015, rainfall was very low at 104 mm (Figure 4.3).

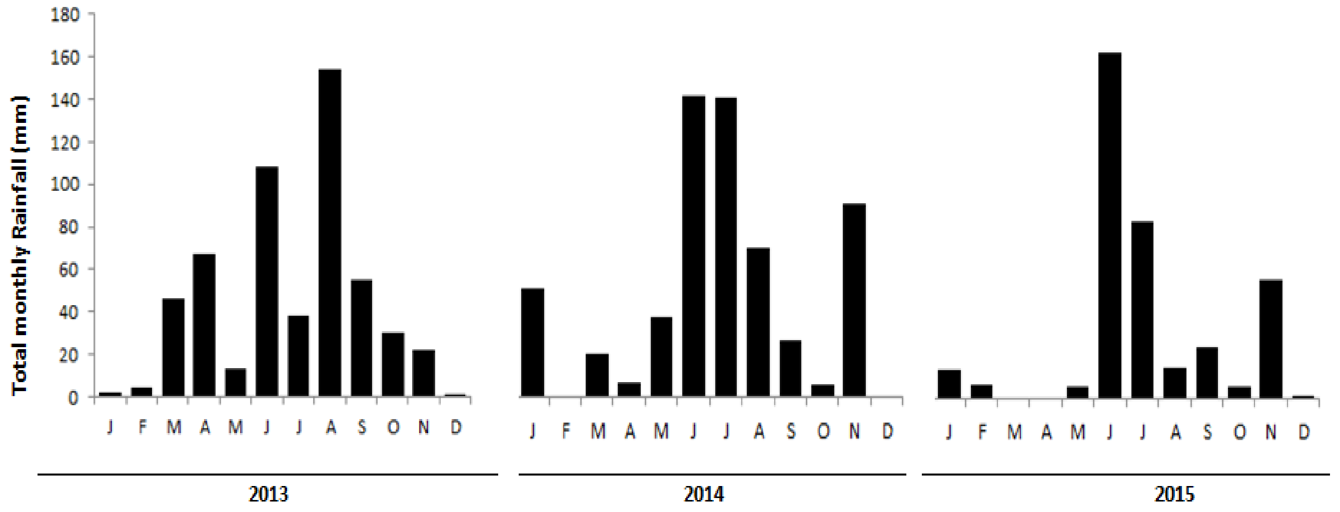


Figure 4.2 Total monthly rainfall in Leliefontein village, for the duration of the study, from the beginning of 2013 to the end of 2015. Data supplied by the ARC weather station.

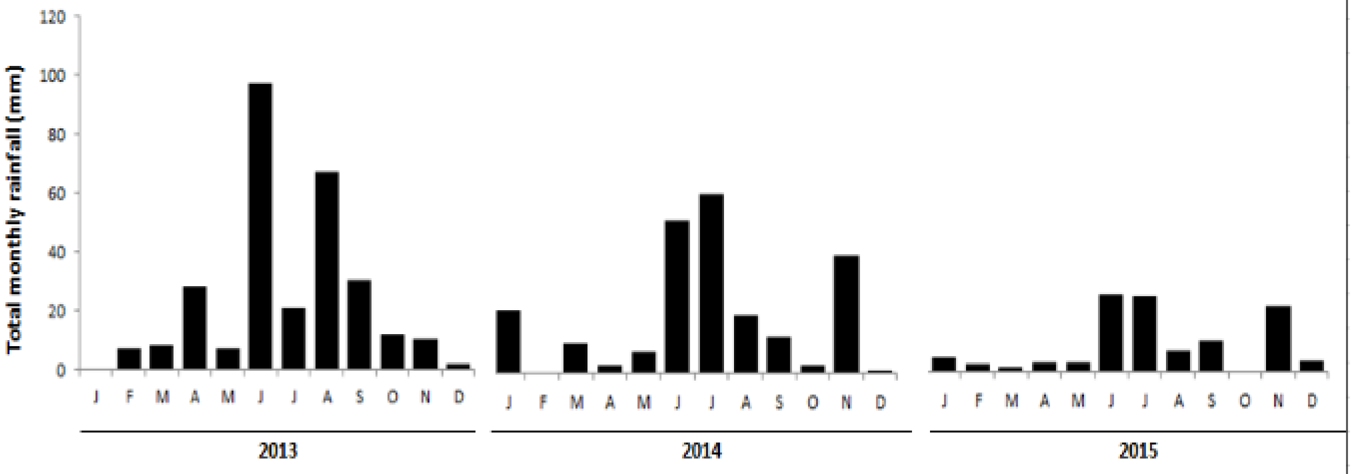


Figure 4.3 . Total monthly rainfall in Tweeriver village, for the duration of the study, from the beginning of 2013 to the end of 2015. Data compiled from the South African Weather service for the nearest station in Kharkams (January – August 2013), thereafter from the CSA weather station in Tweeriver

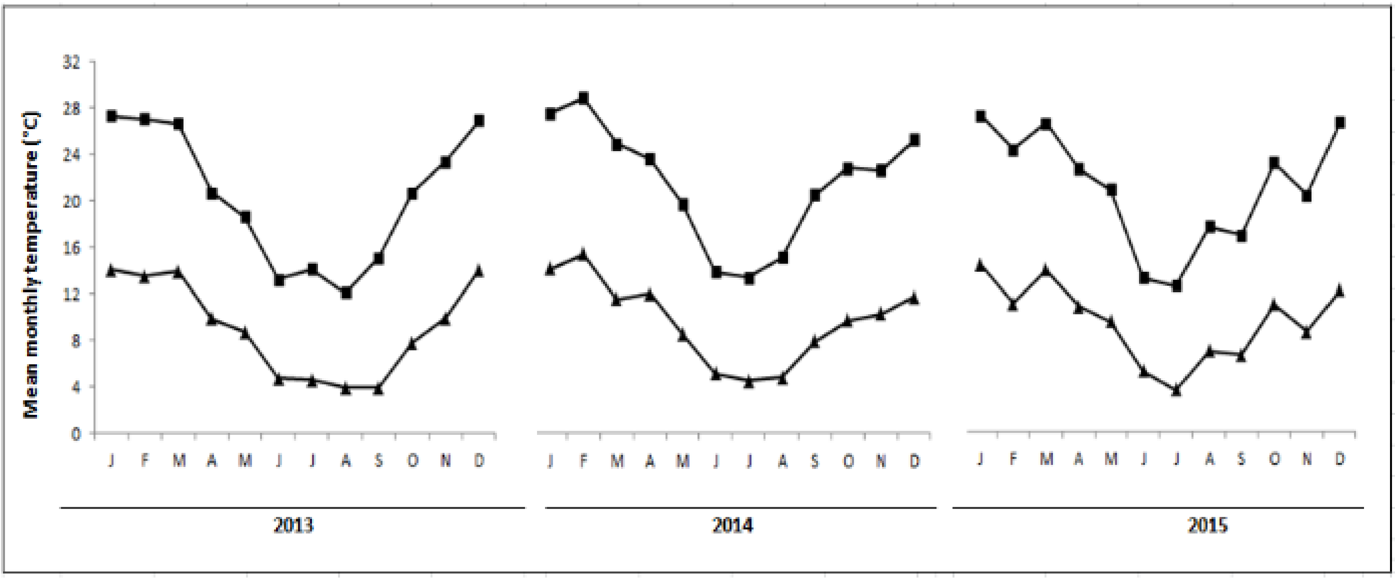


Figure 4.4. Mean monthly temperature (triangles = minimum temperature, squares = maximum temperature) for Leliefontein village, for the duration of the study, from the beginning of 2013 to the end of 2015. Data supplied by the ARC weather station.

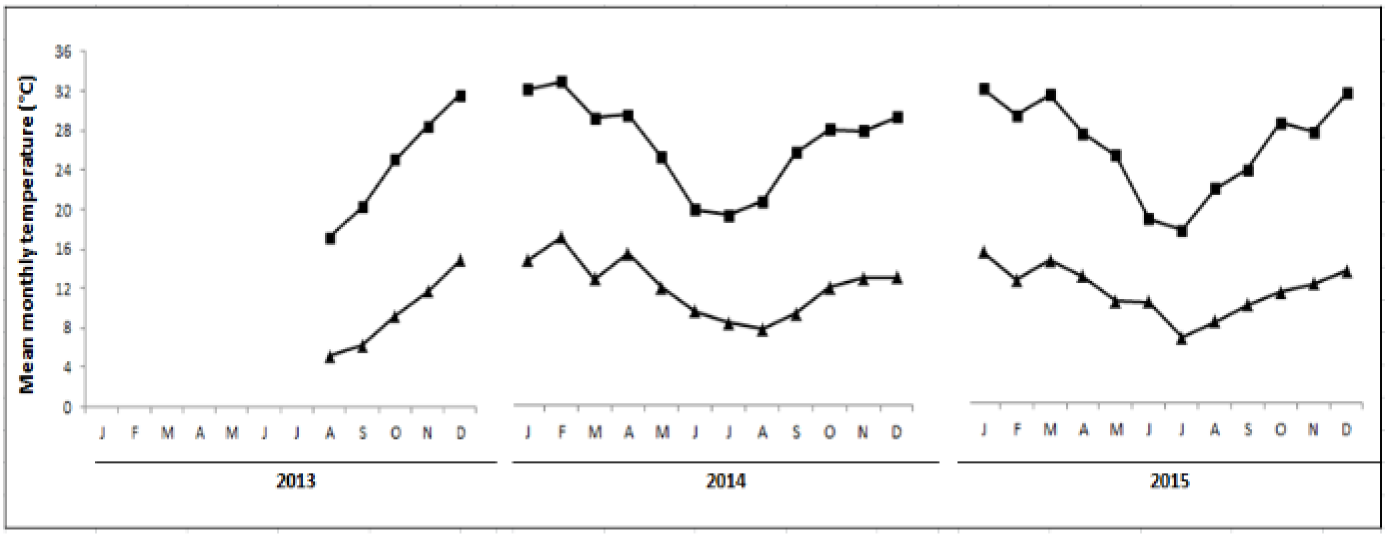


Figure 4.5. Mean monthly temperature (triangles = minimum temperatures, square = maximum temperature) for Tweeriver village, for the duration of the study from August 2013 to the end of 2015. Data supplied by the CSA weather station

4.2.2 Restoration trial methods

Seed Collection, Cleaning and Preparation

A list of seeds to collect for the trial from different plant species was compiled by assessing the natural intact vegetation and identifying the most common and abundant perennial species. These species can tolerate a wide range of conditions and provide vertical structure to the vegetation. The plants were grouped into their major plant growth form types. The aim was to ensure that plant seeds from every functional group were collected (Table 4.2 and 4.3). Seeds, or in most cases, the fruits of plants, were collected from vegetation stands as close to the restoration sites as possible. This is important in conserving the genetic integrity of populations. Locally adapted genotypes are better suited to environmental conditions (Lesica & Allendorf, 1999). Seeds were sourced from natural vegetation around Leliefontein, Tweeriver, Kamieskroon, along the N7 highway, Springbok, and Steinkopf. However, due to differences in seed availability, it was not always possible to collect the desired number of seeds. In such cases, seeds from species that were more abundant were collected so that the total number of seeds per functional group was similar. The Namaqualand Mine Restoration (NMR) company also donated seeds of *Calobota sericea, Chaetobromus involucratus* and *Manochlamys albicans* for this project. All seeds were fumigated with the use of fumi-tabs in an enclosed space as soon as possible after collection to eliminate any beetles, weevils or larvae that were already inside the seeds themselves.

Once the bulk seeds or fruiting bodies had been collected, the individual seeds were carefully extracted from the plant covering bodies that surrounded them (capsules, wings, fruit bodies, etc.), so that they would be able to germinate in the field. Seeds with hard capsules or wings, such as *Tetragonia fruticosa, Zygophyllum morgsana, Conicosa* sp, and *Cheiridopsis denticulata,* were placed in a portable cement mixer to break open the coverings. Seeds with softer coverings or very small seeds, such as *Drosanthemum hispidium, Leipoldtia schultzei, Ruschia* spp., *Pharnaceum confertum,* and *Hypertelis salsoloides,* could be easily removed by crushing the coverings by hand or underfoot on a rough surface. Seeds of certain species did not need to be cleaned because the coverings were known either to not inhibit germination or were unfeasible to remove, such as *Osteospermum oppistifolia, Eriocephalus microphyllus, Pteronia divaricata, Pteronia incana, Hirpicium alienatum, Pentzia incana, Chaetobromus involucratus, Stipagrostis ciliata,* and *Ehrharta calycina.*

A germination trial was conducted in the laboratory at the University of Cape Town in order to understand seed viability and assist in interpreting the results from the field experiment. A germination chamber with a 10 / 25 °C, 12 hr night / 12 hr day temperature and light regime was used for 42 days, where after no germination occurred anymore. Results from the trial are shown in Appendix E.

The quantity of seed from each species to be used was calculated using the Nurture Restore Innovates (NRI) seeding experiment guidelines (P.J. Carrick, personal communication). This considers the size of the seed and assesses the number of seeds that will be in a 50 x 50 cm depression (plot). Slight adjustments were made in cases where collected seed numbers were lower than the targeted amount. With the average weight per seed and the seed number known for each species, the number of seeds needed for the plot was calculated. This included a 5% additional buffer to account for slight measuring errors (Table 4.2 and 4.3). When it came to packing the seeds for the Hardeveld sites, they were separated into small seeds (all the Aizoaceae and others with similar-sized seeds, e.g. *Hypertilis*) and large seeds. This is because many small seeded species need to be located on the soil surface for germination to occur and not buried too deeply, while the larger seeds needed to be covered with more soil (Carrick & Kruger, personal observations). For the Renosterveld sites, there were so few small-seeded species, and only one Mesembryanthemaceae species, that all seed sizes were combined into one packet. Species used were largely grouped into growth forms that follow the groupings set out in chapters 2 & 3. However, due to the low number of species used, small and medium-sized shrubs were not separated into different groups but were rather combined into one category (Table 4.2 and 4.3).

Study site preparation

Each of the six sites comprised an area of 100 m x 50 m and were fenced in by local fencing contractors to protect the sites from grazing livestock and game. The fences did allow for the movement of small wildlife such as tortoises, rodents, and rabbits. A line of wire was strung across the exclosure, known locally as a “camp”, at the 50 m mark (on the longest axis), to create two 50 m x 50 m areas. One half of the camp was used for the seed experiment (often the side closest to a road for ease of access), while the other half was used as a control. At every 5 m interval along the fence, rope was attached and connected to the centre wire to create 10 rows. The two outer rows, at the fence lines, were called “buffer zones” (Figure 4.6). These two rows were not included in the seed planting area or vegetation survey as they had been disturbed during camp construction. They were also the areas most likely to be affected by small mammals and rodents that were able to get through the fence.

Table 4.2. The species and number of seeds in each growth form, sown into each plot in the Hardeveld study sites. The family, and primary seed dispersal mechanism is also indicated. Letters in brackets refer to shrub size shrub: s = small, m = medium, following the classifications outlined in Chapter 2.

Family	**Species**	**Number of seed per plot**	**Seed dispersal mechanism**
Aizoaceae	*Leipoldtia schultzei* (m)	365	water
Aizoaceae	*Ruschia burtoniae* (m)	180	water
Aizoaceae	*Cheiridopsis denticulata* (s)	180	water
Aizoaceae	*Conicosia* sp (s)	23	water
Aizoaceae	*Drosanthemum hispidum* (m)	365	water
Aizoaceae	*Tetragonia fruticosa* (m)	18	wind
Aizoaceae	*Galenia sarcophylla* (m)	45	wind
	Succulent leaf shrubs sub total	***1 176***	
Aizoaceae	*Aizoon canariense*	75	water
Molluginaceae	*Hypertelis salsoloides*	75	passive?
	Herb sub total	***150***	
Asteraceae	*Hipicium alienatum* (s)	25	wind
Asteraceae	*Osteospermum oppistifolia* (m)	18	wind
Asteraceae	*Eriocephalus microphyllus* (m)	55	wind & bird
Asteraceae	*Pentzia incana* (m)	75	wind
Asteraceae	*Pteronia divaricate* (m)	55	wind
Chenopiaceae	*Manochlamys albicans* (m)	320	bird
Fabaceae	*Calobota sericea* (m)	55	explosively dehiscent
Sterculiaceae	*Hermannia disermifolia* (m)	40	animals
Zygophyllaceae	*Zygophyllum morgsana* (m)	18	wind
	Non leaf succulent shrub sub-total	***661***	
Poaceae	*Stipagrostis ciliata*	30	wind
Poaceae	*Chaetobromus involucratus*	440	wind
	Graminoid sub total	***470***	
	Combined seed total	***2 457***	

Table 4.3 The species and number of seeds in each growth form, sown into each plot in the Renosterveld study sites. The family, primary seed dispersal mechanism. Letters in brackets refer to the size shrub: s = small, m = medium, following classifications in chapter 2

Family	Species	Number of seed per plot	Seed dispersal mechanism
Aizoaceae	*Tetragonia fruticosa* (m)	18	wind
Aizoaceae	*Drosanthemum hispidum* (m)	365	water
	Succulent leaf shrubs sub total	***383***	
Aizoaceae	*Aizoon canariense*	75	water
Asteraceae	*Leysera gnaphalodes*	75	wind
Molluginaceae	*Pharnaceum confertum*	70	passive
	Herb sub total	***220***	
Asteraceae	*Eriocephalus microphyllus* (m)	55	wind & bird
Asteraceae	*Helichrysum hamulosum* (m)	75	wind
Asteraceae	*Oedera* sp(m)	75	wind
Asteraceae	*Pteronia incana* (m)	55	wind
Asteraceae	*Pteronia divaricata* (m)	55	wind
Asteraceae	*Pentzia incana* (m)	75	wind
Fabaceae	*Wiborgia* sp (s)	20	wind
Fabaceae	*Calobota sericea* (m)	55	explosively dehiscent
Lamiaceae	*Stachys rugosa* (s)	30	animal
Sterculiaceae	*Hermannia disermifolia* (m)	40	animal
	Non leaf succulent shrub sub-total	***535***	
Poaceae	*Tribolium hispidum*	145	wind
Poaceae	*Ehrarta calycina*	145	wind
	Graminoid sub total	***290***	
	Combined seed total	***1 428***	

Once the study sites had been fenced, a vegetation survey of the section of the site that was to be planted was carried out to obtain an estimate of the density and size of kraalbos and renosterbos prior to the experiment. Once the vegetation survey was completed, 50% of the kraalbos and renosterbos shrubs were removed and laid over the area that they had inhabited. These shrubs were reduced by 50% only, in order to create sites for use in the experiment as well as leave some standing for use as nurse plants. High levels of disturbance could facilitate the invasion of problem plants. Any other vegetation was left untouched as much as possible. The aim was to thin out the density of the bushes and create space for seeding treatments without having a resident shrub too close to the plot. This was done to allow the seeded vegetation to establish amongst the existing shrubs and over time, outcompete the kraalbos and renosterbos shrubs.

Depressions and seed sowing

Seeding began in mid-May 2013, just before the commencement of the rainy season, so as to reduce the number of seeds lost through predation and wind, and was completed by early June. The final site was sown during the first rains of the winter season (1 – 3 June 2013).

Plots were created in two areas. The one area was the inter-patch areas that existed between plants and are hereafter called ‘open’ plots. The second area was created in the space where a shrub had been growing and had been removed, and are referred to as a ‘patch’ or ‘roots’ due to the roots of the shrub being left undisturbed in the soil. Seeds were sown into 50 cm x 50 cm square plots. The plot was shaped into a slight depression wherein water and organic matter could accumulate, creating more favourable conditions for seeds. In this study, any plants and grass tufts were removed so as not to interfere with the experiment. The topsoil (approximately 3 cm) was carefully scraped off and put to one side. Approximately 5 cm of subsoil was removed and used to create a ‘dam wall’ on the top and/or sides of the depressions that were facing downslope to increase the water input to the plot from rain. The edges of the sand outside the plot were smoothed away to prevent the soil from collapsing into the plot. The biologically active topsoil, containing a possible seed bank, micro-organisms, fungi, and nutrients, was then replaced (leaving a few handfuls on the side to be used to cover the sown seeds) and it was ensured that the soil inside the depression was level.

Once the plots had been prepared, the actual sowing of the seeds took place. The seeds were sown into the plot and lightly covered with topsoil (covering them with 1 – 2 cm of soil), then patted down to prevent them from being blown away and to encourage seed contact with the soil (Barnard, 1987).

Treatments

Fifteen replicate plots of each of the following treatments were set out in both open and patch plots respectively at each site (Figure 4.6), creating a full factorial experiment with the following treatments: seeded control Open (O) and roots (patch) (R), nutrients (N), box shelter (Box), brush pack shelter (B), nutrients and brush pack shelter together (BN), nurse plant shelter (Alive), no seeded control open (O/C) and no seeded control roots (R/C).

1) The seeded control treatments in an open and patch area were set out as per the description above for seed sowing.
2) The nutrient treatment consisted of adding an organic slow-release fertilizer, which contained a complete suite of macro- and micronutrients. An amount of 35 g of "Veg 6:3:4(15) SR VITA Organic Fertilizer" was mixed into the top soil before the seeds were sown. The amount of fertilizer is approximately the equivalent amount of nitrogen, phosphorus, and potassium that occurs in undisturbed top soil (700 g.m^{-3}) in patches under perennial shrubs in Namaqualand (Carrick & Kruger, 2007).
3) The treatments containing brush packs consisted of placing a previously removed renosterbos or kraalbos over the plot once the seeds had been sown. The leaves of the shrub were shaken off so that light would still be able to filter through the branches to the soil (Figure 4.7. b). A suitably sized shrub was used to ensure that the shrub covered the entire plot. The shrub was secured in the ground with wire stakes.
4) A treatment that contained both the addition of fertilizer and a brush pack, was set up in the same way as the above two treatments.
5) The box shelter treatment consisted of a plot with cardboard boxes (50 cm x 50 cm and 30 cm deep). The top and bottom flaps of the cardboard box were removed, so that only the four sides of the box remained. The depression for this treatment differed, because approximately half the box had to be submerged in the ground. A hole slightly larger than the box was dug and the cardboard box was inserted 10 – 15 cm deep into the soil. Soil from the hole was put back into the box first, ensuring that the box did not lose its square shape, followed by the topsoil until the soil within the box was 5 cm higher than the soil outside the box. This resulted in the soil pushing the box outwards, which helps prevent the sides of the box from falling inwards (Figure 4.7 a). The box itself still had to be in a slight depression to increase the water input to the depression.
6) The final shelter treatment consisted of creating a plot under a living kraalbos and renosterbos. The nurse plant was in the centre of the plot (Figure 4.7 c) and seeds were sown evenly underneath the nurse plant.

7) In the case of the no seed control treatments, plots were created but no seeds were sown. This was to control for perennial species that might have been present in the seed bank and to account for spontaneous recovery in the absences of grazing.

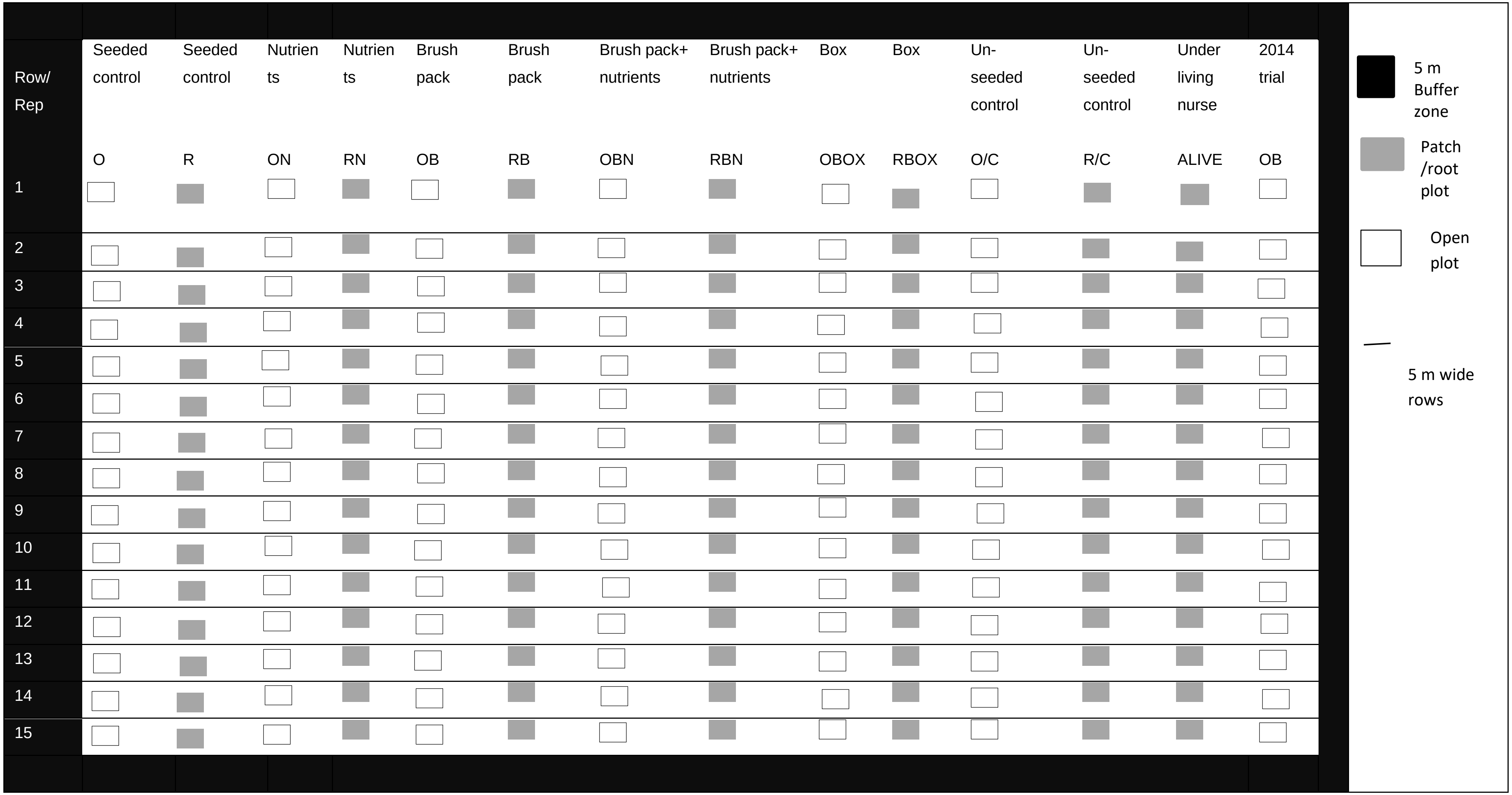
For all the treatments descriped above, there were two plots, one in the open and one in a patch/root. This made for 14 combinations in total (7 treatments x 2 plots) (Figure 4.6, Appendix F.6 & F.7).

In the case of the nurse shelter patch treatment, a matching open treatment could not be created. By definition, this treatment will always be a patch due to the presence of the live plant with its roots in the soil. Therefore, this treatment was used to assess the influence of competition and shelter on seedlings and were analysed with other shelter type treatments. Each of these treatments was repeated 15 times in each of the three camps (Figure 4.6), totalling 45 repetitions of the treatments in each vegetation type.

4.2.3 Monitoring and data collection

The emergence and survival of seedlings were monitored for three years (2013-2015). Data collection took place in winter (August) and in early summer (November) for each of the three years. During each monitoring period, the number of seedlings of the sown species was recorded. This allowed for an assessment of seedling establishment and their suitability for future projects.

After the first year, there was concern over the visible lack of germination from the Renosterveld sites, and given reports of a colder winter than usual, there were concerns that seedlings may have died in the numerous snowfalls that occurred that year (2013). Therefore, it was decided to put in an extra plot every replicate of every camp before the following rains in 2014, in order to compare germination rates under two different starting years and likely two different environmental conditions. This ‘2014 trial’ provided a chance to compare germination trends one year apart, and to assess the impact of different weather conditions and their influence on germination rates. This trial, seeded in May 2014 in all six camps, followed the seeding numbers and sowing design as before and used the “open with brush pack” treatment (Figure 4.6).



Row/ Rep	Seeded control O	Seeded control R	Nutrients ON	Nutrients RN	Brush pack OB	Brush pack RB	Brush pack+ nutrients OBN	Brush pack+ nutrients RBN	Box OBOX	Box RBOX	Un-seeded control O/C	Un-seeded control R/C	Under living nurse ALIVE	2014 trial OB
1	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
2	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
3	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
4	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
5	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
6	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
7	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
8	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
9	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
10	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
11	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
12	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
13	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
14	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐
15	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	☐	▨	▨	☐

Figure 4.6 Diagram showing the layout of the restoration trial comprised of 14 treatment plots (including four controls, seeded and un-seeded) which were implemented in 15 rows. Each plot consisted of a single 0.5 m x 0.5 m depression. Treatment codes are; Open (O), patch/roots (R), nutrients (N), box shelter (Box), brush pack shelter (B), nutrients and brush pack shelter together (BN), nurse plant shelter (Alive).

Figure 4.7 Figure 4.6. Examples of shelter type treatments used in the restoration experiment, placed in a micro-depression, (a) box treatment within the depression, (b) brush packed treatment (kraalbos in photo) and (c) under a nurse plant treatment (renosterbos in photo)

By November 2014 most of the boxes had disintegrated, largely due to the activities of termites and ants. Given that the majority of germination and establishment occurred in the first year (i.e. 2013), the effect of the boxes on germination would have already occurred while the boxes were intact. Because of this, it was decided to remove all boxes from the sites at the end of 2014.

Statistical analysis

Generalized linear mixed models (glmms) were used for the data analysis. A high number of zeros in the data was expected given the nature of the experiment and a Poisson distribution was considered. However in some instances the data was more zero inflated, leading to over-dispersion (Zuur *et al*., 2009). In these instances, a zero-inflated (ZI) model which combines a count response variable (Poisson or Negative binomial distributed) and a distribution with point mass of one at zero was used. This model allows greater flexibility and speed for zero inflation datasets and can be interpreted in the same way as a logistic regression model. A zero-inflated negative binomial model addresses over-dispersion in the data, which arises from the relatively large number of zero counts. The Zero Inflated model was implemented in the R package glmmTMB. Models were tested for zero inflation and distribution and were compared based on the Akaikes Information Criterion (AIC). The model with the minimum AIC was selected as the best fit estimator. I assessed the model's goodness-of fit by plotting a quantile-quantile plot of the residuals and the residuals versus the predicted variable, as provided by the R-package DHARMa.

Once the best glmm was selected, an ANOVA was conducted on the model and, if any significant results were indicated, a posthoc test for the comparisons was run using the R-package emmeans. The adjustment method, "mvt" ("multivariate t") estimates a “multivariate t” distribution of all the hypotheses, which it uses to generate p-values.

In these models, seedling establishment (individuals) was analysed for each growth form as the dependent variable. The last recording date (August 2015) was used in the models, as this would be the most meaningful because it would indicate which growth forms survived the duration of the experiment, thus providing a good idea of which species to use for future restoration efforts.

The first model run was to determine the influence of micro depressions and actively sowing seeds by comparing seeded open and root controls with unseeded open and root controls. The second analysis examined which growth form established better than the others, by comparing the numbers of individuals in the growth forms across the seeded open control treatment.

The third model dealt with a full factorial experiment, where nutrients (two levels), brush pack (two levels) and microsite location (two levels) were compared, as well as their interactions.

The fourth model dealt with different types of shelter. I tested the influence of four different types of sheltering structure on seedling establishment by comparing brush packs (protection from herbivory and climatic elements from above), boxes (protection to seedlings on the sides but more exposed to elements) and under a living kraalbos or renosterbos (protected from above and partly protected on sides) to a no-shelter control. I chose the treatments that were all located on root plots (and the hypothesized fertile island created by a pioneer shrub plant). This allows for a comparison of the above ground aspect where below ground conditions are the same. This then also allows for an analysis of the influence of competition or facilitation, for resources with a nurse plant by comparing a living plant, a ‘dead’ plant (a root plot with a brush pack which mimics similar shade and protection as a nurse plant but without the competition for resources) and a control (root plot with no plant at all).

The fifth model to analyse the influence of seeding numbers in different climatic years, was done by selecting the open with brush pack treatment (OB) set in 2013, and the one set in 2014 (also an open with brush pack treatment called OB 2014 Trial), and comparing the August and November recordings to each other. This was done for two years, to assess how germination and survival differed between years. Data were analysed in the programme R (R Development Core Team, 2009).

4.3 Results

The results of the restoration study are grouped into the two vegetation types of Hardeveld and Renosterveld. In each vegetation type, the four key questions are presented, namely 1) the effect of sowing seeds, 2) the influence of under canopy, nutrients and brush packing, 3) types of shelters and 4) seeding in different climatic years. The results of these studies are presented in terms of the response of the four growth forms used in the study.

4.3.1 Hardeveld

The effect of sowing seeds

No perennial plants germinated from the soil seed bank in the un-seeded control plots (Figure 4.8). Sowing seed of perennial species in plots resulted in establishment. In the first winter season this averaged 20 individuals/plot, and even though this decreased to an average of 2 individuals/plot by the end of the 3rd year, establishment via active seed sowing did occur.

At the end of the three-year study period, 16 species had established out of the 20 that had been sown initially. The five species with the most individuals were *Leipoldtia schultzei, Cheiridopsis denticulata, Drosanthemum hispidum* and *Ruschia burtoniae* (succulent shrubs); and *Chaetobromus involucratus* (grass). Succulent shrubs dominated in each of the three years. *C. involucratus* only became a dominant species from the second year onwards. The shrubs *Pteronia divaricata* and *Zygophyllum morgsana* were dominant in the first year but had died off in subsequent years.

Succulent shrubs were by far the most successful growth form to establish after 3 years in Hardeveld (Figure 4.8) and outperformed the other growth forms across the different treatments. An exception to this was in the case of the root (under kraalbos canopy or patch) with brush pack treatment where grasses established the best. In the control plots, succulent shrubs had significantly better establishment than grasses and non-succulent shrubs (χ^2 (3) = 66.3, $p < 0.0001$), with an average of 2.4 individuals/plot compared to an average of 0.4

individuals/plot of grasses and non-succulent shrubs. Grasses and the non-succulent shrubs performed similarly. Herbs did not establish at all.

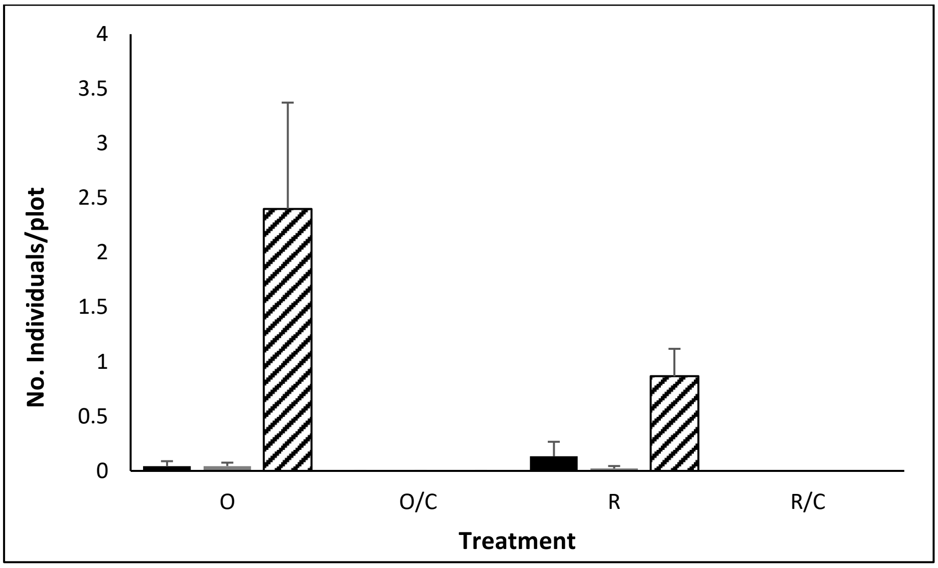


Figure 4.8. Average (±SE) number of individuals per plot of grass (black shading), non-succulent shrubs (grey shading) and succulent shrubs (diagonal stripes) recorded in open plots (O), open unseeded control (O/C), root (R) and root unseeded control (R/C) plots at the end of year three in the Hardeveld trial.

The influence of under canopy patch, nutrients and brush packing

In the factorial model, the effect of seeding on a root (under canopy patch) plot compared to an open plot was analysed in terms of seedling numbers after three years, as well as the effect of adding nutrients and brush packs to the plots. Overall, the model predicted that root plots would result in 0.75 times fewer seedling numbers than open plots (χ^2 (1) = 2.7, p = 0.05, Table 4.4). The root plot treatments all resulted in lower establishment and fewer species than their open plot counterparts. The treatment with the poorest establishment was the control root plot, with an average of 1 individual/plot (Figure 4.9.a). However, it was only succulent shrubs that established well on open plots compared with root plots. The other growth forms showed no difference in establishment on root or open plots.

Across the growth forms, the addition of brush packing (χ^2 (1) = 29.3, p < 0.0001) and nutrients (χ^2 (1) = 6.8, p < 0.0001), as separate treatments, were substantially beneficial for seedlings. Plots without brush packing had 0.4 times fewer individuals than those with brush packing

(Table 4.4). Furthermore, plots with nutrients had 1.5 times more individuals than the control plots. For this experiment, the open plot with nutrients was the best treatment, resulting in an average of 9 individuals/plot (Figure 4.9.a).

Succulent leaved shrubs showed a significant preference (χ^2 (1) = 11.8, $p < 0.0001$, Table 4.4) for open plots compared with root plots. The model estimated that root plots had 0.28 times fewer individuals than open plots (an average of 0.88 vs 2.4 individuals/plot, respectively). The addition of nutrients was also a significant predictor in the model (X^2 (1) = 11.8, $p < 0.0001$) for succulent shrubs, which were 1.5 times more abundant in a nutrient treatment than in a treatment without nutrients. When nutrients were added to an open plot this tripled the establishment, of shrubs, from an average of 2.4 to 8.6 individuals (Figure 4.9.b). The brush packing treatment did not have a significant effect on shrub establishment although the interaction of plot, nutrients, and brush packing was significant (χ^2 (1) = 3.8, $p = 0.05$, Table 4.4). The posthoc test indicated that brush packing on an open plot resulted in better establishment than bush packing on a root plot. Adding nutrients also significantly improved survival, but only when added to an open plot or a root plot with a brush pack (an average of 3.5 individuals/plot). Overall, these results indicated that succulent shrubs establish well on a root plot, but only if conditions were improved by the addition of nutrients or brush packs. For succulent shrubs the treatment that resulted in the best establishment in this model configuration was the open with nutrients treatment, with an average of 8.6 individuals/plot.

Non-succulent leaved shrubs had very low establishment in this study in general, with an average of less than 1 individual/plot. Brush packing was the only factor in the model to have a significant impact on establishment, with 0.22 fewer seedlings in plots without brush packing (χ^2 (1) = 11.5, $p < 0.0001$, Table 4.4). The location of the root or open plot did not have a significant impact on establishment.

For grasses, the effect of the root or open treatment on seedling numbers was minor (χ^2 (1) = 2.9, $p < 0.05$, Table 4.4), with little grass establishment on these plots (Figure 4.9.d). The effect of nutrients was also marginal (χ^2 (1) = 3.8, $p < 0.05$) (Table 4.4). It was the addition of brush packing that had the most noticeable benefit for grass seedlings (χ^2 (1) = 66.9, $p < 0.001$), with the model estimating that plots without brush packing had 0.72 times fewer individuals. However, it was the combination of brush packing and nutrients that had the biggest effect on seedling establishment, with the model estimating 7.8 times more grass seedlings (χ^2 (1) = 8.7, $p < 0.01$, Table 4.4). These treatments increased grass seedling numbers to an average of 1.4 individuals/plot. The treatment that resulted in the best grass establishment was the open treatment with nutrients and brush packing, with an average of 1.4 individuals/plot (Figure 4.9.d).

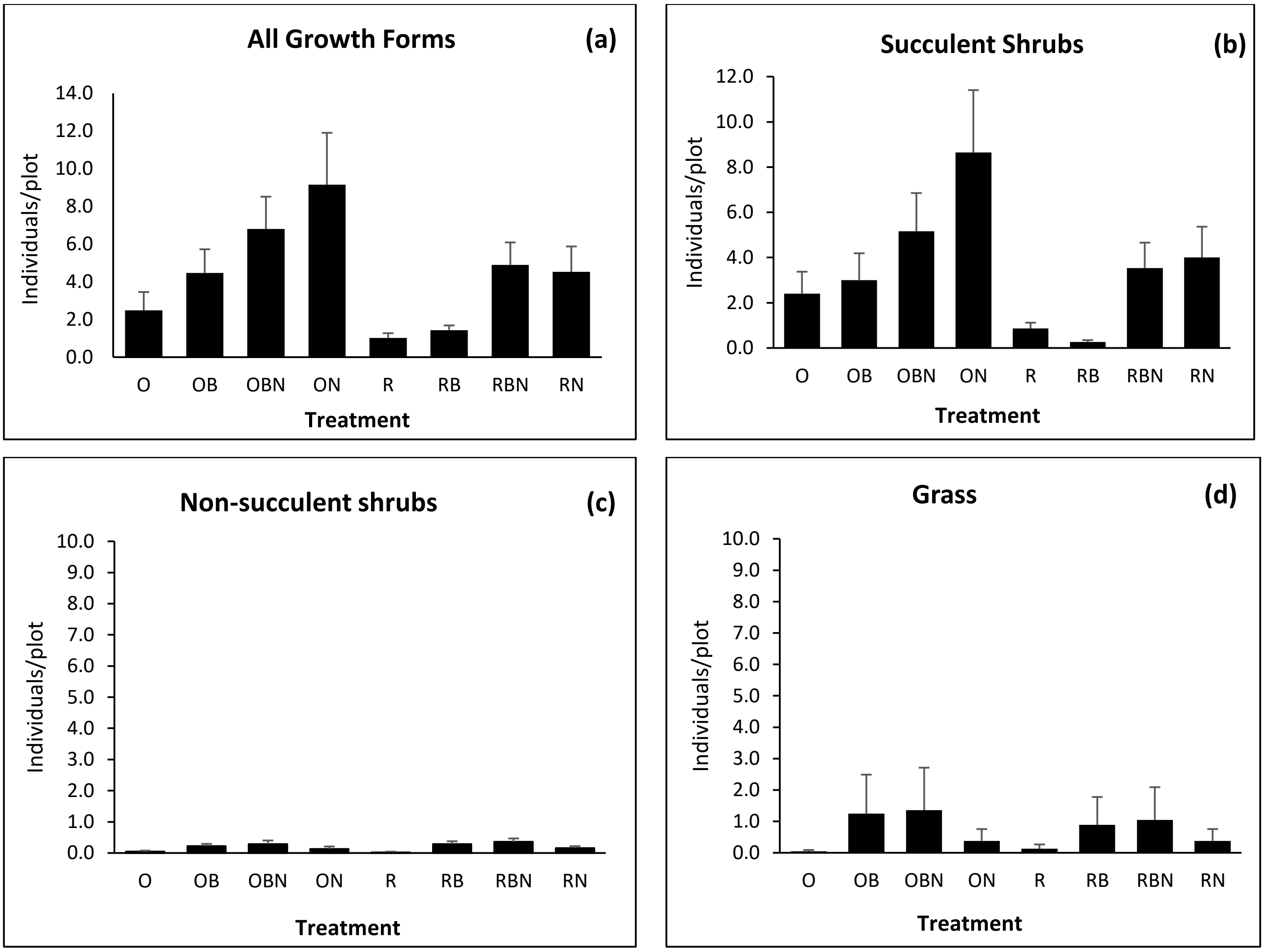


***Figure 4.9** Average (+SE) number of individual seedlings per plot of different growth forms recorded in the Hardeveld trial, a) All growth forms b) Succulent shrubs c) non succulent shrubs d) grass. Treatments are indicated as follows: control open (0) plots, brush packing on an open plot (OB), brush packing and nutrients on an open plot (OBN), nutrients on an open plot (ON), control root (R), brush packing on a root plot (RB), brush packing and nutrients on a root (RBN) and nutrients on root plot (RN).*

Table 4.4 Parameter estimates and error statistics of the GLMM of different growth forms (herbs did not germinate at all) in Hardeveld. Co-efficient results are given on the log scale. BT value indicates the back transformed value of the co-efficient. Significance: * = p 0.05 ≤ 0.01, ** = p ≤ 0.01, *** = p ≤ 0.001.

	All growth forms (n = 1440)				**Succulent shrubs (n = 360)**				**Non-leaf succulent shrubs (n = 360)**				**Grass (n = 360)**			
	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq
Intercept	0.31	1.36	0.27		0.71	2.03	0.58		-1.50	0.22	0.50		-0.11	0.89	0.45	
Treatment (open compared to root)	-0.29	0.74	0.20	2.71	-1.26	0.28	0.40	11.86 ***	0.25	1.28	0.44	0.37	-0.33	0.71	0.20	2.99#
Brush (brush compared to no brush)	-0.91	0.40	0.25	29.33***	-0.31	0.73	0.32	0.25	-1.56	0.21	0.79	11.58***	-3.33	0.03	0.70	66.99***
Nutrients (no nutrients compared to nutrients)	0.14	1.15	0.19	6.87***	0.41	1.51	0.30	12.59 ***	0.29	1.33	0.45	2.80	0.08	1.08	0.18	3.80
Treatment:Brush	0.21	1.23	0.36	0.11	0.94	2.55	0.52	0.23	-0.95	0.38	1.31	0.18	1.43	4.17	0.85	1.81
Treatment:Nutrients	0.13	1.13	0.28	0.06	0.97	2.63	0.51	0.48	-0.05	0.95	0.60	0.02	0.07	1.07	0.27	0.01
Brush: Nutrients	0.38	1.46	0.33	1.31	0.57	1.75	0.41	0.05	0.81	2.24	0.95	2.54	2.05	7.76	0.75	8.72**
Treatment:Brush: Nutrients	-0.26	0.77	0.48	0.23	-1.30	0.27	0.67	3.73	0.87	2.38	1.49	0.34	-1.77	0.17	0.11	1.66

The influence of different types of shelters

Overall, shelters had a significant positive influence on seedling establishment (χ^2 (3) = 9.49, $p < 0.02$). The model predicted that unsheltered control plots would have 0.58 times fewer individuals than box and brush shelters (Table 4.5). There was no difference between seeding under a living kraalbos, brush, or control treatments, which all had an average of 1 individual/plot (Figure 4.10. a), thus indicating no effect of competition. Although not statistically significant, there was a trend that boxes were the most effective form of shelter and increased average seedling numbers to around 5 individuals/plot. However, this result was largely driven by the succulent shrubs, which were the most abundant.

Succulent shrubs established was significantly influenced by different types of shelters (χ^2 (3) = 70.7, $p < 0.001$). Boxes were the best form of shelter, increasing individuals significantly to 4.4 individuals/plot (Table 4.5, Figure 4.10.b). Boxes were significantly better for seedling establishment compared to brush packs, no shelter control, and living under kraalbos. Seedling establishment for succulent shrubs was lowest on a root with brush treatments, with an average of 0.26 individuals/plot. There was no difference between an unsheltered control root plot (1 individual), a brush packed root plot (none) and under a living kraalbos (1.4 individual), indicating no significant impact of competition from a living nurse plant on the establishment of non succulent shrub seedlings.

The non-succulent leaved shrubs had very similar trends in results to the succulent shrubs and were also significantly influenced by shelters (χ^2 (3) = 7.8, $p < 0.05$). Boxes were also the most effective treatment for seedlings (an of average 0.4 individuals/plot), but only significantly differed from the unsheltered control root plot, the latter of which had 0.9 times fewer individuals (Table 4.5, Figure 4.10.c). There was no difference between an unsheltered control root plot, a brush pack, and under a living kraalbos, which all had below 0.3 individuals/plot, indicating no significant impact of competition from a living nurse plant.

Grasses were also significantly influenced by shelters (χ^2 (3) = 27.8, $p < 0.001$), but differed from the shrubs with regard to which type of shelter was more beneficial for seedlings. Although box treatments were also significantly better than the unsheltered root control plots, it was the brush pack treatments that had the best results for grasses, by increasing the number of individuals by 2.66 times (Table 4.5). There was an indication of competition from a living nurse plant, as a root with brush pack treatment resulted in significantly better establishment than under a living kraalbos, with averages of 0.33 to 0.89 individuals/plot, respectively (Figure 4.10.d).

Table 4.5 Parameter estimates and error statistics of the GLMM of different types of sheltering structure on different growth forms in Hardeveld. The growth form herbs did not establish. Results are given on the log scale. BT value indicates the back transformed value of the co-efficient. Significance: * = p 0.05 $\leq$ 0.01, ** = $p \leq 0.01$, *** = $p \leq 0.001$.

	All growth forms (n = 1440)				**leaf succulent shrubs (n = 360)**				**Non-leaf succulent shrubs (n = 360)**				**Grass (n = 360)**			
	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Z value
Intercept	-0.55	0.61	0.26		-0.35	0.70	0.62		-1.04	0.35	0.46		-1.47	2.5	0.49	
Treatment R	-0.54	0.58	0.27	-1.96 *	-0.44	0.64	0.29	-1.45	-2.40	0.90	1.05	-2.28 *	-0.91	0.40	0.46	-1.98*
Treatment RB	0.15	1.16	0.22	0.68	-0.68	0.51	0.46	-1.45	0.15	1.16	0.43	0.35	0.98	2.66	0.29	3.38***
Treatment RBOX	0.24	1.27	0.22	1.07	1.49	4.44	0.24	6.15***	0.48	1.61	0.41	1.18	0.33	1.40	0.32	1.03

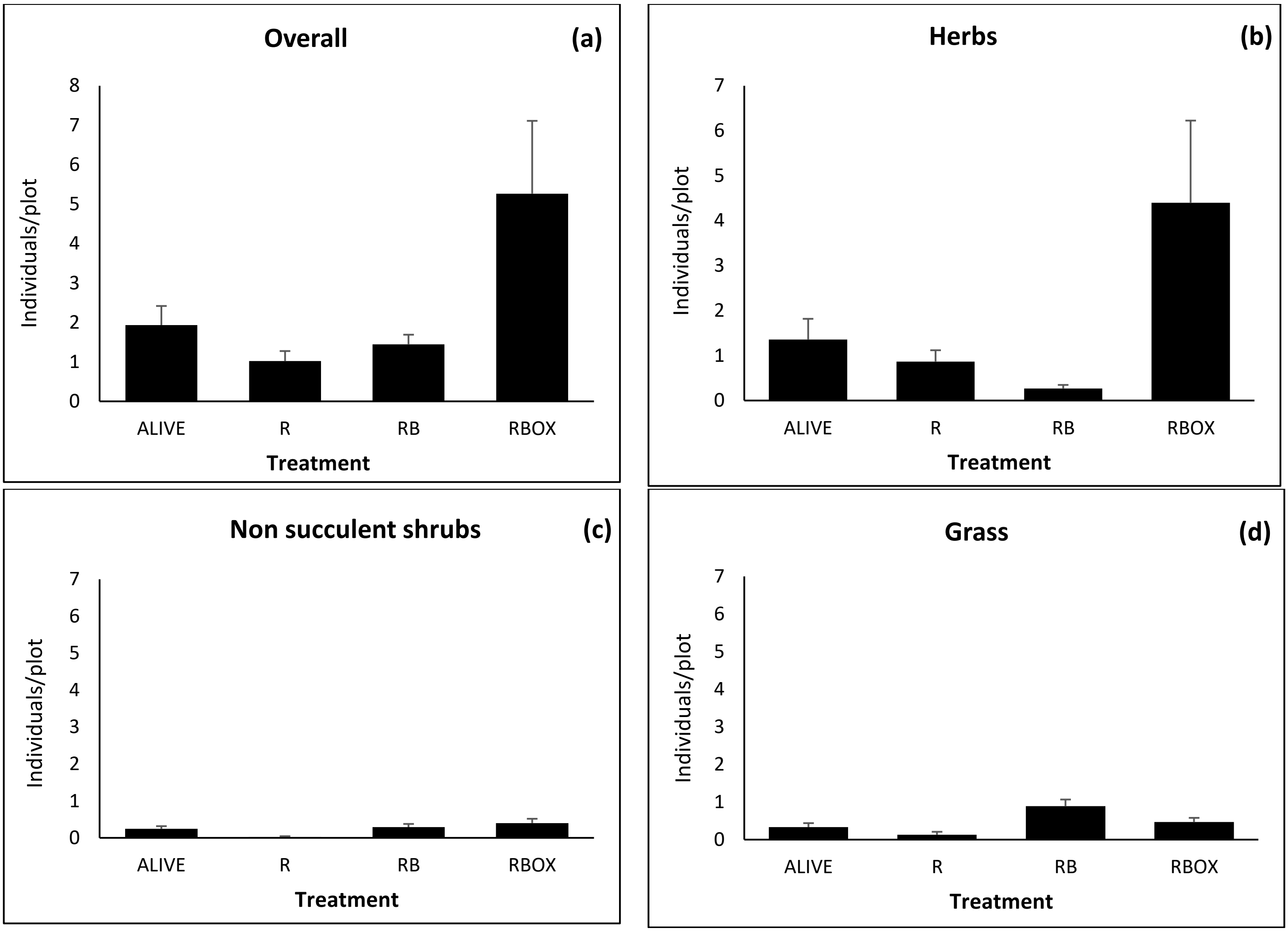


Figure 4.10. Average number of seedlings (± SE) of different growth forms recorded in different types of sheltering structure in the Hardeveld trial, a) overall b) herbs, c) non succulent shrubs d) grass. Treatments are indicated as follows: under a living kraalbos (alive), unsheltered control root plots (R), brush packing on a root plot (RB) and a box on a root plot (RBOX).

Seeding in different climatic years

In 2014 a replica of the 2013 open with brush pack treatment was added to the exclosures. This allowed for a comparison of germination in two different climatic years (2013 verses 2014) over winter and early summer, as well as to track the survival of seedlings over two years for each treatment.

Figure 4.11 demonstrates that there was a significant difference in germination in the Hardeveld between the seeds sown in 2013 and 2014 (χ^2 (1) = 4.1, $p < 0.05$), particularly in their respective first years. In its first winter season, the trial sown in 2013, had an average of 19.5 individuals/plot establish, whilst those sown in 2014 only had an average of 3.5 individuals/plot establish. The other noteworthy difference between the two trials was that the

2013 trial saw a large die-off of seedlings after its first year, whilst the 2014 trial had little change between its two years. Another difference between these two trials was the change in seedling numbers in their respective first summers. In 2013, there was a slight increase from an average of 19.5 individuals to an average of 22.2 individuals/plot, while in 2014 trial there was a slight decrease from an average of 3.5 individuals to an average of 1.3 individuals/plot.

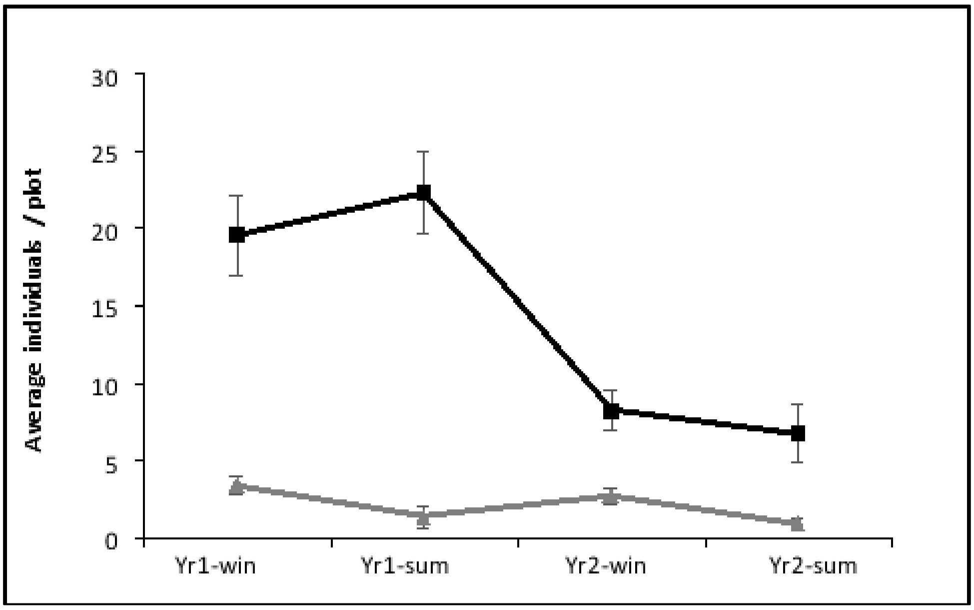


Figure 4.11 Average (± SE) seedling numbers in open with brush pack treatments sown in two consecutive years, in 2013 (black line with squares) and in 2014 (grey line with triangles) in Hardeveld. Each trial is plotted over its two-year winter (win) and summer (sum) recording intervals

4.3.2 Renosterveld

The effect of sowing seeds

Pentameris curvifolia was the only perennial to germinate from the soil seed bank in the un-seeded control plots. This species was not sown in the seeded plots and occurred in low numbers (Figure 4.12). None of the species used in the experiment were recorded in the unseeded plots. Sowing perennial seed species in plots resulted in their establishment. Seedling numbers also increased over the three years. In the first winter season, there was an average of 0.7 individuals/plot. By the end of the third year, this increased to an average of 4.8 individuals/plot.

Of the 17 species sown in the first year, 10 species were established by year three. An interesting trend was that the number of seedlings of herbs, grasses, and non-succulent shrubs all increased over the course of three years, but succulent shrubs decreased. By the end of the first year, germination was low, and only three perennial shrub species germinated: *Drosanthemum hispidum*, *Pteronia divaricata* and a *Wiborgia* sp. This was quite different to the third year where 10 species had established and the five most abundant species were *Tribolium hispidium* (grass), *Leysera gnaphalodes* (herb) and *Pharnaceum confertum* (herb), *Wiborgia* species and *Eriocephalus microphyllus* (both non-succulent leaved shrubs).

Grasses and herbs were the most successful growth forms to establish in the experiment in Renosterveld (Figure 4.12). Succulent shrubs hardly established. In the control treatment, the number of grasses and herb seedlings that established was significantly (χ^2 (3) = 16.3, p < 0.0001) higher than the number of non-leaf succulent shrubs (Figure 4.12).

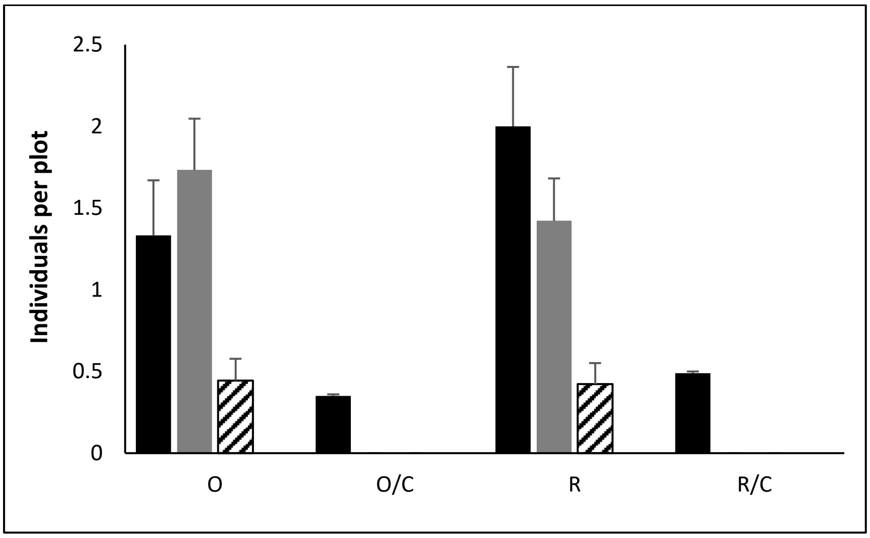


Figure 4.12 The average (+ SE) seedling numbers recorded by the end of the three-year study of the different growth forms: grass (black), herbs (grey), non-leaf succulent shrubs (diagonal lines). Treatments are indicated as the open (O) seeded treatment and unseeded open control (O/C) treatments, the root (R) seeded treatment and the un-seeded root control (R/C) in Renosterveld

The influence of under canopy patch, nutrients and brush packing

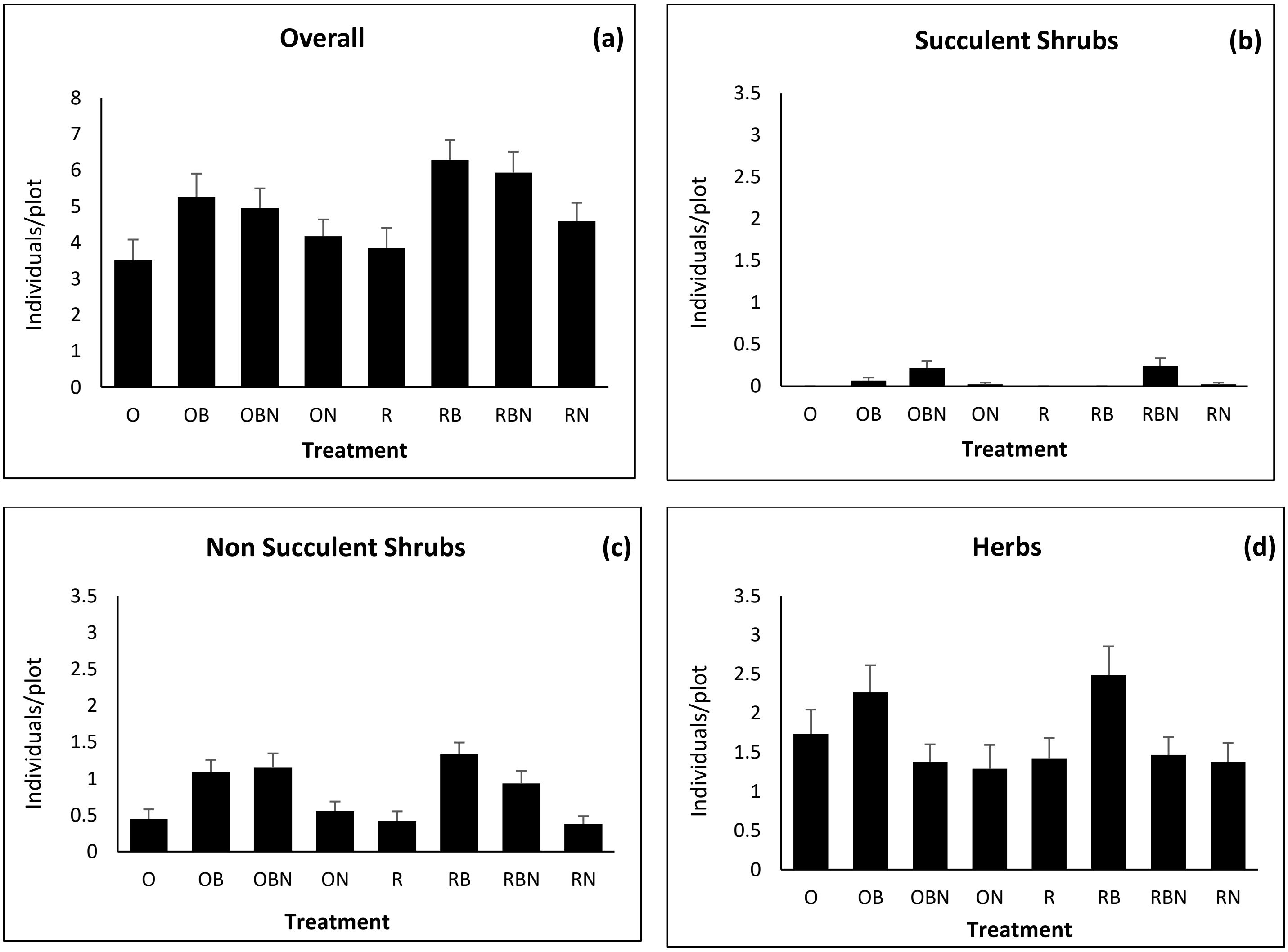
The model to assess the impact of seeding on a patch/root area, addition of nutrients and brush packing, indicated that root treatments resulted in 1.2 times more individuals being established compared to open treatments. This difference was significant (χ^2 (3) = 3.9, p < 0.01, Table 4.6). The average number of individuals/plot was 3.9 in root treatments compared to an average of 3.5 in open treatments. The model also indicated that the addition of brush packing had a significant beneficial effect on seedling seedling establishment (χ^2 (3) = 21.9, p < 0.0001, Table 4.6), with plots without brush packing having 0.6 times fewer individuals. The addition of nutrients had no impact on seedling success. For this analysis, the root with brush pack emerged as the best treatment, resulting in an average of 6.3 individuals/plot. The treatment with the worst establishment was the open control plot, with an average of 3.5 individuals/plot (Figure 4.13.a).

For succulent leaved shrubs, *Drosanthemum hispidum* was the only species to occur in this study and it occurred in very low numbers. Due to these low numbers, suitable models could not be created for either the brush or plot treatments. The model run estimated that nutrients had an effect on seedling establishment. However, this effect was minor (χ^2 (3) = 3.5, p < 0.05, Table 4.6). Plots with nutrients had 3.3 times more individuals than plots without nutrients. Despite there being insufficient data to allow for an analysis, there did appear to be an increase in the numbers of individuals established with the addition of nutrients (Figure 4.13.b).

For non-succulent leaved shrubs, the glmm indicated that brush packing was a significant predictor of seedling establishment (χ^2 (1) = 36.7, p < 0.0001, Table 4.6), with an estimated 0.39 times fewer individuals in non-brush packed treatments. This resulted in an increase in seedling numbers from an average of 0.4 individuals than without a brush pack to average of 1 individual per plot with a brush pack. The addition of nutrients was not a significant predictor, nor were the interactions. The best treatments for the establishment of non-leaf succulent shrubs were the brush pack and nutrient treatments, with an average of 1 individuals/plot (Figure 4.13.c).

Herbs established well in the Renosterveld restoration experiment. As with the shrubs, there was also no effect of open or root treatment herb seedling establishment. The model indicated that the effect of brush packing (χ^2 (1) = 5, p < 0.05) and nutrients (χ^2 (1) = 10, p < 0.001) were significant, but there was no effect of interactions. For herbs, brush packing had a positive effect on seedlings, with 0.75 times fewer individuals without brush packing. Plots with brush packs had an average of 2.8 individuals/plot, compared to those without brush packs, which had an average of 1.4 individuals/plot. The addition of nutrients had a negative impact on seedling establishment (Figure 4.13.d), reducing seedling numbers in the model by 0.6 times. The open with nutrients treatment had the lowest establishment overall. The open and root plots with brush packs had the best establishment with an average of 2.4 individuals/plot (Figure 4.13.d).

Grasses were the only growth form in the model where the root treatment was significantly better than open plots (χ^2 (1) = 12.4, $p < 0.0001$, Table 4.6), with an estimated increase of 1.5 times. Root treatments had an average of 2 individuals, compared to an average of 1.3 individuals/plot in open treatments. The addition of nutrients was also a significant predictor (χ^2 (1) = 15.7, $p < 0.0001$), with the model predicting a positive increase of 1.36 times. Treatments with nutrients had an average of 2.6 individuals/plot compared to the control, which had an average of 1.6 individuals/plot. Brush packing and the interactions of all factors were not significant. However, the brush pack and nutrient plots had the best establishment, with an average of 2.7 individuals/plot (Figure 4.13.e).



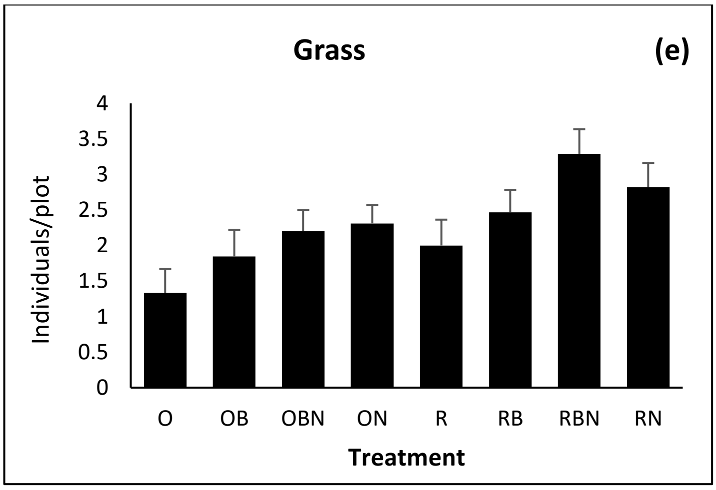


Figure 4.13 Average number of seedlings (± SE) of different growth forms recorded in in the Renosterveld trial, a) overall, b) Succulent shrubs, c) non succulent shrubs, d) herbs, and e) grass. Treatments are indicated as follows: control open (O) plots, brush packing on open plot (OB), brush packing and nutrients on open plot (OBN) and nutrients on open plot (ON). Control root (R) plot, brush packing on a root plot (RB), brush packing and nutrients on a root (RBN) plot and nutrients on a root (RN) plot.

Table 4.6 Parameter estimates and error statistics of the GLMM of different growth forms in Renosterveld. Results are given on the log scale. BT value indicates the back transformed value of the co-efficient. * = p 0.05 ≤ 0.01, ** = p ≤ 0.01, *** = p ≤ 0.001. Where suitable models could not be created due to very low numbers of seedlings, this is indicated as "--------".

	All growth forms (n = 1440)				**Herbs (n = 360)**				**Succulent shrubs (n = 360)**				**Non-leaf succulent shrubs (n = 360)**				**Grass (n = 360)**			
	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq	Co-efficient	BT value	Std. Error	Chisq
Intercept	0.43	1.53	0.24		0.77	2.16	0.26		-3.21	0.04	0.67		0.14	1.15	0.27		0.43	1.53	0.28	
Treatment (open compared to root)	0.19	1.20	0.14	3.94*	-0.00	1.00	0.19	0.00	-------	-------	------	-------	0.17	1.18	0.21	0.26	0.41	1.50	0.21	12.44***
Brush (brush compared to no brush)	-0.47	0.62	0.16	21.97***	-0.28	0.75	0.20	5.01*	-------	-------	------	-------	-0.92	0.39	0.31	36.79***	-0.35	0.70	0.25	2.52
Nutrients (no nutrients compared to nutrients)	-0.01	0.99	0.14	0.85	-0.51	0.60	0.21	10.28**	1.20	3.32	0.65	0.07	0.08	1.08	0.25	0.10	0.32	1.37	0.21	15.70***
Treatment:Brush	-0.03	0.97	0.23	0.23	-0.17	0.84	0.29	0.09	-------	-------	------	-------	-0.23	0.80	0.41	0.48	0.13	1.13	0.31	0.30
Treatment:Nutrients	-0.02	0.98	0.20	0.15	0.06	1.06	0.29	0.61	-------	-------	------	-------	-0.39	0.67	0.32	1.97	-0.3	0.74	0.27	0.99
Brush: Nutrients	0.26	1.30	0.22	2.08	0.15	1.16	0.31	1.56	-------	-------	------	-------	0.16	1.17	0.41	0.39	0.41	1.50	0.31	0.89
Treatment:Brush: Nutrients	-0.08	0.92	0.31	0.06	0.23	1.25	0.44	0.28	-------	-------	------	------	0.06	1.06	0.59	0.01	-0.38	0.68	0.39	0.94

The influence of shelters

Overall, shelters had a significant influence on seedlings (χ^2 (1) = 14.9, $p < 0.001$). Brush packs had 1.51 times more individuals with an average of 6.3 individuals/plot (Table 4.7) than under a living plant (average of 4.5 individuals/plot) or an unsheltered root control (an average of 3.7 individuals/plot). There was no statistical difference between boxes and brush packs (Figure 4.14.a). The unsheltered control plots had the lowest establishment (Figure 4.14.a).

No succulent shrub seedlings established in the unsheltered root control, boxes, brush packs, or alive treatments used in this analysis. Therefore, no analysis was conducted for this growth form in the Renosterveld study sites.

For non-succulent leaved shrubs, the type of shelter had a significant effect on seedling establishment (χ^2 (1) = 19.8, $p < 0.001$). However, brush packs were the only type of shelter to significantly improve seedling establishment, from no establishment in unsheltered control plots to an average of 1.2 individuals in brush pack plots (Table 4.7, Figure 4.14.b). Treatments in the box and under the living shrub had similarly low seedling numbers and did not differ from other treatments (Figure 4.14.b). There were no noticeable facilitation benefits for seedlings or indications of competition between the living nurse plant and non-succulent seedlings in Renosterveld.

Herbs and grasses, which made up most of the established seedlings, were the only growth forms whose seedlings were noticeably impacted by a nurse plant. There was a significant influence (Table 4.7) of shelters on herbs (χ^2 (1) = 12.5, $p < 0.01$). There were significantly more seedlings growing under a living shrub (an average of 2.3 individuals/plot) and under a brush pack (an average of 2.5 individuals/plot), compared to unsheltered control plots (an average of 1.5 individuals/plot). Boxes had no discernible influence on herb seedling establishment (Figure 4.14.c). For grasses, shelters were significantly (χ^2 (1) = 10.1, $p < 0.01$) influential for seedling establishment (Table 4.7). A brush pack was significantly better for seedlings (average 2.5 individuals/plot) than under a living renosterbos (average 1.8 individuals/plot) and marginally better than a box treatment (average 1.4 individuals), see Figure 4.14.d).

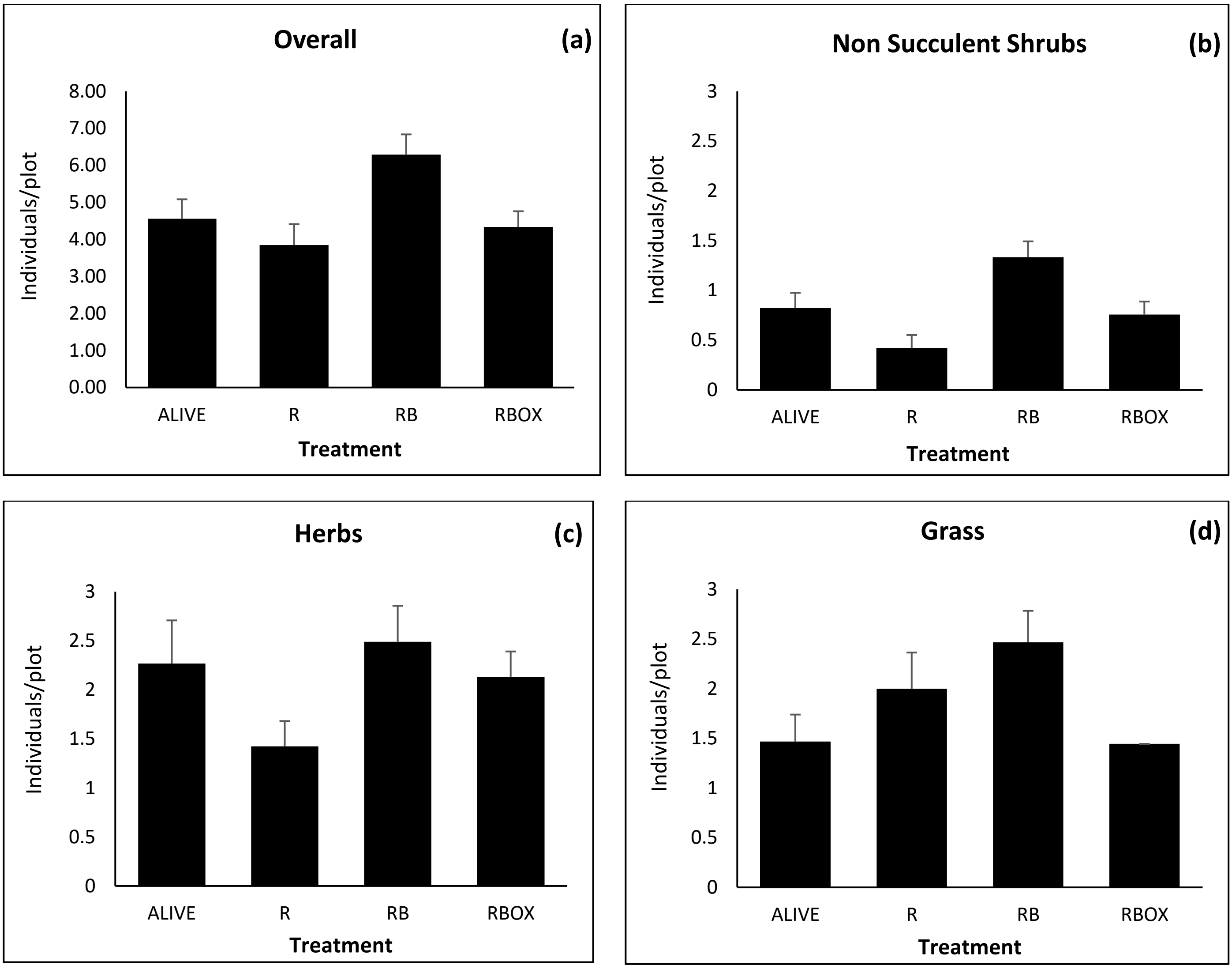


Figure 4.14 Average number of seedlings (± SE) of different growth forms recorded in different types of sheltering structure in the Renosterveld trial. a) Overall, b) non succulent shrubs, c) herbs and d) grass. Treatments are indicated as follows: under a living kraalbos (alive), unsheltered control root plots (R), brush packing on a root plot (RB) and a box on a root plot (RBOX)

Table 4.7 Parameter estimates and error statistics of the posthoc of the GLMM of different types of sheltering structure on different growth forms in Renosterveld. Results are given on the log scale. BT value indicates the back transformed value of the co-efficient. Significance: * = p 0.05 ≤ 0.01, ** = p ≤ 0.01, *** = p ≤ 0.001.

	All growth forms (n = 1440)				**Herbs (n = 360)**				**Non-leaf succulent shrubs (n = 360)**				**Grass (n = 360)**			
	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Z value	Co-efficient	BT value	Std. Error	Chisq
Intercept	0.21	1.23	0.19		0.67	1.95	0.16		-0.20	0.81	0.19		0.27	1.30	0.34	
Treatment R	-0.12	0.89	0.16	-0.77	-0.27	0.76	0.23	-1.16	-0.73	0.48	0.31	-2.32*	0.31	1.36	0.21	1.46
Treatment RB	0.41	1.51	0.14	2.78 **	0.23	1.25	0.21	1.10	0.50	1.64	0.22	2.23*	0.54	1.71	0.20	2.7 **
Treatment RBOX	0.10	1.01	0.15	0.67	0.21	can	0.21	0.99	-0.07	0.93	0.25	-0.27	0.03	1.03	0.22	0.15

Seeding in different climatic years

Sowing seeds in two consecutive years had a significant impact on germination and survival (χ^2 (1) = 25.5, p 0.0001), particularly with regard to the first summer season. In their respective first winter seasons, the 2013 trial had an average of 1.4 individuals/plot compared to the 2014 trial, which had an average of 0.8 individuals/plot. However, the stark contrast between the two trials was how the seedling numbers fluctuated by the start of the first summer (Figure 4.15) and had completely opposite trends. Across all the treatments in which seeds had germinated in 2013, the same pattern occurred, which was that by early summer 2013, the seedling numbers decreased to around a third of those recorded in winter. Over the course of the following two years, the seedling numbers rose quite sharply, irrespective of the season. However, with the trial sown in 2014, the seedling numbers did not fall in the first summer, but rather increased into early summer. Thereafter, seedling numbers in the second year increased slightly, but the numbers mostly plateaued over the course of the second year. Thus sowing in different years resulted in different patterns of seedling survival over two year.

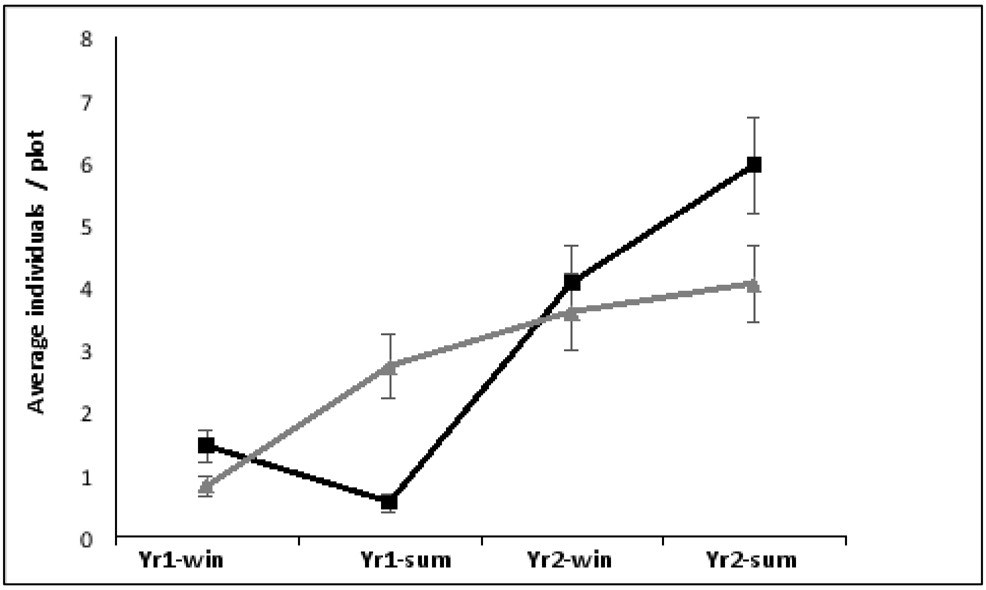


Figure 4.15 Average (+ SE) seedling numbers in open with brush pack treatments sown in two consecutive years, in 2013 (black line with squares) and in 2014 (grey line with triangles) in Renosterveld. Each trial is plotted over its two-year winter (win) and summer (sum) recording intervals

4.3.3 Summary of results

Table 4.8 provides a scoring system of treatments used in the restoration trial, where the treatments are scored a percentage of the maximum individuals of all treatments. It indicates how different growth forms responded to treatments, as well as scoring which treatments were the most effective. It demonstrates that even the same growth form in different vegetation types, responds quite differently. The results also indicated that different growth forms established better than others, irrespective of treatment, which could indicate that certain growth forms can only establish at certain stages of succession.

In Hardeveld it is clear that adding a form of shelter considerably improved seedling success, and that boxes and brush packs located on open plots had the best results. Adding nutrients benefitted grasses and succulent shrubs. In Renosterveld, shelters, especially brush packs, were also very beneficial for seedlings. Boxes had very mixed results but were overall less effective than brush packs. The most effective treatments were the brush pack and nutrient treatments, irrespective of where these were applied. The addition of nutrients is only effective if applied together with brush packs (Table 4.8).

Table 4.8. Scoring system of treatments used in the restoration trial in Hardeveld and Renosterveld. Treatments scored a percentage of the maximum individuals of all treatments. Score of 0 – 4 assigned to each percentage range in order to calculate a total score for the treatment. The scores are: 'No response' (0 points, grey colour) indicates no successful establishment, 1 – 25 % individuals (1 point, red colour), 25 – 50 % individuals (2 points, blue colour), 50 – 75 % individuals (3 points, yellow colour) and 75 – 10% individuals (4 points, green colour). Treatments are listed, from top to bottom, as under a living kraalbos or renosterbos (Alive). Open control (O), open with brush pack (OB), open with brush pack and nutrients (OBN), open with box (Obox) and open with nutrients (ON). Root control (R), root with brush pack (RB), root with brush pack and nutrients (RBN), root with box (RBox), and root with nutrients (RN).

	Hardeveld					**Renosterveld**				
Treatment	grass	Herb	non-succulent leaf shrub	succulent leaf shrub	Total score	grass	herb	non-succulent leaf shrub	succulent leaf shrub	Total score
ALIVE	1	0	2	1	4	2	4	3	0	9
O	1	0	1	1	3	2	3	2	0	7
OB	3	0	2	2	7	3	4	4	1	12
OBN	4	0	2	3	9	3	3	4	4	14
OBOX	2	0	4	4	10	2	4	2	0	8
ON	2	0	1	4	7	3	3	2	1	9
R	1	0	1	1	3	3	3	2	0	8
RB	4	0	2	1	7	3	4	4	0	11
RBN	3	0	2	2	7	4	3	4	4	15
RBOX	2	0	3	2	7	2	4	3	0	9
RN	2	0	1	2	5	4	3	2	1	10

4.4 Discussion

The aim of this study was to identify abiotic resources that can be manipulated to restore biodiversity and the structure of the vegetation in two vegetation communities. The experiments were located across the landscape and monitored for three years, which allowed for an assessment of seedling establishment in these vegetation communities and the suitability in future projects. The field trial demonstrated that restoring a structurally diverse ecosystem is challenging in both vegetation communities, and often mirrored findings by Bourne *et al.* (2017) in the Steinkopf area of Namaqualand as well as the findings of Kruger (2010) along Namaqualand's west coast. Researchers in drylands need to strive to improve the efficiency and restoration by understanding the conditions required for establishment (Carrick & Kruger, 2007; Erickson, 2015; Erickson *et al*., 2016; Madsen *et al*., 2012; Turner *et al*., 2013). The results from this trial highlight the importance of recognising that different growth forms have their own requirements to establish, which must be taken into consideration in restoration planning.

4.4.1 Creation of micro-depressions and sowing seeds

The creation of micro-depressions is a proven technique in the rehabilitation of arid areas. Micro-depressions accumulate water and organic matter which increases soil nutrient levels and assists in germination and establishment (Critchley *et al*., 1994; Lesoli, 2011; Matthee, 2015). The formation of micro-depressions in this trial differed slightly from other studies. In most cases, depressions are created by removing the upper layer of the soil (topsoil) and leaving it outside the depression. In my study, the topsoil, which is the biologically active component that contains a possible seed bank, micro-organisms, fungi, and nutrients, was conserved (Tongway & Hindley, 2004) and returned to the depression after subsoil was removed to create the depression. Topsoil plays an important role in rehabilitation (De Villiers *et al*., 2002; Holmes, 2001; Koch, 2007). Therefore, any seeds in the soil could germinate and reap the benefits derived from the depression, such as increased soil moisture. However, even with care taken to return the top soil, and even though grazing was excluded from the camps, the unseeded treatments failed to establish perennial species, indicating that there is no spontaneous recovery in the absence of grazing. These findings have been recorded previously in rangeland restoration trials in Namaqualand (Bourne *et al*., 2017), and support the findings from Chapter 3. These results support the hypothesis that the soil seed bank is depleted of indigenous perennial species after cultivation in both vegetation types. The assumptions of De Villiers, Van Rooyen and Theron (2003) and Schmiedel *et al.* (2010) that successful restoration will require the active reintroduction of perennial plants via seeding is also confirmed by the results outlined in this chapter.

4.4.2 Using fertile islands created by pioneer plants

I tested the hypothesis that the unwanted pioneer shrubs of kraalbos and renosterbos could be removed and their fertile islands used to improve seedling establishment. This concept has been successful with Wyoming sagebrush seedlings that had 40% higher survival in former canopy sites compared to open sites (Davies *et al*., 2020). Results from chapter 2, as well as findings from other researchers, indicated that kraalbos does improve soil fertility in degraded areas by increasing organic matter, carbon, potassium, sodium and phosphorus (Allsopp, 1999; Carrick, 2001). Removing adult kraalbos plants would provide a cost-effective way to generate material for brush packing and reduce fertilizer input. However, the results from this trial did not support this hypothesis. The number of individuals of some growth forms (herbs and non-succulent shrubs) was not noticeably different between open and root plots. In the Hardeveld, the possible benefit for grasses of a root plot with its fertile island patch was inconclusive, while in the Renosterveld, grasses were the only growth form that established well on root plots. It was the high numbers of grass individuals that established on root plots in Renosterveld that contributed towards the overall result that root plots were more beneficial for seedlings than open plots, even though none of the other growth forms showed a preference for root plots. In Hardeveld, succulent shrubs showed an overwhelming preference for open areas, with a significantly lower number of seedlings in root plots. There was a clear trend that succulent shrubs preferred all the treatments on the open plots over the corresponding treatments on the root plots. It was hard to tell if this pattern with succulent shrubs occurred in Renosterveld due to the very low establishment success and only one succulent species being used.

One explanation for the succulents not growing on the root plots could be due to the effects that kraalbos has on the soil under its canopy. Chapter 2 has indicated, along with research from others (Allsopp, 1999; Carrick, 2001) that kraalbos increases pH, phosphorus and potassium levels relative to what is found in soils beneath succulent shrubs growing on reference sites. Soil from open sites on fallow fields had similar acidic pH values (4 -5) as soil from intact vegetation, but soil under kraalbos is relatively alkaline (pH 7.6). The same trend was found for potassium, sodium, and phosphorus concentrations. Although kraalbos does create a fertile island, it could also contribute to its own success, by creating a more basic or alkaline soil environment, suitable for its own species (Allsopp, 1999)*, i.e. creating a reinforcing (positive) feed-back loop. This is also seen for some alien invasive species* (Gaertner *et al*., 2012)*.*

In natural vegetation in the Karoo, the dominant growth form is succulent shrubs. It has been reported that succulent shrubs also create islands of fertility under their canopies by enriching the soil with organic matter, and nutrients and by increasing pH levels in the soil (Stock *et al*., 1999). This could account for the increase in abundance of other plant species around *Cephalophyllum spissum* which is also a succulent shrub (Schmiedel *et al*., 2010). Fertile islands created by succulents are shorter lived in Namaqualand, compared to islands created by shrubs in other arid areas (Stock *et al*., 1999). Phosphorus, for instance, takes a considerable period of time to accumulate, is relatively immobile in most soil systems, and its mobility is controlled by pH (Bhat & Nye, 1974). Phosphorous is most available in soils with pH levels 6 – 7.5 (Bandel *et al*., 2002) and its availability decreases rapidly under pH of 6. This could point to an over saturation of phosphorous for succulent shrubs, which are used to lower pH and phosphorous values. The accumulation levels indicate that kraalbos is similar to other desert shrubs and creates a more ‘permanent’ island with higher nutrient levels and higher pH, beyond the levels that succulent shrubs can tolerate. Other growth forms of shrubs, grasses, and herbs seem to not be as sensitive to the kraalbos altered soil. However, the notion of using kraalbos induced fertile islands to improve seedling establishment is not recommended, as this does not benefit the establishment of the key growth form in the Karoo, the succulent shrubs.

Results from Chapter 2 indicate that renosterbos does not really create a fertile island in degraded areas, which explains the lack of definitive results in the restoration trial. Renosterbos has been seen to recolonise furrows in ploughed lands in the Swartland Renosterveld which have higher levels of soil moisture, pH, nitrogen, carbon and sodium compared to ridges where renosterbos does not grow (Ruwanza, 2017). This could indicate that renosterbos is taking advantage of more fertile zones and is not necessarily creating its own fertile island. There is a general lack of understanding of Renosterveld (Krug, 2004a) and it is not known what role patch dynamics play in vegetation communities of Kamiesberg Renosterveld. Some Renosterveld ecosystems are more shrub based, whilst others consist mainly of grass with isolated bush clumps (Walton, 2006). There is little known about the role renosterbos could play in facilitating restoration. My results indicate that other than increasing potassium to similar levels found in natural vegetation, which may benefit grass establishment, there is no clear benefit or disadvantage to using renosterbos patches for plant establishment

A novel suggestion would be to transfer top soils from intact vegetation communities to degraded sites (Ruwanza, 2020). The transfer would ensure that soil physicochemical properties, organic matter, native seed bank, and microbial biomass are brought to the degraded ecosystem (Bulot *et al*., 2017). This has been seen as a promising restoration tool in Swartland Renosterveld where tree and shrub (e.g., *Asparagus* sp., *Aspalathus* sp., *Stoebe* sp, *Eriocephalus africanus*, and *Hermannia* sp) richness was increased. Species that were not present in the old field returned through this method (Ruwanza, 2020). However, caution must taken to not cause destruction of the intact communitities during transfer and this would only be recommended for small scale projects. In such projects gradually introducing small amounts of soil to the degraded site thereby creating pockets of seeds from where restoration can start (Ruwanza, 2020). These findings concur with similar studies in Mediterranean areas (Jaunatre *et al*., 2014), and require further research.

4.4.3 Aspects of patch dynamics – the role of nutrients and shelters

The addition of nutrients (fertilizer) increases the cost of restoration activities, and it is therefore crucial to evaluate whether the increased cost is worth the return. Due to the impact of cultivation on the soil the reduction of fertility, I hypothesized that adding fertilizer to treatments would increase the success of seedling establishment. The addition of nutrients would re-create the more nutrient rich environment seedlings would be growing in, within a patch. My results had very mixed responses from the different growth forms and largely did not support the hypothesis. It was only succulent shrubs (Hardeveld) and grasses (Renosterveld) that responded well to nutrient addition. The other growth forms in both vegetation types, had no noticeable benefit. An unexpected result was that nutrients had a negative effect on herb seedlings in Renosterveld.

In the Hardeveld, it was only the succulent shrubs that responded well to nutrient additions, and it was this contribution of succulent shrubs that influenced the overall result. Non-succulent shrubs and grasses derived no noticeable benefit from the added nutrients. Kruger (2010) had the complete opposite result to mine, where nutrition addition did not affect succulent shrub survival and it did increase non-succulent shrub seedling survival. Such differences could be attributed to the difference in soil types and conditions between his trial in Coastal Duneveld (Sandveld) which had been mined and my trial in Hardeveld after cultivation. In Renosterveld, nutrient addition in general posed little benefit for seedlings in this study. Grasses were the only growth form in Renosterveld to see an increase in seedling numbers from nutrient addition. As stated earlier, succulent shrub establishment was very low, so trends were difficult to detect. There was also no benefit to nutrient addition for non-succulent shrubs, and there was a negative effect on herbs. Renosterveld vegetation is normally located on relatively fertile soils (Cowling *et al*., 1986). Given that cultivation had a negative impact on soil fertility, and that renosterbos does not appear to improve soil fertility over time, it was anticipated that the addition of nutrients would be beneficial. Other studies on restoring Renosterveld have not included nutrient addition because previous farming practices increased nutrients in the soil (Midoko-Iponga *et al*., 2005; P. A. Waller *et al*., 2016). Further research is required to understand soil fertility in granite derived Renosterveld ecosystems.

4.4.3.1 Shelters

Seedlings in arid areas can be exposed to harsh weather conditions and are vulnerable to grazers, but growing in a patch protects them from these impacts. I hypothesized that seedling establishment would be greater in sheltered micro-sites. Results from this study confirmed this hypothesis, as box and brush pack treatments were very successful for increasing seedling numbers across both vegetation types, but nurse plants were not effective. There were only two growth forms, succulents in the Hardeveld and grasses in the Renosterveld that did not show significant benefits from being sown under a brush pack. Unlike living vegetation, brush packs and boxes do not compete for resources with other plants, but do provide some sheltering benefit, which can easily be applied to increase restoration success. Creating depressions and brush packing have been successful restoration interventions in Paulshoek and Steinkopf (Bourne *et al*., 2017; Simons & Allsopp, 2007), as well as in semi-arid environments in general (Coetzee, 2005; Tongway & Ludwig, 1991). Brush packs are a successful means to protect the soil against erosion, improve soil moisture conditions (Schmiedel *et al*., 2010), simulate the protective effect of a natural plant but do not compete with seedlings for resources. They can also trap soil particles and organic matter to initiate the formation of a resource island. Studies have found that in the Karoo soil water content immediately after a rainfall event is almost doubled under a brush pack and takes considerably longer to dry out, compared to open soil (Hanke *et al*., 2011; Schmiedel *et al*., 2010).

An unusual finding in both vegetation types was that the combination of brush packing and nutrients did not yield significantly better establishment than that of each treatment on its own. It was expected that in these arid, resource limited environments, the addition of both nutrients and brush packs would create very favourable germination sites. It was only with the grasses in Hardeveld that an impact was seen. Nutrients did not have a strong influence on grasses, but when a brush pack was added, it doubled or tripled the seedling numbers. There is a finely poised balance between different factors, where nutrients only have a positive effect when other factors such as shelters are present (Grubb, 1992).

Hardeveld boxes in particular were very effective for non-succulent shrubs and resulted in the doubling of seedling numbers. They were also effective for the establishment of succulent shrubs, in which seedling numbers increased fourfold. The addition of nutrients further enhanced establishment success. Shelter of some kind resulted in more non-succulent shrub seedlings and if sufficient shelter is provided to non-succulent shrubs, it is likely to mean they will become nurse plants with time (Kruger, 2010).

Higher survival rates of succulent seedlings when sheltered in a box were also recorded by Kruger (2010) in Strandveld, Namaqualand. Succulent shrubs of the Aizoaceae family are water dispersed and most likely suited to establishment in inter-patch areas, where there is not much protection from sunlight, an important requirement for succulents (Esler, 1999). Thus, the box treatment is advantageous for succulents as it provides some protection from the elements but is open enough to allow sunlight to reach seedlings, unlike a brush pack would. For grass, brush packs were most beneficial but did not differ from boxes. Perennial grasses respond well to reduced UV radiation (Bosco *et al*., 2018) created by shelters. The wind dispersed seeds of grasses and non-succulent shrubs are likely to be trapped in the branches of shrubs and would naturally germinate in a sheltered location (van Oudtshoorn & Van Rooyen, 1999).

In Renosterveld, all growth forms did well under a brush pack. Boxes did not function that well, and they were only really effective for herbs. For grasses and non-succulent shrubs, brush packs were more effective than boxes, which had a similar number of plants as under a living renosterbos. The results demonstrate that shelter was an important factor for seedling establishment and they hold promise for future restoration activities as brush packs have not yet been used in Renosterveld restoration.

4.4.3.2 The role of nurse plants

Nurse plants have been recommended as a restoration intervention in dryland and Mediterranean ecosystems (Callaway & Walker, 1997; Castro *et al*., 2002; Padilla & Pugnaire, 2006). This is because they are thought to facilitate the establishment of seedlings by providing benefits such as protection from solar radiation, increased soil moisture, and nutrient availability, which are the main factors affecting seedling biomass (Bosco *et al*., 2018). There is strong evidence for facilitation among adult plants and seedlings in the Karoo (Carrick, 2001; Eccles *et al*., 1999), and near Paulshoek, seedling numbers under kraalbos were higher (L. Simons & Allsopp, 2007). Nurse plants also trap soil particles, and attract small wildlife seeking refuge, which contributes to nutrient input under the nurse plant (Callaway, 1995; Chambers, 2000; Garcia-Moya & McKell, 1970; Schlesinger *et al*., 1996; Stock *et al*., 1999). I hypothesized that a nurse plant would be beneficial to seedling establishment, if there was no competition between the seedling and the nurse plant. However, my findings did not support this hypothesis, and nurse plants were largely ineffective. In most cases there was no difference in seedling success between unsheltered plots and those under nurse plants. This has also been seen in Strandveld (De Villiers *et al*., 2001) where non-succulent shrubs are disadvantaged by nurse plants, probably due to competition for soil resources (Philips & MacMahon, 1981).

There is no motivation for using kraalbos or renosterbos as a nurse plants as they had similar results to unsheltered controls for all growth forms. The only growth form to establish well under a living renosterbos was herbs. Kruger's (2010) results also did not support the notion that nurse plants facilitate the establishment of succulent or non-succulent shrubs. However, in Kruger's (2010) trial, he transplanted nurse plants, just prior to seeding. Therefore, in his experiment, the micro-environment had not had much time to be influenced by the nurse plant, unlike the pioneer plants in my trial which were mature, established plants that had occupied their growing site for years. Brush packs, made from dead kraalbos, were very effective as a shelter and kraalbos nurse plants should have provided the same type of protection. The treatments with kraalbos were not significantly worse than root plot treatments or root plots with brush packs. Root plot and brush pack treatments mimic the same conditions as under a nurse without competing for resources. This suggests that there was no influence of competition or competing for root space (De Villiers *et al*., 2001). Therefore the reason all three treatments performed poorly likely comes back to the increased pH and phosphorous levels in kraalbos soil. It has been reported that renosterbos has a facilitatory role as a ‘nurse’ site for geophytes, herbs, dwarf shrubs, and perennial grasses, as recorded by Walton (2006) on Swartland Shale Renosterveld, but this was only found for herbs in my study. As renosterbos does not create a fertile island there was little difference between alive and other open treatments.

Schmidt (2002) found that more seeds germinated below the combined canopy of three nurse plants than under isolated nurse plants in Strandveld, Namaqualand, that were transplanted to the site. Therefore, facilitation may only be effective for seedlings if multiple adult plants are involved, and is an area that could be explored further. It is also possible that other species could function as nurse plants. Transplanted *Brownanthus* and *Cephalophyllum* species increased the abundance of other plants (Schmiedel *et al*., 2010). The shrub *Osteospermum sinuatum* forms positive associations with the succulent *Ruschia robusta* (Todd, 2000)*. O. sinuatum* and *Hirpicium alienatum* established beneath various succulent shrubs (Carrick, 2004). More research on the creation of fertile islands by succulent shrubs is required, as well as their use as possible nurse plants for other seedlings. These shrubs established well in the trial in open sites and should be used in restoration. It would be interesting to see if establishing succulent shrubs as an initial step in restoration, to get them to create islands of fertility, could be followed by seeding underneath them.

4.4.4 Seeding in different climatic years

Weather patterns need to be taken into account when attempting restoration. Over the course of the three-year experiment annual rainfall decreased, which very likely had an impact on results. The two vegetation types also had very different responses with regard to seedling numbers, even though rainfall decreased in both areas over time.

Considerable die off of seedlings after the first year of a restoration experiment is a normal phenomenon, especially in arid areas. Re-seeding trials in the Karoo see few seedlings survive the first year (Kruger, 2010; Milton, 1994; Saayman *et al*., 2017). Variable rainfall has an impact on seedling survival, which is naturally higher in years receiving more autumn rain (Milton, 1995b). This was the trend with the Hardeveld sites where seedling numbers dropped to around half from the first year (2013) to the second (2014). However, the extra 2014 treatment did not show this clear trend. Instead, its numbers started off low and stayed fairly consistent into the following year, with not as pronounced a drop off in numbers, even though 2015 had the lowest rainfall of the three years. An interesting point emerges when considering which species which did not perform well in the 2014 trial were mostly the succulent shrubs. Generally seedlings of succulent shrubs are more drought tolerant that seedlings of non-succulent shrubs and should not have been as badly affected. A plausible explanation is the seed quality and viability, which was only tested in 2013 and not after being stored for a year. The same seed batch collected in 2013 were used in the 2014 trial. Succulent shrubs have small seeds that are stored in canopies with very little dormancy (Baskin & Baskin, 1998; Esler, 1999). Therefore seeds stored for a year may have lost their viability.

In Renosterveld, germination of the 2013 treatments was very low initially. However, in the following year germination had increased significantly and continued to increase into the summer of 2014. Initially, this delayed germination response was attributed to long seed dormancy. However, the extra trial set in 2014 showed less of a ‘delay’ period, and by the end of 2014, the number of seedlings had tripled. This contradicted the assumption of long seed dormancy. These different responses in germination can probably best be explained by differences in temperature and not rainfall, which also decreased over the three-year period. The first winter season (2013) in Leliefontein was not necessarily colder, but it was a longer winter, in which average minimum temperatures of 3 - 5°C lasted into September. This could account for a delayed germination response, when minimum temperatures only started peaking above 9°C in November, when monitoring took place.

4.4.5 Limitations of the study

Seed quality

Out of the 31 plant species used in this experiment, nine species did not germinate at all or in extremely low numbers for only one or two recording intervals. These were *Hypertelis salsoloides, Aizoon canariense, Restio* sp, *Calobota sericea, Tetragonia fruticosa,* and *Pteronia incana.* Seeds of the latter four species also did not germinate in the germination trial, but *Hypertelis salsoloides* and *Aizoon canariense* did, just in very low numbers (Appendix E). The seeds for *C. sericea*, which were donated by Namaqualand Mine Restoration (NMR), had been stored for several years in unknown conditions. Therefore, these seeds could have been old, damaged and un-viable. *T. fruticosa* was collected in late summer and most seeds showed signs of predation. This is the most likely cause for the lack of germination, both in the field and in the germination trial of this species. Swart (2019) noted that harvesting the seeds as soon as they ripen and while they are still on the adult plants should mitigate this problem.

Fire

One aspect not covered in this study was the influence of fire, in the form of heat or smoke treatment. Renosterveld, like Fynbos, is a fire driven system, where species show a clear germination response to smoke extract. While fire ecology has been extensively researched in fynbos, little is documented on the role of fire in renosterveld (Bond *et al*., 2004; Curtis, 2009). However, research from Heelemann *et al*. (2013) found in Renosterveld that, on average, ten more indigenous species germinated after smoke treatment, than without smoke treatment, but only at certain sites. Their results were consistent with the few fire studies conducted in abandoned fields in Renosterveld, where species composition and germination improved in burnt plots relative to plots that had not burnt (Cousins *et al*., 2017; Curtis, 2013; Heelemann *et al*., 2013; Simons, 2017; Van Der Merwe & Van Rooyen, 2011a). No seeds in this study were treated with smoke, which could have contributed to low species establishment. The species of *Restio* recorded in this study are part of the Restionaceae family, and germinate significantly better when exposed to smoke from wild fires (Brown *et al*., 1994). In Swartland Renosterveld annuals and grasses displayed higher species richness after burning and certain species only recruited after burning. This suggests that Swartland Renosterveld is a fire driven system (Cousins *et al*., 2017). The role of fire in the restoration of Renosterveld vegetation is limited requires further research, particularly of Kamiesberg Renosterveld.

4.5 Recommendations for future restoration efforts and research

This restoration trial used a variety of growth forms and species, but there needs to be recognition that recovery is a slow process and that returning the entire species community into an altered environment is not possible. Instead, focus should be on returning hardy species across growth forms to 'kick start' the ecosystem on a trajectory of recovery. It is recommended to research the effectiveness of introducing growth forms in stages, instead of seeding all at once and having only one or two growth forms establish well in the first year. This would prevent time consuming seed collecting of species which may need improved conditions before they can establish.

Non-succulent shrubs germinated reasonably well, but in low numbers and struggled to survive past the first year. This is consistent with other studies in the Karoo (Bourne *et al*., 2017; Milton, 1994; Simons & Allsopp, 2007). In some cases, however, my results were in direct contrast to Kruger's (2010) findings along Namaqualand's west coast. In his study, the germination and establishment of succulents were always lower than those of non-succulents. Therefore, land managers need to be aware that interventions cannot necessarily be applied across broad areas. Restoration interventions need to be planned for each vegetation community according to the requirements of the plants that grow there. Kruger's (2010) sites were located on the west coast of Namaqualand and received substantially more precipitation in the form of mist, as well as cooler weather, compared to the Hardeveld which is further inland and experiences significantly higher temperatures. This could also account for why non-succulent shrub establishment was higher in Renosterveld, which is located at higher elevations than Hardeveld and experiences cooler weather and more precipitation.

These findings also have important implications for the desired outcome of different management objectives. For example, management interventions that need to increase grass cover for grazing, will be different from those aimed at increasing the diversity of the succulent component of the Karoo.

Hardeveld

The results do not support the hypothesis that the fertile soil islands created by kraalbos can be used to increase seedling success. It is recommended to sow seeds in open plots and to add a form of shelter. Care must be taken to not sow succulent seeds near to kraalbos. It is still recommended to thin kraalbos prior to seeding to reduce the density and obtain material for brush packing. Seedlings require some form of shelter, and boxes and brush packs located on open plots resulted in the best establishment. Adding nutrients would increase the cost considerably, but should be considered as part of future restoration efforts because of its benefit to grasses and succulent shrubs.

Rainfall is likely to become more irregular, and temperatures are likely to increase with ongoing climate change. Re-seeding with species such as succulents that are more able to tolerate drought conditions will increase the resilience of the ecosystem (Carrick, 2001; Hoffman *et al*., 2009; Kruger, 2010) and will also be more cost effective. For the initial stages of restoration, it is recommended to use succulent shrubs such as *Leipoldtia schultzei* and *Cheiridopsis denticulata* and the grass *Chaetobromus involucratus,* as these species establish well.

These species have also been successful in the restoration trials of Bourne *et al.* (2017) undertaken in Steinkopf, in those of Simons and Allsopp (2007) near Paulshoek as well as the restoration experiments of Saayman *et al.* (2017) in the Cederberg, which confirms their suitability for restoration efforts in the larger Karoo area. Herbs did not establish in this trial but only one species was used and seeds were collected late in the year.

Future research should consider using a different type of nurse plant, besides only kraalbos, as well as exploring whether succulent shrubs could be used as nurse plants for non-succulent shrubs in a staggered seeding approach.

Renosterveld

The most effective treatments in Renosterveld were the brush pack and nutrient treatments, irrespective of where these were applied. As there were no differences between root and open plots, and root plots benefited grasses, it is recommended to still sow seeds into the former canopy space. Brush packs were key in increasing establishment for all the growth forms. Boxes are not recommended in Renosterveld. The addition of nutrients is not strongly recommended, due to its negative impact on herbs although nutrient additions do favour grasses.

Herbs and grasses, such as the grass *Tribolium hispidum* and the herb *Leysera gnaphalodes,* are recommended in Renosterveld as they established well and contribute to stabilising the soil. The latter species is an early pioneer herb species that establishes rapidly and maintains consistent numbers over time. This was also observed in the results of Chapter 2. Only one species of succulent shrub was used in this trial, and it is recommended to try other succulents to get a better understanding of their use in this vegetation type. Non-succulent shrubs also established but not as well. This was also documented by Heelemann *et al.* (2012), even though non-succulent shrubs showed promising potential in greenhouse studies. Indigenous shrubs in Renosterveld face challenging barriers to establishment (Heelemann *et al*., 2012) and further research into their germination requirements is needed, as is research into the relationships between renosterbos and other species with which they co-occur.

4.6 Conclusion

Restoration of degraded rangelands in the Kamiesberg area of Namaqualand, is still in its infancy. This study will contribute towards generating knowledge on the functioning and restoration of these vegetation types, topics that are particularly poorly known in Renosterveld. This study also highlighted the importance for restoration practitioners to recognise that restoration activities from one area may not necesarrily be effectively applied across all vegetation types of the same biome. Individual vegetation units function differently from each other, and care must be taken to work within the dynamics of that ecosystem. Individual growth forms also appear to have their own requirements for establishment, which must be taken into consideration in restoration planning.

Several hypotheses, aimed at using pioneer shrubs in various restoration treatments were not supported by the data. For example, the results do not support the hypothesis that the fertile island created by kraalbos and renosterbos can be used to significantly increase seeding success, nor that these plants can function as nurse plants to facilitate the establishment of seedlings. In Hardeveld seeding should occur in open plots, in order to avoid soil that has been influenced by kraalbos, while in Renosterveld it seems not to matter whether seed is sown in the open or under a renosterbos canopy. However, this study has supported the hypothesis that the provision of shelters is beneficial to the germination and establishment of seedlings. Brush packs and boxes (only in Hardeveld) are recommended in restoration practice. In the Hardeveld, succulent shrubs and grasses established well over the three years and are recommended for future restoration activities. Non-succulent shrubs struggled to establish in Hardeveld, and further research is required to understand their germination and survival needs. In Renosterveld, grasses, herbs and non-succulent leaf shrubs established well over the three years and are recommended for future restoration activities.

Chapter 5 Synthesis and recommendations

5.1 Key findings

This thesis set out to determine the impact of grazing on natural Hardeveld and Renosterveld vegetation of the Kamiesberg and whether passive restoration of cultivated fields is an effective strategy for the region. It also set out to explore the effectiveness of active restoration interventions and the use of different techniques in promoting vegetation recovery. This has been done with a view to informing the future drafting of feasible, landscape-scale, ecological restoration strategies for Hardeveld and Kamiesberg Renosterveld. A starting point for this approach is the theory of patch dynamics. This has been used as a model for describing the structure and function of Namaqualand vegetation (Stock *et al*., 1999) and has provided the framework for the research undertaken in this thesis.

5.1.1 Motivation for using the theory of patch dynamics in arid land restoration ecology

The goal of restoration ecology is to reproduce an ecosystem founded on the ecological principles that were present prior to degradation (Higgs, 2005). To achieve this, it is vital to understand the dynamics and drivers of the intact vegetation community that could shape the envisaged, restored community. This information is needed to understand what key ecological functions have been removed and are therefore required to return the ecosystem to something resembling an original state.

The concept that patches are dominated by a variety of plant growth forms that accrue soil nutrients and create fertile islands (Howard *et al*., 2012) is key to this thesis. My findings support this theory, and indicate that it is critical for the functioning of arid ecosystems (Val *et al*., 2020). In both Hardeveld and Renosterveld vegetation, patches of plants growing together did positively influence the quality of the soil under their canopies, by increasing the organic matter fraction, carbon, sodium, and nutrients such as potassium and magnesium.

Patches consisting of multiple species was well demonstrated in Chapter 2, where in the case of Hardeveld vegetation, around 40 – 63 % of all plants occur in a patch, with all grasses, most herbs, and half the succulent and non-succulent shrub species following this trend. These findings re-iterate the value that growing in a patch must have to plants. However, in

Renosterveld the results indicated that there was no real preference for growing in a patch. Patches also positively influenced soil quality under their canopies, but only grasses showed a strong preference for growing in a patch. Although it has been reported that renosterbos could have a facilitatory role as a 'nurse' site for geophytes, herbs, and dwarf shrubs (Walton, 2006), my results indicated that most species grew in the open.

5.1.2 The impact of grazing on Hardeveld and Renosterveld vegetation

Most of this thesis is concerned with the effect of cultivation on the vegetation of the Kamiesberg and how to restore old fields that have lain fallow for years or even decades. A smaller component of the thesis described reference conditions for the two vegetation types in the region (Hardeveld and Renosterveld) and their response to grazing under communally managed and privately owned land tenure regimes.

In Hardeveld, the intact reference sites were relatively diverse and abundant in succulent shrubs. Grasses also constituted a major part of these communities. There were very few *Galenia africana* (kraalbos) individuals in undisturbed Hardeveld vegetation. The grazing impact in this study was not severe enough to alter community structure, diversity or richness, which reflects findings from Todd and Hoffman (1999). The impact was observed in the higher proportion of bare ground cover and lower vegetation cover, which has been recorded in Namaqualand before (Anderson & Hoffman, 2007) and by the substantially lower seed numbers found in the soil of communal reference sites especially. This is likely due to the more intense browsing of flowers and fruit on shrubs in communal areas, greatly reducing seed production and consequently seed input into the soil (Milton, 1994; Todd & Hoffman, 1999).

In Renosterveld the intact community was dominated by non-succulent shrubs, including renosterbos, grass and herbs. The impact of grazing was not pronounced and differences between the three reference sites were attributed largely to spatial differences in elevation and rainfall, and not to grazing.

5.1.3 The nature and effectiveness of passive restoration in fallow fields

Understanding the natural recovery of vegetation without any intervention after an area has been cultivated is important for a variety of reasons. Land managers need to know the extent of natural recovery, what is required to make active revegetation more effective (Abella, 2010), and whether active revegetation is worth the expense.

I hypothesized that cultivation had removed and compromised the structure and functioning of vegetation patches, and that this does not improve over time. I also hypothesized that the recovery of vegetation on fallow fields in Namaqualand is hindered by a decline in soil condition, the removal of the fertile island, as well as a depleted perennial soil seed bank. These factors reduce the ability of the ecosystem to provide favourable germination sites for seeds to establish. Models of alternative states recognise that the dynamics of the degraded state can greatly differ from those of the original state, and that restoration efforts need to manipulate more than the single factor that led to the ecosystems change (Suding & Hobbs, 2009), which in this case is cultivation. This is why passive restoration, which assumes that once the main cause of degradation has been removed, and the ecosystem is left to "self-repair" (Esler *et al*., 2008), does not always work. Succession is also not always linear or in the desired trajectory. Instead, the alternative ecosystem that arises after cultivation is held in its current state until the thresholds, needed to return the original community, are crossed (Gaertner *et al*., 2012; Galatowitsch, 2008; Le Maitre *et al*., 2011). This process has been recorded in the Succulent Karoo and Renosterveld, which undergo a shift towards an alternative stable ecosystem and are unlikely to return to a pre-disturbed state (Bosco *et al*., 2018; Hobbs *et al*., 2013).

Decades of ploughing removes all vegetation, decreases soil nutrients and destroys the seed bank (Colbach *et al*., 2014; Hobbs &Walker, 2007). The findings from chapters 2 and 3 show that passive restoration is not effective for these alternative ecosystems in either vegetation type. Fallow fields that have been resting between 6 to 70 years are not distinguishable from each other, indicating that there has been little improvement or change in species composition and cover with time. The removal of a diverse community leads to the establishment of pioneering plants of renosterbos and kraalbos*,* with few other species present in fallow fields. Bare soil cover increases and persists for decades. These findings are consistent with results from previous research in both vegetation types (Cowan & Anderson, 2019; Heelemann *et al*., 2013; Kemper *et al*., 1999; Midoko-Iponga *et al*., 2005; Whisenant *et al*., 1995), as well as with research in arid environments in general, where recovery periods are long (Bainbridge, 2012). Recovery is further limited by the continuous impact of grazing, which might remove the few perennial and palatable plants that do manage to establish before they have a chance to reproduce themselves. Nutrient accumulation in the soil of plant patches is vital to the high productivity of the patch (Carrick, 2001; Austin, 2011). The success of passive restoration can largely be linked to soil recovery and whether fertile islands are able to reform or not. After cultivation, soil condition and fertility are significantly reduced and barely improves after seven decades. This could prevent the establishment of species that are accustomed to germinating in fertile islands. My findings confirm this hypothesis that the ecosystem is 'stuck' in its current state and significant barriers exist which hinder it from recovering.

In Hardeveld there was evidence that the pioneer kraalbos, which colonises fallow fields, does create a fertile island under its canopy by gradually accumulating organic matter and carbon, albeit at very low levels, even after 70 years. These findings are similar to those from nearby Paulshoek (Allsopp, 1999; Carrick, 2001). However, kraalbos also increased the pH and phosphorus levels beyond levels found in the pre-disturbed ecosystem. Soil in these patches has become relatively alkaline (pH 7.6), whereas under patches in intact veld the soil is relatively acidic (pH 4.5). The proposal by Allsopp (1999) that kraalbos could facilitate the re-establishment of the original community without the need of expensive soil intervention is only applicable for plants that can tolerate the high pH and phosphorous level.

Given that renosterbos dominates both degraded and intact Renosterveld, I speculated that soil conditions under it would be similar. However, this was not the case. Although soil under renosterbos in pre-disturbed communities indicated fertile island formation, on fallow fields there was no indication that fertile islands had formed under renosterbos or that there had been any improvement in the nutrient status of the soils under renosterbos. It also raised questions as to what might be contributing to the formation of the fertile islands under renosterbos in intact areas, but not on fallow lands. Is it possibly the complement of other species, together with renosterbos, that enriches the soil? Or is it related to time, and that soil fertility is only improved over longer periods than 70 years? This requires further research.

Pioneer plants in both Hardeveld and Renosterveld vegetation are not facilitating the return of other plants, as less than 20 % of other plants were found to form a patch with kraalbos and renosterbos in old fields. Most plants grew in the open spaces between patches. Patches consist of multiple pioneer plants growing together with a handful of other species, whose numbers tend to decrease over time. Even in the case of kraalbos which showed some improvement in soil fertility beneath its canopy, seedlings are barely able to establish because of the particular characteristics of these soils described earlier.

The only perennial plants to form a considerable component of the seed bank were kraalbos and renosterbos. These unpalatable plants have an advantage in heavily grazed areas as their flowers are not grazed and they, therefore, contribute a disproportionate amount of seed to the seed bank. This likely contributes to their successful establishment on fallow fields. Chapter 3 confirmed the hypothesis that the soil seed bank is depleted of other perennial seeds, which I suggested was due to three factors. Firstly, the removal of the above ground perennial plants for many years results in no seed input from these plants. Secondly, long term dormancy is a not feature of Karoo seed species (Carrick, 2001; Esler, 1999; Milton *et al*., 1997). Lastly, seed dispersal from the mother plant in arid areas occurs over a relatively short distance. This ranges from 1.5 – 5 m in the case of succulent shrubs, to 20 – 30 m for most other perennial shrubs (Wiegand & Milton, 1996). Also, seeds in arid environments usually germinate within the patch of the mother plant where conditions are suitable, instead of dispersing far away into possibly unsuitable and hostile conditions where they do not survive (Esler & Cowling, 1993).

Therefore seeds in intact vegetation are unable to reach fallow fields, resulting in a large portion of the original community that cannot return. The scarcity of perennial seeds has been recorded in the Southern Karoo (Milton, 1994; Milton & Dean, 1990) and from studies from other Mediterranean-type ecosystems (Krug & Krug, 2007; Heelemann *et al*., 2013). The lack of perennial plants in fallows fields is reflected in the results of Chapter 2 and 3, with a reduction in diversity, species richness and plant abundance in the soil seed bank and the above ground vegetation.

In fallow fields in Hardeveld vegetation where active restoration intervention has not occurred, there is a shift in community structure from succulent shrubs of various sizes to a community of non-succulent shrubs and herbs. An important finding is that after 70 years succulent plant diversity is significantly lower than in reference sites and around 22 non-succulent shrubs do not return. This confirms the results of other sites in Namaqualand (Allsopp, 1999; Hoffman & Rohde, 2007; Todd & Hoffman, 1999).

In the case of Renosterveld, renosterbos dominates degraded and intact vegetation, both in the seed bank and in the vegetation. Vegetation structure shows some signs of passive recovery in Renosterveld as growth forms occurred in similar proportions to reference sites.

However, the passive recovery of species in fallow fields of Renosterveld vegetation does not occur. Species composition remains different from reference sites and 20 species did not return at all to fallow fields. This is in line with other studies (Anderson *et al*., 2010; Krug & Krug, 2007; Walton, 2006), indicating that the recovery of Renosterveld fallow fields takes many decades (Midoko-Iponga *et al*., 2005; Saayman & Botha, 2008; Shiponeni, 2003). The recovery of Renosterveld could also be due to incorrect fire regime. Simons (2017) found that communal farmers in this area tend to burn fields every 4.2 years in Kamiesberg Renosterveld, which is below the optimum frequency of her suggested 7 year frequency to increase biodiversity. Although Renosterveld is a fire driven system, too frequent fires, coupled with grazing soon after burning, will alter the structure of vegetation (Van Der Merwe & Van Rooyen, 2011a).

I suggest that because seeds of natural, uncultivated vegetation have attributes and evolved traits that results in dispersal across a short distance to a suitable safe site of a patch with a nurse plant, recovery on open fields will not occur without active intervention and removal of grazing. Fallow fields cover extensive areas and large parts of fallow lands are located too far from intact vegetation. Even those areas bordering on intact, natural vegetation do not offer hospitable germination sites. This highlights the importance of the role of patch dynamics in the functioning of vegetation in the arid ecosystems and that without the development of patches in the landscape, the alternative state is unable to move to a trajectory of recovery.

5.1.4 The theory of patch dynamics and its practical use in the restoration of old lands

The introduction of seed

The results from the seed bank chapter, the results from the un-seeded treatments in the experimental trial, together with other research, confirm the hypothesis that the seed bank is depleted of indigenous perennial species after cultivation in both vegetation types (Bourne *et al*., 2017; Heelemann *et al*., 2013; Krug, 2004b; Shiponeni, 2003; Simons, 2005). This provides convincing evidence that for restoration to be effective, seeds need to be actively re-introduced to fallow lands. Active restoration goes beyond the removal of just the disturbance factor to include manipulative interventions (Suding & Hobbs, 2009). Restoration will be more cost effective for land managers if the efficiency is improved (Davies *et al*., 2020). In this study, livestock was excluded from the research area and therefore discussions around the results should be viewed in light of this fact which is vital to allow seedlings to establish and improve outcomes. Another way to improve success is through the careful identification of seedling requirements. Considering that seeds in arid areas germinate under nurse plants in a sheltered environment, on a fertile island, I suggest that seedling establishment could be increased by mimicking aspects of a patch. By providing the structure of a patch to improve establishment, the ecosystem can be set on a trajectory towards its original state (Suding & Hobbs, 2009).

The importance of growth form selection

I predicted that different growth forms would respond differently to the different restoration treatments used in the experimental trial (Chapter 4). Throughout this thesis species have been grouped into growth forms and their different responses to the experimental treatments has validated their use. Findings such as these have important implications for management in planning future restoration work and in the selection of species. Although the aim of restoration ecology is return the diversity, resilience and functioning of an ecosystem, the costs involved need to be taken into consideration. Costs could be reduced if the focus was to sow species that establish well and in a short period.

Succulent and non-succulent seedlings displayed different establishment and survival patterns. My results contrasted with those of Kruger (2010) who reported that the establishment success of succulents was always lower than that of non-succulents. In my study, non-succulent shrubs germinated reasonably well but still in low numbers. They also struggled to survive past the first year in the Hardeveld trials, which is consistent with findings from the Karoo in general (Bourne *et al*., 2017; Milton, 1994; Simons & Allsopp, 2007). The same species of non-succulent shrubs had considerably better survival in the Renosterveld trials. Given their success in Renosterveld and along the coast in Kruger (2010) research, I suggest that the establishment success of many non-succulent shrubs is strongly linked to water availability and, therefore, may be more suitable for use in locations that receive more rainfall.

In the Hardeveld trials succulent shrubs established well. Their ability to survive drier periods makes them excellent candidates for dryland restoration. *Leipoldtia schultzei* and *Cheiridopsis denticulata* were particularly effective, which is a finding supported by Bourne *et al* (2017). The palatable grass *Chaetobromus involucratus* established well, which supports the recommendations from others to use this grass in Karoo restoration (Saayman *et al*., 2017; Simons & Allsopp, 2007). Using these species in restoration would return the succulent component of the vegetation to the ecosystem which is lacking in degraded sites. In the Renosterveld trial, the grass *Tribolium hispidum* and the herb *Leysera gnaphalodes* established well. Non-succulent shrubs established but not as effectively as grasses and herbs. Using these species in restoration would return the grass and herb component.

The use of pioneer plant induced fertile islands in restoration

I hypothesized that pioneer plants create a fertile island that could improve seedling establishment success, and that by removing the above ground portion of the plant, the seeds would be able to maximise the soil resources without competition from the living plant. However, the findings from this study did not support the idea that the so-called 'root plots' (Chapter 4) would be advantageous for the establishment of different species. In Hardeveld, most growths forms showed no noticeable benefit to growing on a kraalbos root plot as compared to an open area. Conversely, succulent shrubs showed an overwhelming preference for open areas. I propose that because kraalbos increases alkalinity in the soils, this in turn increases the availability of phosphorous (Bandel *et al*., 2002). Succulent shrubs that are accustomed to more acidic soils and consequently lower phosphorous levels, struggle to establish and grow on kraalbos soil. Considering that establishing the succulent component of Karoo vegetation is vital, this largely nullifies the use of kraalbos patches as an aid in the restoration of fallow fields in Namaqualand.

Renosterveld is a poorly understood biome (Krug, 2004a) with some areas consisting of isolated bush clumps and others characterised by an even spacing of shrubs without noticeable bush-clumping (Curtis, 2013). It is not known what role, if any, patch dynamics play in vegetation communities of Kamiesberg Renosterveld. The results from chapter 2 indicate that renosterbos does create a fertile island, but only in relatively undisturbed environments and not on degraded land or on fallow fields. Therefore, the lack of a noticeable difference in seedling establishment on Renosterveld root plots compared to open areas is not surprising. Grass was the only growth form that established successfully on root plots. This concurs with the findings of Davies, Bates and Clenet (2020) who showed that perennial grasses had greater establishment in former sagebrush canopy sites.

The role of nutrients

There is a large cost to management that comes with adding nutrients and it is therefore crucial to evaluate whether the increased cost would be worth the return of investment. Due to the impact of cultivation on the soil and reducing fertility, I hypothesized that adding fertilizer to treatments would increase success of seedling establishment. Addition of nutrients would re-create the more nutrient rich, patch environment that seedlings needed to grow in. My results showed a mixed response from the different growth forms. It was only succulent shrubs (Hardeveld) and grasses (Renosterveld) that responded positively to nutrient addition. The other growth forms appeared not to have derived a noticeable benefit from the addition of nutrients. The most unexpected result was that this treatment resulted in a decline of herb seedlings in Renosterveld. These results emphasize how important it is to consider the response of different growth forms to different treatments when planning a restoration intervention in an area.

The role of shelters

Seedlings in arid areas can be exposed to harsh weather conditions and are also vulnerable to grazers. Growing in a patch, however, may protect them from some of these impacts. I hypothesized that seedling establishment would be greater in sheltered micro-sites. Three different types of shelters provided varying degrees of protection. Results generally supported this hypothesis, as box and brush pack treatments were very successful in increasing seedling numbers. Unlike nurse plants, brush packs and boxes do not compete with seedlings for resources, but still provide some form of protection, trap soil particles and organic matter and create a cooler environment. These features can easily be applied to increase restoration success.

In Hardeveld vegetation, boxes were especially effective for non-succulent and succulent shrubs, as well as for grasses. For succulent shrubs, boxes were the most effective treatment, even more so than adding nutrients or brush packing. This indicates that succulent shrubs respond well to boxes because it affords them some protection from the elements but allows more sunlight in than a brush pack, which is an important requirement for succulents (Esler, 1999). For non-succulent shrubs, boxes and brush packs were equally beneficial indicating that some form of protection is required. Bourne *et al.* (2017) and Simons and Allsopp (2007) found that brush packing yielded the greatest success in their restoration studies. These results are also supported by earlier findings that in the intact community, all the growth forms showed a preference for growing in a patch. In Renosterveld there was a clear preference by all growth forms for the complete cover provided by the brush packs, while the open boxes appeared not to have much influence on seedling establishment. The results with brush packs hold promise for future restoration activities because brush packs have not been used in Renosterveld restoration trials to date.

It was expected that the treatment that provided the addition of both nutrients and brush packs would create favourable germination sites for all growth forms and would show the greatest success in terms of seedling establishment. However, this was not the case for the majority of growth forms across both vegetation types. It was only grasses in Hardeveld that an impact was seen. These results suggest that different factors influence each other to affect seedling establishment. For example, nutrients only had a positive effect when other factors such as a shelter were present (Grubb, 1992).

In natural vegetation that has not been cultivated, seedlings growing in a patch would have nurse plants that they interact with. Thus nurse plants have been recommended as a restoration intervention because they provide benefits to seedlings such as added nutrients, cooler environments, and protection from herbivory (Kruger, 2010). I hypothesized that nurse plants would be beneficial to seedling establishment especially if there was no competition between the seedling and the nurse plant. The results indicate, however, that the use of nurse plants as a tool to aid in the restoration of Namaqualand's dryland ecosystems are not effective even though there is strong evidence for facilitation among adult plants in the Karoo (Carrick, 2001; Eccles *et al*., 1999). No difference in seedling survival between those seedlings located in unsheltered environments (i.e. in the open) and under nurse plants was seen in Strandveld (De Villiers *et al*., 2001). In some cases non-succulent shrubs are even disadvantaged by nurse plants, probably due to competition for soil resources (Philips & MacMahon, 1981). These results indicate that even if seeds of the original ecosystem were able to disperse to degraded fields, they would not establish well under those pioneer shrubs (kraalbos and renosterbos) which currently dominate fallow fields across large parts of Namaqualand.

Kraalbos, as a nurse plant, provided no noticeable benefit to seedling establishment as they had similar results to unsheltered controls for all growth forms. This is similar to findings from Kruger (2010). Therefore, despite possible positive effects that nurse plants could provide for seedlings, it was not enough to significantly increase seedling survival. There was not much evidence for competition between nurse plants and seedlings for resources. The results are due to the soil conditions under kraalbos, which discussed earlier, provide no benefit to seedlings. The only indication of facilitation by a nurse plant was with renosterbos and herb seedlings. These results indicate that the relationship between nurse plants and seedlings is complex. Findings from Kruger (2010) and Schmidt (2002) suggested that the size of the nurse plant could be factor, and that nurse clumps of three or more plants had benefit to seedlings, which is possible given that only individual pioneer plants were used as nurse plants in my study. Further research is required into the nurse plant and seedling relationship.

5.1.5 Seeding in different climatic years

Weather patterns need to be taken into consideration when attempting restoration, because different conclusions can arise from studies done on the same area but over different years. Inter-annual differences have impacts on seed production and predation (Milton, 1995a), seed viability (Carrick & Kruger, 2007) and seedling survival (Schmidt, 2002). Setting the same treatment with the same seeds mixture in two consecutive years (2013 and 2014) demonstrated this. It is also possible that individual treatments might respond differently under different climatic conditions. Although this thesis did not replicate all the treatments in 2014, it is possible that in drier and hotter years, treatments with shelter would result in better survival. The two vegetation types also had very different responses with regard to seedling numbers over three years. Over the course of the three year experiment the annual rainfall decreased, which very likely had an impact on the Hardeveld trial, but did not seem to have an influence on the Renosterveld trial. In fact, seedling numbers increased in Renosterveld over the three years, while rainfall decreased, indicating that rainfall is not a big an influence on germination in Renosterveld. I predict that in the case of Renosterveld, it was temperature that had an influence. The first year (2013) had a longer winter, which could have resulted in delayed germination. The extra treatment (2014) was set in a year with a milder winter and germination occurred faster, supporting the notion that temperature is an important influence on germination and establishment. In Hardeveld, the extra treatment in 2014 had dismal results, and the lack of germination is likely a cause of low rainfall or poor seed quality after storage. No seed viability or germination tests were conducted on the seeds after being stored for a year. These results have implications for future restoration planning and the functional groups that should be re-introduced with increased climate change.

5.2 Recommendations for future research and management

One of the key findings from this thesis is the importance of not using the same restoration techniques over different locations, but to carefully consider the environment one is working in. For example, there were major differences between the two vegetation types in this thesis even though they are in close proximity to each other. In order to further our understanding of the role of grazing in passive restoration, it is recommended to assess the long term impact of excluding grazing from the abdoned fields, particularly those that directly border natural or intact vegetation, to see if natural colonisation by seeds would be improved. The design for the restoration experiment used in this study was similar to that of Kruger (2010), which was also carried out in Namaqualand. However, the results for the same growth forms and in some cases even the same species, differed vastly. Restoration conducted in other Renosterveld types in the Western Cape also had results which contrasted from those for Kamiesberg Renosterveld. This research has shown that “one size does not fit all” and that different restoration techniques need to be tailored for each area.

Recovery is a slow process and returning the entire community of species in a single intervention is unlikely. I recommend that focus should be centred on returning those growth forms that established well on degraded land, to ‘kick start’ the ecosystem on the right trajectory. It is recommended to research the effectiveness of introducing growth forms in stages, by allowing one or two growth forms to establish over a few growing seasons and see if this results in improved establishment of other growth forms. This would focus seed collecting efforts, and reduce seed wastage. It is not recommended to use fertilizers, due to their limited positive impact on seedling establishment and the associated costs of purchasing fertilizer.

The results from this thesis indicate that manipulating the environment, along the lines suggested by the theory of patch dynamics, can be used successfully for restoration purposes. Due to the requirements of different growth forms, there is no universally-acceptable treatment, and recommendations for land managers will be influenced by their restoration objective. For example, do they wish to return biodiversity or fodder for livestock? Although the theory that fertile islands created by pioneer plants would increase seedling establishment did not occur, that does not mean that the material and space they provide cannot be used. It is still recommended to reduce the density of pioneer plants, such as kraalbos and renosterbos, prior to seeding in order to obtain material for brush packing on site. Future research should consider using different types of nurse plants, in both vegetation systems, as well as assess if nurse plant size is a factor to be considered. In the Karoo, it is suggested to explore whether established succulent shrubs, which also increase organic matter and nutrients under their canopies (Stock *et al*., 1999), could be used as nurse plants for non-succulent shrubs.

In Hardeveld, soil under the canopy of kraalbos individuals should largely be avoided. It is also recommended to re-seed with succulent shrubs and grasses, as both growth forms established well in this vegetation. Adding nutrients increases the cost considerably but tripled the establishment success of succulent shrubs establishment and is recommended. Boxes and brush packs, are also recommended as shelters for seedlings and were the most effective treatments. Considering future climate change impacts, which suggest that there will be an increase in the frequency of droughts (Hewitson *et al*., 2005), restoration interventions that provide some form of shelter from heat and reduce evaporation, are likely to become even more important to ensure seedling survival.

Although sowing seeds directly under renosterbos did not necessarily improve seedling success, the results were similar to open areas, and therefore sowing under a renosterbos can still be recommended. Especially for grasses that did show a benefit to being under a renosterbos. Brush packing is highly recommended as a shelter structure, because they cost effective, easily applied and a readily available resource on site, especially if the density of pioneer plants is reduced to create space for seed sowing. Boxes are more labour intensive to install correctly, as it requires more physical digging and time, and did not significantly enhance establishment success in Renosterveld and are therefore not recommended. Herbs and grasses are recommended as they established well in Renosterveld and contribute to stabilising the soil. Non-succulent shrubs also established but not as well.

Active restoration needs to exclude livestock grazing for a number of years. In communal areas this type of restoration activity, which then prohibits the community from using the land, will only be successful if there is community buy-in. The community should be involved in the restoration work and take a vested interest in it, as well as reap some benefits from it, such as through paid labour and monitoring work.

The recommended active restoration interventions mentioned here should be viewed as experiments. There is a need to build the knowledge base of suitable approaches for different ecosystems and loactions and ongoing research, as well as monitoring there-of is recommended. Renosterveld is a poorly understood ecosystem and there is considerable scope for further research. Kamiesberg Renosterveld is unlike other Renosterveld types where alien grass invasion is a major obstacle to restoration. Alien grass invasion is not a common feature in Kamiesberg Renosterveld. However, more research is required into the ecological functioning of intact Renosterveld and what contributes towards fertile island development. Renosterbos is not a suitable nurse plant, so investigations should be undertaken to identify a species which could function in this capacity. I also recommend researching the role of fire or smoke treatments in restoration of Renosterveld species. The role of fire was not tested in this thesis, but it is recognised that Renosterveld is a fire-driven system and increased species establishment and diversity after burning has been recorded by simons (2017) in Kamiesberg Renosterveld vegetation, as well as in Roggeveld Renosterveld (Van Der Merwe & Van Rooyen, 2011a), and Swartland Rensoterveld (Cousins *et al*., 2017; Heelemann *et al*., 2013).

5.3 Conclusion

In this thesis, I contribute conceptually and theoretically to our understanding of patch dynamics, by analysing its role in intact ecosystems and how it recovers over time after degradation. Passive recovery of old fields in Renosterveld and Hardeveld environments occurs extremely slowly, if at all. Decades after cultivation has ceased the land is not on a trajectory to recovery. Short distance seed dispersal, a lack of suitable shelter sites and nurse plants, and altered soil conditions beyond what the seeds can survive, are the barriers that keep fallow fields in their alternative state. Therefore active manipulations and seed introduction is required to restore these ecosystems.

This thesis has contributed towards generating knowledge on how Hardeveld and Kamiesberg Renosterveld ecosystems function. I have also demonstrated that restoration activities from one area cannot be applied across all vegetation types of the same biome. Individual vegetation types appear to function differently from each other. Restoration efforts should be aware of the dynamics that exist within a particular environment. I also demonstrated that individual growth forms have their own requirements for establishment, which must be taken into consideration in restoration planning.

Two hypotheses, aimed at using pioneer shrubs as nurse plants and the fertile island they created, did not prove successful, apart from the response of grasses in Renosterveld. Fertile islands do not significantly increase seedling success and there was little difference between these areas and open areas. Kraalbos and renosterbos do not make suitable nurse plants. This study did support the hypothesis that the use of shelters is beneficial to the germination and establishment of seedlings of a range of growth forms. The success of brush packs and especially boxes in Hardeveld, suggests that their use should be promoted in future restoration endeavours. The addition of nutrients to increase seedling success had only limited success, and was only beneficial to succulents in Hardeveld and grass in Renosterveld. In the Hardeveld areas succulent shrubs and grasses established well and are recommended for future restoration activities. In Renosterveld, grasses and herbs established well and are recommended for future restoration activities.

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Appendix

A

Abundance (mean ± SD) of all perennial species and plant families, in Kamiesberg Hardeveld grouped in their relevant growth form types, recorded in 100 m transects at each site, from the following land uses: young fields, old field, private reference farms and communal reference farms.

		Land use category			
Species	**Family**	**Young fields (n = 4)**	**Old fields (n = 4)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 4)**
Perennial Graminoid					
Ehrharta barbinodis	Poaceae			8.5 (12.9)	
Ehrharta sp	Poaceae				13.7 (24.8)
Fingerhuthia africana	Poaceae				0.1 (0.3)
Pentameris (Pentaschistis) curvifolia	Poaceae	10.8 (20.5)	3.3 (6.4)		
Stipagrostis ciliata	Poaceae			0.1 (0.3)	
Stipagrostis sp	Poaceae	0.3 (0.3)	0.6 (1.2)		17.5 (19.7)
Tribolium hispidum	Poaceae	0.1 (0.3)			
Perennial herb					
Aizoon canariense	Aizoaceae	2.5 (4.1)			3.6 (11.5)
Blepharis sp	Acanthaceae	2.6 (5.2)			
Hypertelis salsoloides	Molluginaceae		0.2 (0.4)	0.1 (0.3)	
Leysera gnaphalodes	Asteraceae	13.4 (16.9)	0.5 (0.9)	0.1 (0.3)	0.0 (0.0)
Microloma sagittatum	Apocynaceae	0.3 (0.6)	0.1 (0.25)	0.5 (0.6)	1.1 (1.5)
Othonna sp cf cuneata/ filicaulis	Asteraceae			0.3 (1.0)	2.0 (5.3)
Pharnaceum confertum	Molluginaceae	7.0 (10.9)	25.8 (35.4)	0.9 (1.8)	
Perennial small leaf Succulent (SLS) shrub					
Cephalophyllum spissum	Aizoaceae			1.8 (5.6)	
Cephalophyllum sp	Aizoaceae			5.1 (9.8)	
Cheirodopsis sp	Aizoaceae			0.3 (1.3)	
Conicosia elongata	Aizoaceae	1.4 (2.2)	0.4 (0.6)	1.2 (2.3)	0.1 (0.3)
Crassula hemisphaerica	Crassulaceae			0.4 (1.7)	
Crassula muscosa	Crassulaceae	0.1 (0.3)		2.1 (3.8)	5.8 (9.8)
Pelargonium karooicum	Geraniaceae			2.4 (3.9)	
Phyllobolus nitidus	Aizoaceae	0.1 (0.3)		0.2 (0.4)	
Perennial medium leaf succulent (MLS) shrub					
Aridaria sp	Aizoaceae		0.1 (0.3)	0.6 (1.3)	4.8 (10.4)
Crassula sp	Crassulaceae				0.8 (3.2)
Crassula subaphylla	Crassulaceae			0.3 (1.3)	0.3 (0.7)
Drosanthemum hispidum	Aizoaceae	0.8 (1.7)	0.3 (0.5)	0.2 (0.4)	

Drosanthemum sp	Aizoaceae				0.2 (0.8)
Lampranthus sp	Aizoaceae				8.3 (10.4)
Leipoldtia schultzei	Aizoaceae		0.6 (2.5)	16.6 (22.6)	42.5 (34.5)
Othonna cylindrica	Asteraceae			0.3 (0.7)	
Ruschia burtoniae	Aizoaceae			0.8 (1.9)	0.2 (0.5)
Ruschia cf fugitans	Aizoaceae			11.1 (12.8)	
Ruschia goodiae	Aizoaceae			5.7 (11.1)	
Ruschia cf aggregata	Aizoaceae	0.3 (1.0)	0.6 (2.0)	4.0 (4.7)	6.9 (8.7)
Tetragonia fruticosa	Aizoaceae	0.1 (0.3)		4.7 (5.2)	1.6 (2.8)
Zygophyllum leptopetalum	Zygophyllaceae			0.1 (0.3)	0.1 (0.3)
Zygophyllum morgsana	Zygophyllaceae	0.1 (0.3)		0.1 (0.3)	
Perennial small non-leaf succulent (SNLS) shrub					
Chrysocoma ciliata	Asteraceae			0.3 (0.3)	0.1 (0.3)
Hirpicium alienatum	Asteraceae			1.4 (2.2)	3.8 (7.1)
Hirpicium sp	Asteraceae			0.8 (1.5)	0.3 (0.8)
Wiborgia sp	Fabaceae	0.4 (1.2)		2.9 (2.8)	0.9 (1.9)
Stoebe sp	Asteraceae	0.6 (0.5)	1.1 (2.7)	2.1 (4.8)	
Perennial medium non-leaf succulent (MNLS) Shrub					
Asparagus sp	Asparagaceae				0.1 (0.3)
Berkheya sp	Asteraceae			2.1 (3.7)	0.8 (0.1)
Didelta spinosa	Asteraceae			0.4 (0.9)	2.3 (3.2)
Eriocephalus ericoides	Asteraceae	0.1 (0.3)	0.8 (1.3)	6.6 (6.8)	6.8 (5.8)
Eriocephalus sp	Asteraceae		0.1 (1.2)	1.6 (2.2)	2.9 (2.7)
Galenia africana	Aizoaceae	23.5 (15.1)	24.4 (9.6)	0.9 (1.2)	2.6 (3.4)
Hermannia disermifolia	Sterculiaceae	0.1 (0.3)	0.1 (0.2)	0.5 (1.1)	1.9 (2.9)
Hermannia sp	Sterculiaceae	0.2 (0.4)	0.1 (0.2)	0.1 (0.3)	0.3 (0.7)
Calobota (Lebeckia) sericea	Fabaceae	0.6 (0.8)		1.1 (1.9)	3.8 (4.2)
Lycium sp	Solanaceae			0.4 (1.0)	0.6 (0.7)
Manochlamys albicans	Chenopodiaceae		0.1 (0.3)		0.4 (1.0)
Montinia caryophyllacea	Montiniaceae				0.1 (0.3)
Pelargonium crithmifolium	Geraniaceae				7.4 (6.7)
Pelargonium spinosum	Geraniaceae			0.1 (0.3)	
Pentzia incana	Asteraceae	0.3 (0.7)	1.6 (3.6)	1.1 (1.4)	0.1 (0.3)
Pteronia divaricata	Asteraceae	0.3 (0.4)	1.9 (4.3)	0.1 (0.3)	1.0 (2.7)
Pteronia incana	Asteraceae				0.1 (0.3)
Pteronia sp 1	Asteraceae			0.7 (1.5)	
Pteronia sp 2	Asteraceae			2.0 (4.6)	
Searsia incisa	Anacardiaceae			0.3 (1.3)	
Searsia undulata	Anacardiaceae	0.1 (0.3)		0.3 (1.3)	1.4 (1.2)
Senecio sp	Asteraceae			0.3 (1.3)	
Solanum sp	Solanaceae			0.0 (0.0)	0.3 (1.0)
Thesium lineatum	Santalaceae			0.0 (0.0)	0.1 (0.3)
Osteospermum (Tripteris) sinuatum	Asteraceae	0.1 (0.3)	0.1 (0.3)	0.6 (1.4)	0.3 (0.5)
Osteospermum sp	Asteraceae	0.1 (0.3)		0.6 (1.0)	

Perennial stem succulent (SS) shrub					
Euphorbia braunsii	Euphorbiaceae			0.4 (0.8)	
Euphorbia decussata	Euphorbiaceae	0.1 (0.3)		3.0 (2.6)	3.9 (6.2)
Euphorbia mauritanica	Euphorbiaceae			2.0 (2.5)	4.6 (4.5)
Pelargonium cf alternans/ dasyphyllum	Geraniaceae	0.2 (0.5)	0.1 (0.3)	0.2 (0.5)	
Psilocaulon sp	Aizoaceae			0.1 (0.2)	
Quagua incarnata	Apocynaceae			0.3 (0.6)	0.1 (0.3)
Sarcocaulon l'heritieri	Geraniaceae			0.1 (0.2)	
Tylecodon wallichii	Crassulaceae				0.1 (0.3)

B

Abundance (mean + SD) of all perennial species and plant families, in Kamiesberg Renosterveld, grouped in their relevant growth form types, recorded in 100 m transects at each site, from the following land uses: young fields, old field, private reference farms and communal reference farms.

		Land use category			
Species	**Family**	**Young fields (n = 4)**	**Old fields (n = 3)**	**Communal reference farms (n = 4)**	**Private reference farms (n = 3)**
Perennial Graminoid					
Ehrharta calycina	Poaceae	18.3 (21.6)	7.2 (10.9)	11.3 (7.8)	3.7 (5.9)
Ficinia sp	Cyperaceae		3.0 (4.0)	0.8 (1.5)	
Restio (Ischyrolepis) gossypina	Restionaceae		0.4 (1.4)	33.9 (34.0)	
Tenaxia (Merxmuellera) stricta	Poaceae			1.6 (2.3)	1.4 (1.8)
Pentameris (Pentaschistis) curvifolia	Poaceae	116.4 (34.1)	65.7 (23.0)	16.1 (12.3)	8.2 (8.4)
Tribolium hispidum	Poaceae	7.6 (12.9)	1.75 (3.1)	14.6 (14.6)	11.3 (9.6)
Perennial herb					
Blepharis furcata	Acanthaceae			1.9 (3.0)	
Euphorbia tuberosa	Euphorbiaceae			2.6 (4.8)	
Heliophila carnosa	Brassicaceae		1.2 (3.1)	1.6 (2.1)	0.5 (1.0)
Lessertia diffusa	Fabaceae				0.1 (0.3)
Leysera gnaphalodes	Asteraceae	12.4 (16.4)	9.2 (8.2)	12.3 (16.5)	
Limeum africanum	Molluginaceae		0.1 (0.2)		
Othonna filicaulis	Asteraceae		0.1 (0.2)	0.9 (1.2)	
Pharnaceum confertum	Molluginaceae	2.5 (5.7)	10.2 (12.0)	6.6 (6.6)	10.0 (10.4)
Perennial Leaf Succulent (LS) shrub					
Conicosia elongata	Aizoaceae	0.2 (0.4)	0.1 (0.2)		
Crassula cf orbiculata	Crassulaceae				0.1 (0.2)
Drosanthemum hispidum	Aizoaceae				1.5 (2.3)
Ruschia sp	Aizoaceae		0.1 (0.2)	0.7 (1.5)	
Zygophyllum leptopetalum	Zygophyllaceae				1.1 (1.1)

Perennial small non-leaf Succulent (SNLS) Shrub					
Chrysocoma ciliata	Asteraceae	22.3 (21.6)	24.5 (27.2)	13.0 (11.8)	2.5 (4.2)
Euryops sp	Asteraceae		0.4 (0.7)		3.2 (4.6)
Hermannia disermifolia	Sterculiaceae		0.1 (0.2)		0.1 (0.3)
Lotononis cf digitata	Fabaceae	1.0 (1.9)	2.8 (4.6)	3.6 (4.6)	
Melolobium adenodes	Fabaceae			0.1 (0.2)	
Pentzia incana	Asteraceae	0.3 (5.7)			9.2 (12.6)
Selago sp	Scrophulariaceae				1.1 (2.4)
Senecio sp	Asteraceae		2.5 (3.8)	3.1 (4.1)	0.8 (1.4)
Stoebe cf microphylla	Asteraceae	0.3 (0.7)		0.1 (0.2)	2.1 (2.5)
Ursinia pilifera	Asteraceae			0.1 (0.2)	
Wiborgia sp	Fabaceae	8.0 (7.0)	9.6 (10.5)	8.6 (15.2)	0.1 (0.3)
Perennial medium non-Leaf Succulent (MNLS) Shrub					
Anthospermum cf spathulatum	Rubiaceae	0.1 (0.2)		4.0 (5.8)	
Aspalathus sp	Fabaceae	1.6 (2.5)	1.5(2.4)	0.5 (0.7)	0.2 (0.4)
Asparagus rubicundus	Asparagaceae			0.1 (0.2)	
Chironia baccifera	Gentianaceae			0.1 (0.3)	0.1 (0.2)
Cliffortia ruscifolia	Rosaceae		1.9 (3.3)	1.7 (3.9)	0.1 (0.2)
Dodonaea viscosa	Sapindaceae			0.1 (0.2)	
Dicerothamnus rhinocerotis	Asteraceae	21.9 (9.9)	20.3 (13.4)	22.7 (11.2)	20.2 (5.6)
Eriocephalus africanus	Asteraceae	0.4 (1.0)	0.0 (0.0)	20.2 (15.9)	0.1 (0.2)
Eriocephalus ericoides	Asteraceae			0.8 (1.1)	0.3 (0.9)
Eriocephalus long leaf	Asteraceae			0.4 (1.5)	0.0 (0.0)
Euryops lateriflorus	Asteraceae		0.1 (0.2)	1.7 (2.6)	9.1 (12.2)
Felicia filifolia	Asteraceae			0.1 (0.2)	0.1 (0.3)
Gnidia nitida	Thymelaeaceae	0.9 (2.5)	1.4 (2.1)	2.2 (2.3)	
Helichrysum hamulosum	Asteraceae		0.3 (0.4)	11.6 (8.2)	10.9 (9.4)
Indigofera sp	Fabaceae			0.1 (0.2)	
Calobota (Lebeckia) sericea	Fabaceae	0.1 (0.5)			
Lycium sp	Solanaceae			0.2 (0.5)	
Nenax sp	Rubiaceae		0.16 (0.5)	1.1 (2.2)	
Muraltia spinosa	Polygalaceae		0.1 (0.3)	1.2 (0.8)	0.1 (0.3)
Oedera genistifolia	Asteraceae			4.2 (5.5)	7.4 (13.1)
Pelargonium cf. scabrum	Geraniaceae			0.1 (0.3)	
Polygala sp	Polygalaceae			0.3 (0.6)	
Pteronia incana	Asteraceae			3.9 (10.5)	
Salvia sp	Lamiaceae			0.2 (0.5)	
Selago glutinosa	Scrophulariaceae			1.6 (2.8)	
Stachys rugosa	Lamiaceae			0.8 (1.7)	
Sutherlandia sp	Fabaceae				0.5 (1.0)

C

Species abundance (mean ± SD) of all germinating seeds and plant families, in Kamiesberg Hardeveld, grouped into their relevant growth form types, germinated from soil collected (12 x 600 g replicates) along the skirts of the most dominant shrub in each site from the following land uses: young fields (four sites), old field (four sites), private reference farms (four sites) and communal reference farms (four sites).

		Land use category			
		Young fields	**Old fields**	**Communal reference farms**	**Private reference farms**
Species	**Family**	**(n = 48)**	**(n =36)**	**(n = 48)**	**(n = 36)**
Annual herb					
Adenogramma glomerata	Molluginaceae	2.60 (4.5)	0.04 (0.3)	0.02 (0.1)	0.79 (1.9)
Aizoon canariense	Aizoaceae	0.00 (0.0)	0.02 (0.1)		
Conyza bonariensis	Asteraceae	0.06 (0.2)	0.14 (0.6)	0.15 (0.5)	1.08 (2.3)
Cotula sp	Asteraceae	0.33 (1.2)	0.31 (0.9)	0.04 (0.2)	0.06 (0.4)
Crassula glomerata	Crassulaceae	1.79 (5.9)	2.35 (5.0)	1.58 (2.6)	3.78 (7.4)
Crassula thunbergiana	Crassulaceae	0.85 (1.8)	0.21 (0.7)	0.54 (0.1)	0.54 (1.47)
Erodium cicutarium	Geraniaceae	0.1 (0.4)	0.02 (0.1)		
Felicia australis	Asteraceae	1.92 (3.2)	4.16 (4.7)	0.64 (1.5)	0.44 (0.9)
Hebenstretia cf parviflora or integrifolia	Scrophulariaceae				0.02 (0.1)
Helichrysum leontonyx	Asteraceae	0.85 (1.3)	5.87 (2.7)	1.32 (2.1)	0.88 (1.5)
Heliophila sp	Brassicaceae	0.04 (0.2)	0.08 (0.2)	0.04 (0.2)	0.17 (0.6)
Hypertelis sp	Molluginaceae			0.02 (0.1)	
Limeum africanum	Molluginaceae	0.08 (0.4)			
Leysera gnaphalodes	Asteraceae	0.06 (0.2)	0.35 (0.9)	0.02 (0.1)	0.06 (0.3)
Mesembryanthemum guerichianum	Aizoaceae	0.04 (0.2)			
Oncosiphon suffructicosum	Asteraceae	0.35 (0.6)	0.75 (0.7)	0.04 (0.2)	
Petrorhagia sp	Caryophyllaceae				0.12 (0.6)
Pharnaceum croceum	Molluginaceae	0.35 (1.7)	0.21 (0.6)	0.2 (0.5)	

Plantago cafra	Plantaginaceae	0.04 (0.2)	0.06 (0.3)		0.02 (0.1)
Polygonum cf aviculare	Polygonaceae				0.02 (0.1)
Senecio sp 1	Brassicaceae	0.02 (0.1)			0.06 (0.3)
Senecio sp 2	Brassicaceae	0.17 (0.5)			
Wahlenbergia androsacea	Campanulaceae	0.06 (0.2)		0.02 (0.1)	0.06 (0.3)
Wahlenbergia annularis	Campanulaceae	0.14 (0.4)	0.12 (0.4)	0.08 (0.3)	0.27 (1.2)
Wahlenbergia prostrata	Campanulaceae	0.25 (1.5)		0.02 (0.1)	0.17 (1.1)
Wahlenbergia sp	Campanulaceae			0.02 (0.1)	0.06 (0.3)
Zaluzianskya benthamiana	Scrophulariaceae	0.25 (0.6)	0.56 (1.5)	0.21 (0.6)	0.08 (0.2)
Zaluzianskya minima	Scrophulariaceae		0.02 (0.1)		
Annual Graminoid					
Aristida sp	Poaceae	0.75 (1.4)	2.45 (4.8)	1.12 (3.7)	0.90 (2.3)
Bromus pectinatus	Poaceae	0.08 (0.3)	0.12 (0.7)	0.02 (0.1)	0.17 (0.6)
Bromus sp	Poaceae	0.01 (0.6)	0.16 (1.0)	0.06 (0.3)	
Cyperus sp	Cyperaceae		0.0 (0.0)	0.02 (0.1)	
Pentameris airoides	Poaceae	0.54 (1.3)	2.71 (6.5)	1.33 (3.5)	0.77 (1.5)
Tribolium echinatum	Poaceae	0.69 (1.7)	0.43 (1.7)	0.48 (1.6)	0.094 (2.2)
Geophyte					
Moraea spp	Iridaceae			0.02 (0.1)	
Oxalis pes-caprae	Oxalidaceae		0.02 (0.1)	0.02 (0.1)	
Oxalis sp 1	Oxalidaceae	0.14 (0.4)	0.04 (0.2)	0.06 (0.2)	0.08 (0.3)
Oxalis sp 2	Oxalidaceae	0.04 (0.2)			
Perennial Graminoid					
Digitaria argyrograpta	Poaceae	0.06 (0.2)	0.04 (0.2)		0.06 (0.3)
Ehrharta sp	Poaceae				0.33 (1.6)
Ficinia sp	Cyperaceae	0.08 (0.3)	0.08 (0.3)	9.1 (17.1)	1.42 (4.0)
Pentameris curvifolia	Poaceae	0.14 (0.5)	0.04 (0.2)		
Perennial Leaf succulent (LS) shrub					

Crassula muscosa	Crassulaceae			0.14 (0.5)	
Leipoldtia sp	Aizoaceae			0.04 (0.2)	3.54 (7.9)
Ruschia goodiae	Aizoaceae			0.12 (0.4)	
Ruschia sp	Aizoaceae				0.02 (0.1)
Tetragonia sp	Aizoaceae			0.02 (0.1)	
Perennial Non-leaf succulent (NLS) shrub					
Galenia africana	Aizoaceae	1.40 (3.8)	0.64 (1.3)	0.02 (0.1)	0.19 (0.4)
Hermannia sp	Sterculiaceae				0.04 (0.2)
Manochlamys albicans	Chenopodiaceae				0.02 (0.1)
Pentzia incana	Asteraceae			0.02 (0.1)	
Wiborgia sp	Fabaceae	0.17 (0.5)	0.21 (0.4)	0.04 (0.2)	

D

Species abundance (mean ± SD) of all germinating seeds and plant families, in Kamiesberg Renosterveld, grouped into their relevant growth form types, germinated from soil collected (12 x 600 g replicates) along the skirts of the most dominant shrub in each site from the following land uses: young fields (four sites), old field (three sites), private reference farms (three sites) and communal reference farms (four sites).

		Land use category			
Species	**Family**	**Young fields**	**Old fields**	**Communal reference farms**	**Private reference farms**
Annual herb					
Adenogramma glomerata	Molluginaceae	0.56 (2.1)	0.27 (0.8)	0.02 (0.1)	0.03 (0.2)
Conyza bonariensis	Asteraceae			0.23 (0.7)	0.14 (0.8)
Cotula sp	Asteraceae	0.02 (0.1)	0.25 (1.2)		
Crassula glomerata	Crassulaceae	0.40 (1.1)	0.36 (0.9)	0.67 (1.7)	2.81 (5.9)
Crassula sp 1	Crassulaceae				1.19 (5.9)
Crassula sp 2	Crassulaceae		0.03 (0.2)		0.11 (0.7)
Crassula thunbergiana	Crassulaceae	1.31 (2.9)	2.22 (4.7)	0.31 (0.8)	0.11 (0.7)
Erodium cicutarium	Geraniaceae	0.08 (0.4)	0.11 (0.3)	0.10 (0.6)	0.03 (0.2)
Felicia australis	Asteraceae	1.21 (1.7)	2.25 (3.0)	0.46 (1.0)	0.44 (1.1)
Gamochaeta sp	Asteraceae		0.25 (1.5)	0.02 (0.1)	0.03 (0.2)
Helichrysum leontonyx	Asteraceae	0.94 (2.1)	0.14 (0.4)	0.21 (0.8)	0.50 (0.9)
Heliophila sp	Brassicaceae	0.06 (0.3)	0.36 (1.0)	0.04 (0.2)	
Limeum africanum	Molluginaceae	0.29 (1.4)			
Mesembryanthemum crystallinum	Aizoaceae	0.10 (0.5)	0.06 (0.3)	0.06 (0.2)	
Pharnaceum croceum	Molluginaceae		0.06 (0.3)	0.31 (1.5)	0.78 (2.6)
Rumex cordatus	Polygonaceae	0.02 (0.1)			
Selago sp 1	Scrophulariaceae			0.08 (0.6)	
Selago sp 2	Scrophulariaceae			0.38 (1.6)	0.03 (0.2)
Senecio sp	Asteraceae				0.19 (0.8)
Ursinia ck cakilefolia	Asteraceae		0.06 (0.3)		
Wahlenbergia androsacea	Campanulaceae				0.03 (0.2)

Wahlenbergia annularis	Campanulaceae		0.03 (0.2)	0.10 (0.6)	
Wahlenbergia prostrata	Campanulaceae		0.03 (0.2)		0.06 (0.3)
Zaluzianskya benthamiana	Scrophulariaceae	0.29 (0.8)	0.17 (0.6)	0.25 (0.9)	0.53 (0.8)
Zaluzianskya pusilla	Scrophulariaceae				0.53 (3.2)
Annual Graminoid					
Aristida sp	Poaceae	6.94 (16.9)	4.56 (8.0)	1.83 (3.7)	1.25 (3.5)
Bromus pectinatus	Poaceae	10.23 (21.0)	2.00 (4.7)	0.08 (0.6)	0.56 (0.2)
Cyperus sp	Cyperaceae		0.03 (0.2)	0.35 (2.3)	0.33 (1.7)
Pentameris airoides	Poaceae	0.77 (5.2)	0.72 (2.1)	2.71 (6.6)	3.14 (5.8)
Tribolium echinatum	Poaceae	1.60 (5.7)		1.90 (6.4)	1.72 (3.9)
Vulpia myuros	Poaceae	0.13 (0.5)		0.02 (0.1)	3.42 (7.1)
Restio sp	Restionaceae	10.23 (18.0)	2.72 (9.7)	0.27 (1.0)	0.17 (0.6)
Perennial Graminoid					
Ehrharta calycina	Poaceae	0.04 (0.2)	0.06 (0.3)	0.02 (0.1)	
Chaetobromus sp	Poaceae		0.03 (0.2)		
Pentameris curvifolia	Poaceae	3.96 (7.6)	3.36 (5.4)	0.54 (1.9)	0.22 (0.7)
Tribolium hispidum	Poaceae			0.17 (1.0)	0.03 (0.2)
Perennial Leaf succulent (LS) shrub					
Drosanthemum sp	Aizoaceae				0.03 (0.2)
Perennial Non-leaf succulent (NLS) shrub					
Dicerothamnus rhinocerotis	Asteraceae	0.17 (0.5)	0.42 (0.7)	1.04 (1.7)	0.94 (2.2)
Euryops lateriflorus	Asteraceae			0.02 (0.1)	
Hermannia sp	Sterculiaceae			0.02 (0.1)	
Leysera sp	Asteraceae	0.04 (0.2)	0.03 (0.2)	0.02 (0.1)	
Solanum sp	Solanaceae	0.02 (0.1)	0.03 (0.2)	0.04 (0.3)	0.03 (0.2)
Sutherlandia sp	Fabaceae				0.03 (0.2)
Wiborgia	Fabaceae	0.08 (0.4)	0.19 (0.5)	0.13 (0.9)	0.08 (0.3)
Geophyte					

Oxalis sp	Oxalidaceae	0.06 (0.2)	0.02 (0.1)

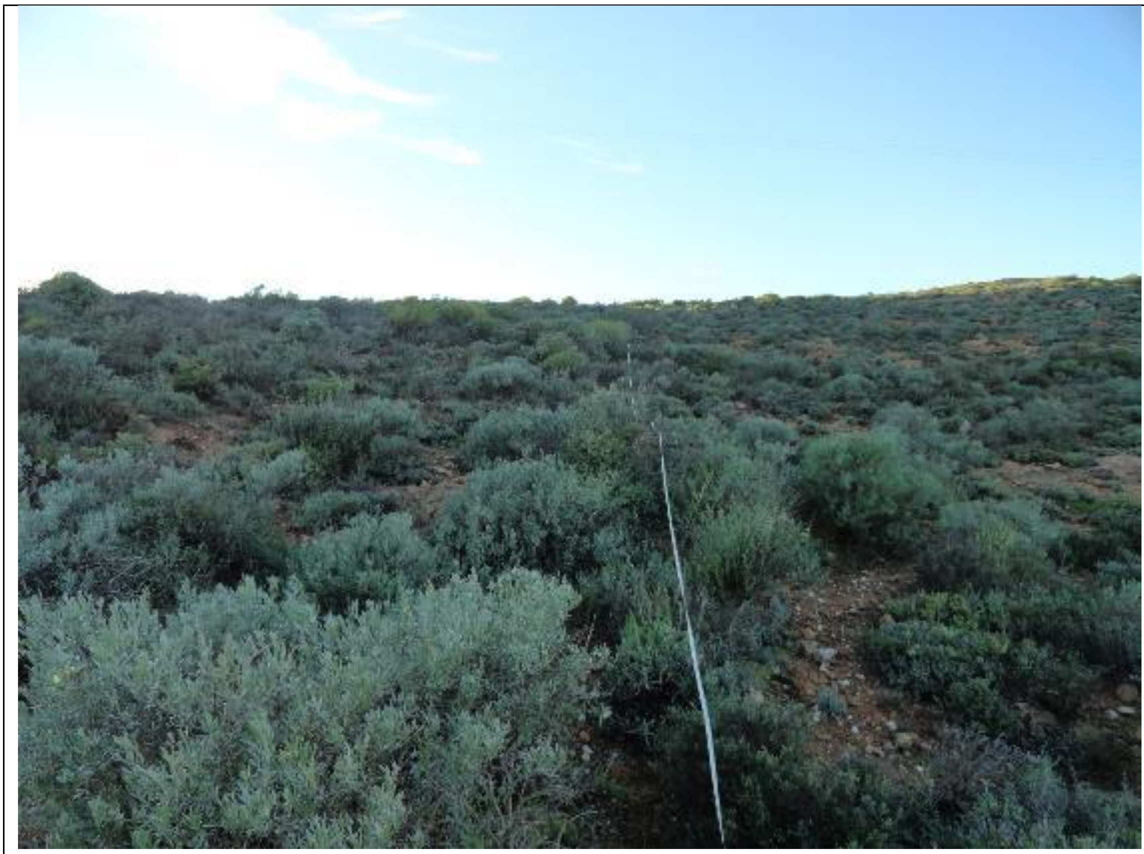
E

Germination trial results on the seeds used in the restoration experiments, after 42 days in a germination chamber with 10 / 25 C, 12 hr night/ 12 day temperature and light regime. NSA = no seeds were available for the trial due to low collecting numbers

Family	**Species**	**Number of seeds used**	**Germinated %**
Aizoaceae	*Leipoldtia schultzei*	*100*	70
Aizoaceae	*Ruschia* sp	*100*	5
Aizoaceae	*Cheiridopsis denticulata*	*100*	88
Aizoaceae	*Conicosia* sp	NSA	NSA
Aizoaceae	*Drosanthemum hispidum*	*100*	25
Molluginaceae	*Hypertelis salsoloides*	*100*	20
Aizoaceae	*Galenia sarcophylla*	*100*	36
Aizoaceae	*Aizoon canariense*	*100*	35
Asteraceae	*Hipicium alienatum*	*100*	30
Asteraceae	*Osteospermum oppistifolia*	*100*	35
Chenopiaceae	*Manochlamys albicans*	*100*	50
Asteraceae	*Pteronia divaricata*	*100*	26
Aizoaceae	*Tetragonia fruticosa*	*100*	0
Asteraceae	*Eriocephalus microphyllus*	*100*	1
Sterculiaceae	*Hermannia disermifolia*	*100*	47
Asteraceae	*Pentzia incana*	*100*	30
Zygophyllaceae	*Zygophyllum morgsana*	*NSA*	NSA
Poaceae	*Stipagrostis ciliata*	*NSA*	NSA
Poaceae	*Chaetobromus involucratus*	*100*	0
Fabaceae	*Calobota sericea*	*100*	0
Asteraceae	*Helichrysum hamulosum*	*100*	50
Asteraceae	*Pteronia glomerata*	*100*	33
Lamiaceae	*Stachys rugosa*	*100*	0
		100	0
Asteraceae	*Pteronia incana*	*100*	0

Restionaceae	*Restio* sp	*40*	0
Poaceae	*Ehrharta calycina*	*100*	0
		100	0
Poaceae	*Tribolium hispidum*	*100*	55
Asteraceae	*Leysera gnaphalodes*	*100*	87
Molluginaceae	*Pharnaceum confertum*	*NSA*	NSA
Asteraceae	*Elytropappus rhinocerotis*	*100*	1
Fabaceae	*Wiborgia* sp	*100*	26
Fabaceae	*Calobota sericea*	*100*	0

F



F.1. Vegetation surveys in intact or reference sites in Renosterveld

F.2. Vegetation survey in intact or reference sites in Hardeveld

F.3. Vegetation survey on old fields in Hardeveld

F.4. Vegetation survey on old fields in Renosterveld

F.5. Greenhouse experiment on the seed bank

F.6. Layout of restoration trial in Hardeveld. Seeded plots are visible buy the square shape

F.7. Restoration trial in Renosterveld, with boxed and removed renosterbos visible.

F.8. Seedlings growing in a box

F.9. Restoration plot in Hardeveld after three years, with kraalbos in the back ground

F.10. Restoration plot in Renosterveld after three years