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Seed bank strategies in a Kalahari ecosystem in relation to grazing and habitats

by

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Submitted in partial fulfillment for the degree

MAGISTER SCIENTIAE

In the Faculty of Natural and Agricultural Sciences
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Supervisor: Prof MW van Rooyen

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I declare that the thesis/dissertation, which I hereby submit for the degree Magister Scientiae at the University of Pretoria, is my own work and has not been previously submitted by me for a degree a this or any other tertiary institution.

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DATE:

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ABSTRACT

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The seed bank dynamics of five habitats as well as a grazing gradient in the southwestern Kalahari, South Africa were studied. Soil samples were collected in the following habitats: dune crests, dune slopes, dune streets, a calcrete outcrop and a riverbed on the farm Alpha. Soil samples were also collected along a grazing gradient from a watering point.

Three methods of soil seed bank analysis were used to analyse the soil samples and to gain insight into soil seed bank response to habitat type and to grazing pressure, over four seasons in the year 2004. Results from the three methods of analysis were also compared to each other. They included the direct seedling germination method, the seedling germination re-examination and the seed extraction method. These analyses were used to (a) estimate seed bank size and composition in response to habitat type and grazing pressure; (b) the differences between the standing vegetation- and the seed bank-flora in different habitats and along a grazing gradient and (c) the type of seed banks that tend to form in certain habitats and in response to grazing pressure.

Analyses of soil seed bank size along a grazing gradient showed that the seedling emergence re-examinations estimated a larger size for the seed bank than the direct seedling emergence method. The seed extraction method estimated a significantly larger seed bank size than the other two methods. Heavy grazing pressure favoured annual/opportunistic species such as *Schmidtia kalahariensis*, which formed very large seed banks in heavily trampled areas. When *Schmidtia kalahariensis* data was removed from the seed bank analyses, it was found that, in contrast to previous results, the direct germination method mostly estimated a larger seed bank size than the re-examination. Also, the estimation of seed bank size by the flotation method , in this case, was much smaller. The flotation method produced data mostly for hard-seeded species, while the seedling emergence method produced data for species with small seeds and which were readily germinable.

In all seasons, the dune crest habitat always had the smallest seed bank and the riverbed habitat always had the largest seed bank. All the dune habitats were characterised by perennial grasses. Perennial grasses formed transient seed banks which were relatively small. The riverbed habitat's vegetation was mostly composed of annuals. Annual plants formed persistent seed banks which were relatively large. Species richness of the readily germinable seed bank in all habitats, fluctuated between the four seasons and was usually largest in summer. The difference in species richness between the above- and belowground floras fluctuated over four seasons. The dune habitats showed a large difference between the species richness of the above- and the below-ground flora, while the riverbed habitat showed a much smaller difference. The dune habitats had many species with transient seed banks while the riverbed was characterised by many species with short-term persistent and 'permanent' seed banks.

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CHAPTER 1

INTRODUCTION

The southwestern Kalahari is situated in the border-zone of Namibia, Botswana and South Africa. This region is characterised by long, parallel-running sand dunes (van Rooyen, 2001) and is also called the Kalahari duneveld. The vegetation in this area can be described as arid savanna (van Rooyen *et al*., 1984) or Kalahari Thornveld (Leistner, 1967). The plant communities within this vegetation type are grouped according to habitat, namely on sand, calcrete outcrops, pans and riverbeds (Werger, 1978; van Rooyen *et al*., 1984). The Mier area in the southwestern Kalahari has three land-use types namely village use, communal grazing and commercialised stock farming. The primary productivity of the southwestern Kalahari is very low and the area is also prone to degradation. Communal grazing areas are often overgrazed, causing this area to become desertified (van Rooyen, 1998).

Seeds are a crucial and integral part of an arid ecosystem (Kemp, 1989; van Rooyen, 1999). Seeds in the soil can be the most prevalent or only viable forms of desert plants for many years (Pake & Venable, 1996; Guo *et al*., 1999; Cabin & Marshall, 2000; Kinloch & Friedel, 2005). Desert climate governs life-form distributions and productivity of plants, which in turn affects seed production and consequently seed bank size (Pake & Venable, 1996). An understanding of the population dynamics of buried viable seeds is of practical importance in conservation and agriculture (Fenner, 1985; Fenner & Thompson, 2005). The re-eappearance of plant species after disturbance to vegetation often depends on the persistence of seeds in the soil (Bakker *et al*., 1996). The type of seed bank in a plant community will often determine how the plant community will react to disturbance. Thus an understanding of persistent seed banks is the key to many aspects of practical management of agriculuture and conservation (Kinucan & Smeins, 1992).

This study aimed to gain a better understanding of soil seed bank dynamics in five habitats of the Kalahari duneveld. The seedling emergence method and seedling emergence re-examinations were used to determine seed bank size and species composition within each habitat. In addition, comparisons were made between the standing vegetation and seed bank floras in each habitat, and species were grouped into seed bank types according to germination responses in the germination trials.

In addition to studying habitat type as a factor in influencing seed bank dynamics, grazing pressure on duneveld vegetation was also studied as a potential factor governing seed bank dynamics. Gradients of grazing over increasing distances from watering points have been used extensively in rangeland research to investigate the impact of livestock on rangeland vegetation (Smet & Ward, 2006; Solomon *et al*., 2006). Gradients of animal impact known as piospheres tend to develop around artificial watering points, particularly in arid zones (Todd, 2006). In this study a transect was laid out from a watering point along a dune street, to investigate the effect that grazing pressure has on soil seed banks. The seedling emergence method, the re-examination method and the seed extraction/flotation method were used to gain an understanding about seed bank dynamics along a grazing gradient in this arid area. Seed bank size and species richness were compared at distances away from the watering point. In addition, seed bank types that form in response to grazing pressure were investigated.

CHAPTER 2

STUDY AREA

2.1 LOCATION

2.1.1 The southwestern Kalahari

The entire Kalahari region stretches from the Orange River (about 29° S latitude) to deep into the Congo Basin (about 1° N latitude) in Zaire (Werger, 1978). This area covered by Kalahari sands extends over some 2.5 million km² of the interior of central southern Africa (Thomas & Shaw, 1991). These wind-blown sands form the world's largest continuous mantle of sand (Figure 2.1) stretching over nine countries (van der Walt & le Riche, 1999). The area constituting the Kalahari duneveld forms only a small part (Figure 2.5), in the southwestern corner of this vast expanse (van Rooyen, 2001). For the purposes of this study, the study area will be referred to as the southwestern Kalahari.

The southwestern Kalahari, situated in the border-zone of Namibia, Botswana and South Africa, is the southwesternmost part of the Kalahari sand area. It lies at an altitude of about 1000 m, in the lowest part of a very gently sloping inland plateau (Werger, 1978). This region is characterized by long sand dunes running in parallel rows, in a northwest-southeast direction (van Rooyen, 2001). The sands in the southern Kalahari display two reasonably distinct surfaces. In the extreme west and southwest the sands are piled into a belt of dunes 800 km long and 200 km wide, which is known as the southern Kalahari duneveld (or the southwestern Kalahari), while eastwards the dunes are less conspicuous and the country is flat or only slightly undulating (van Rooyen & van Rooyen, 1998).

2.1.2 The Mier area within the southwestern Kalahari

The Mier rural area is situated in the southwestern Kalahari, Northern Cape Province, South Africa. It lies south of the Kgalagadi Transfrontier Park and between the Namibian and Botswana borders, i.e. between 26° and 26° 40'S and between 20° and 20° 40'E. The total Mier area comprises some 420 000 ha, 34 000 ha of which is occupied by villages and communal grazing areas. About 37 000 ha are managed as game ranches while the rest of the 125 fenced ranches are either leased from the Mier Transitional Council (MTC) or individually owned. In 1998, the Mier community numbered between 4 000 and 5 000 people, most of which live in the villages (van Rooyen, 1998).

There are three land-use types in the area namely: village use, communal grazing areas and commercialized stock farming by individuals who lease land. Sheep, goats and cattle are the most important livestock. As the Mier area holds no other natural resources, the community is highly dependent on agriculture. Primary productivity of this area is very low and therefore large areas are required for economically viable stock farming. The individual farms in the Mier area are too small for any production of meat other than subsistence farming while the communal areas are overgrazed and have therefore become desertified (van Rooyen, 1998). This is due to the vulnerability of the Kalahari-Namib region to degradation. As John Acocks (1953) (in Acocks, 1988) wrote before stock farming had expanded into this area: “the sparse tuftedness of the grass and the looseness of the virtually bottomless sand, make this veld extremely vulnerable to grazing pressure, and it is indeed fortunate that the absence of surface water has kept it largely uninhabited”.

2.1.3 Study site: The farm Alpha

Alpha is the name of the farm on which the present study was conducted (Figure 2.3). It was previously used as a cattle ranch but is managed as a nature reserve at present. It is situated on the border between South Africa and Botswana and borders on the Mier area of the southwestern Kalahari duneveld. The Nossob River forms the easternmost border of the farm. The farm is situated 35 km south of Twee Rivieren which is the southernmost entrance to the Kgalagadi Transfrontier Park. The farm covers approximately 3 500 ha and is covered by 18 longitudinal dunes. The dunes lie in a northwest – southeast direction due to the prevailing dominant wind direction (van der Walt, 1996). The co-ordinates of the corners of the farm are: 26º45’01”S, 20º37’34”E (NE); 26º47’15” S, 20º37’17” E (SE); 26º46’07”S, 20º33’17”E (SW); 26º43’28” S, 20º33’17” E (NW).

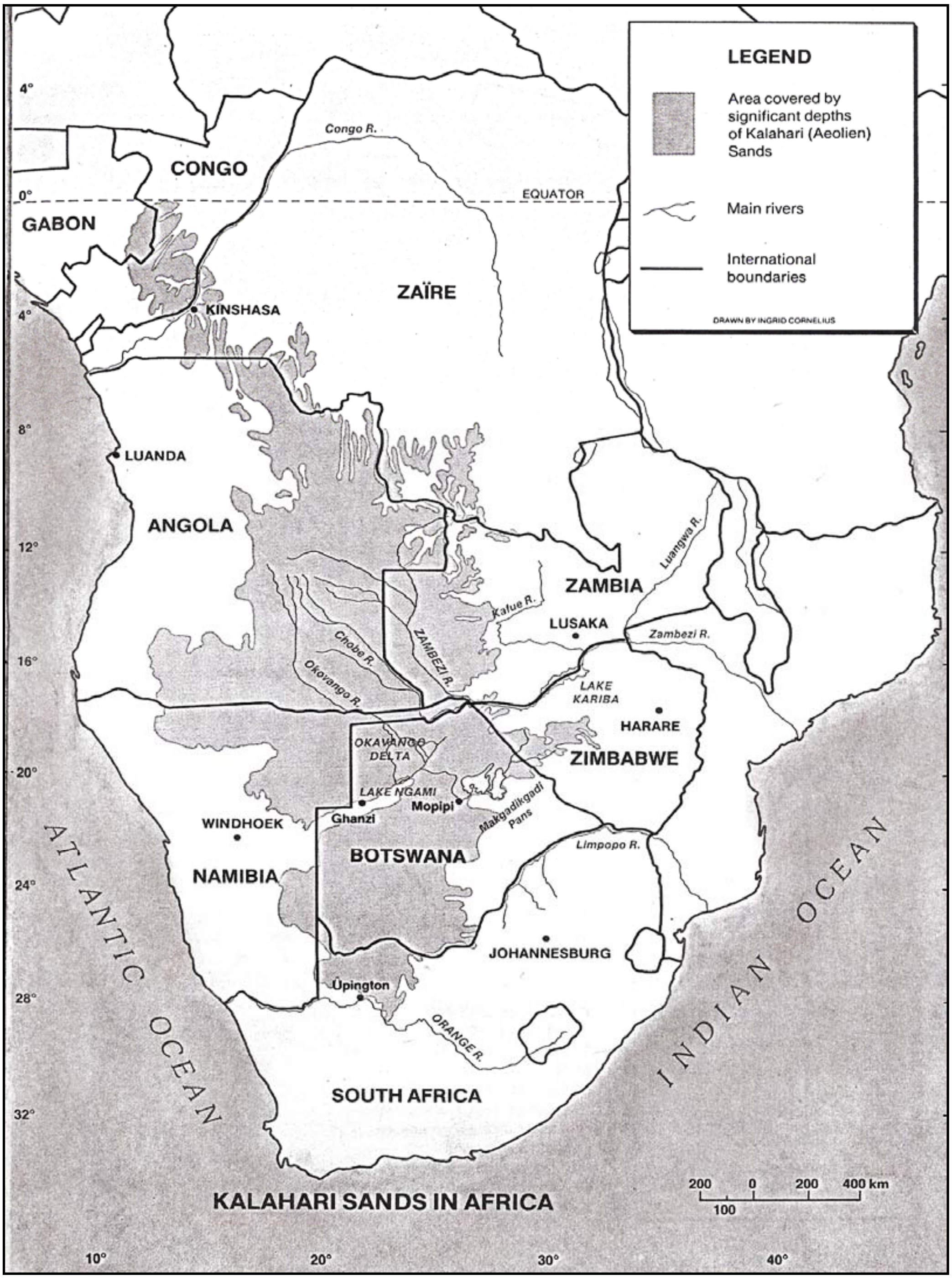


Figure 2.1 Extent of Kalahari sands across Africa (Main, 1987).

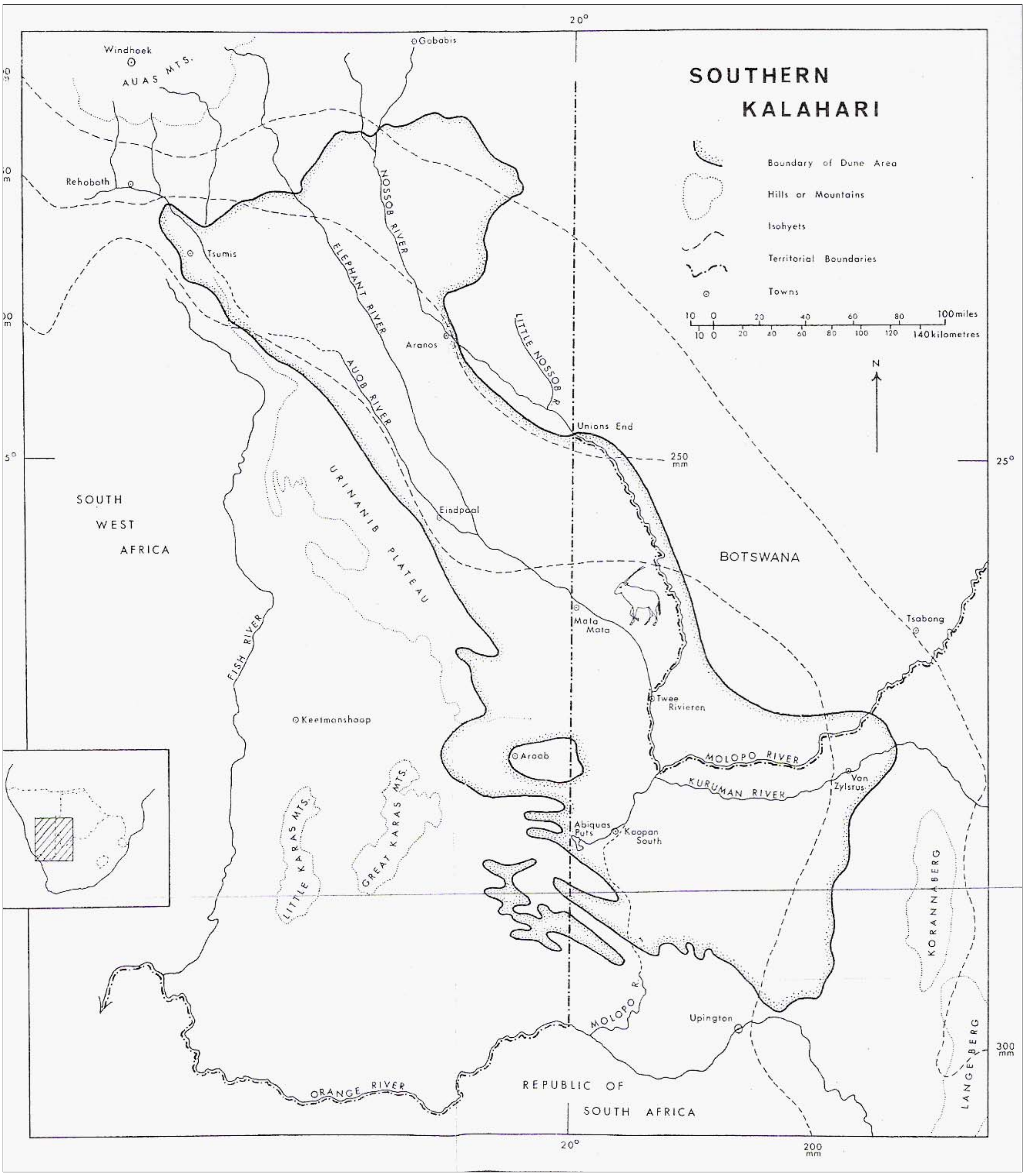


Figure 2.2 Extent of the duneveld region in the southwestern Kalahari (Leistner, 1967).

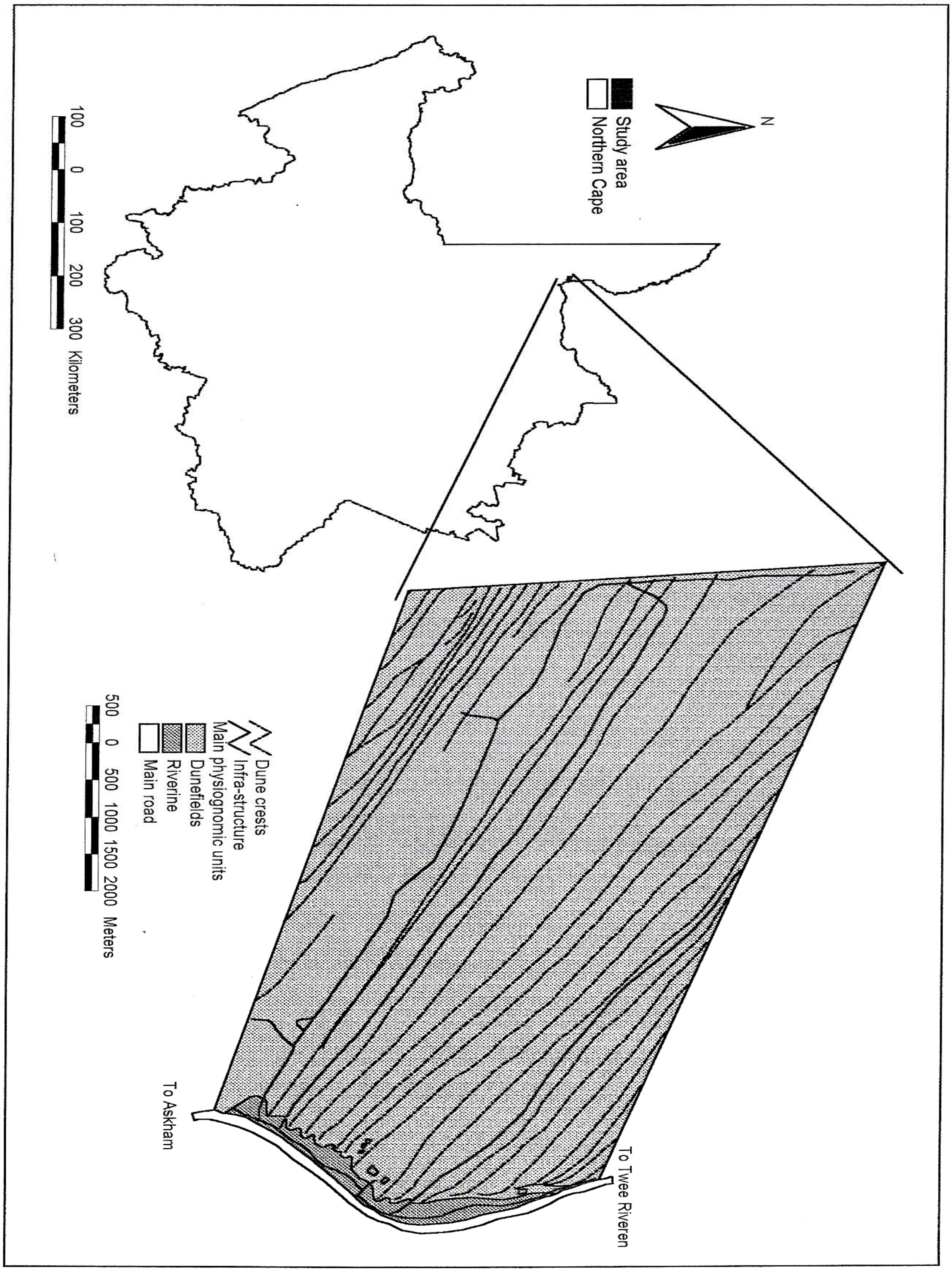


Figure 2.3 Location map of the study site: the farm Alpha in the Northern Cape, South Africa (van der Walt, 1996).

2.2 CLIMATE

The climate of virtually all of southern Africa is dominated by anticyclonic circulation patterns. The result is that the southwestern Kalahari experiences a dry, hot desert climate (Werger, 1986). It is often also referred to as an arid savanna. However, the classification for deserts can overlap with this area as well. The world's deserts can be classified according to mean annual precipitation, into extremely arid (less than 100 mm), arid (from 60 –250 mm) and semi-arid (150 – 500 mm) deserts. According to this classification, the southwestern Kalahari can be classified as an arid or semi-arid desert, as the annual rainfall lies between 150 – 450 mm (van Rooyen & van Rooyen, 1998). The Kalahari is however not a true desert and is quite densely covered with grasses, shrubs and trees (van Rooyen, 2001).

The southwestern Kalahari is the driest part of the entire Kalahari region with mean annual rainfall varying from 150 mm per annum at the southwestern boundary to approximately 300 mm further north. This is due to a rainfall gradient that exists from southwest (Kalahari duneveld) to northeastern Botswana (Palmer & van Rooyen, 1998).

The southwestern Kalahari falls within a summer rainfall area (Figure 2.4) with 80% of the precipitation falling in summer. Rainfall occurs from January to April, with a peak in March (Figure 2.5). Rainfall is highly erratic and at a specific locality can vary from less than 100 mm to up to more than 700 mm per annum (van Rooyen & van Rooyen, 1998) and falls mostly in the form of thunderstorms (van der Walt & le Riche, 1999). The riverbeds are usually dry and flood only episodically after exceptionally high rainfall. No natural permanent surface water is present in the Kalahari region and pans and riverbeds hold water for only short periods after sporadic heavy rainstorms (Knight *et al*., 1988).

Severe weather conditions are characteristic of a desert-like environment (van der Walt & le Riche, 1999). Temperatures in the southwestern Kalahari are extreme with winter lows reaching –10.3°C and summer highs reaching up to 45.5°C (van Rooyen & van Rooyen, 1998). The mean daily maximum temperature of the hottest month (January) is about 34°C and the mean daily minimum of the coldest month (July) is about 1°C (Leistner, 1967). Night frosts are common during the winter season, but they are not severe (Werger, 1978).

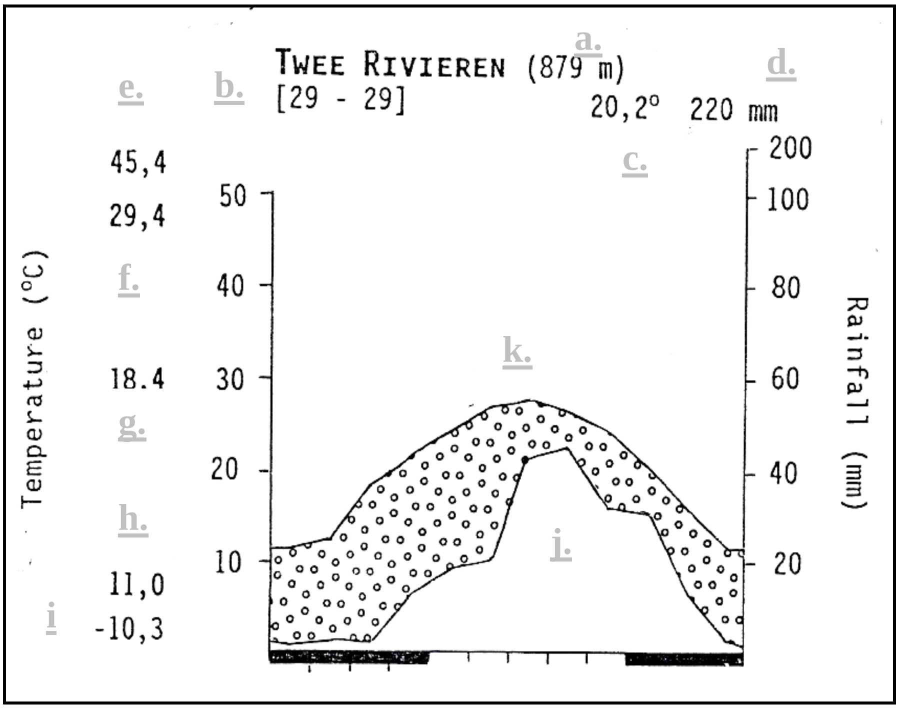


Figure 2.4 A climate diagram of Twee Rivieren, southwestern Kalahari, South Africa. (a=altitude; b=duration of observation in years; c=mean annual temperature; d=mean annual precipitation; e=highest temperature recorded; f=mean daily temperature of the warmest month; g=mean daily temperature variations; h=mean daily temperature of the coldest month; i=lowest temperature recorded; j=mean monthly rainfall; k=mean monthly temperature) (van Rooyen *et al.*, 1990).

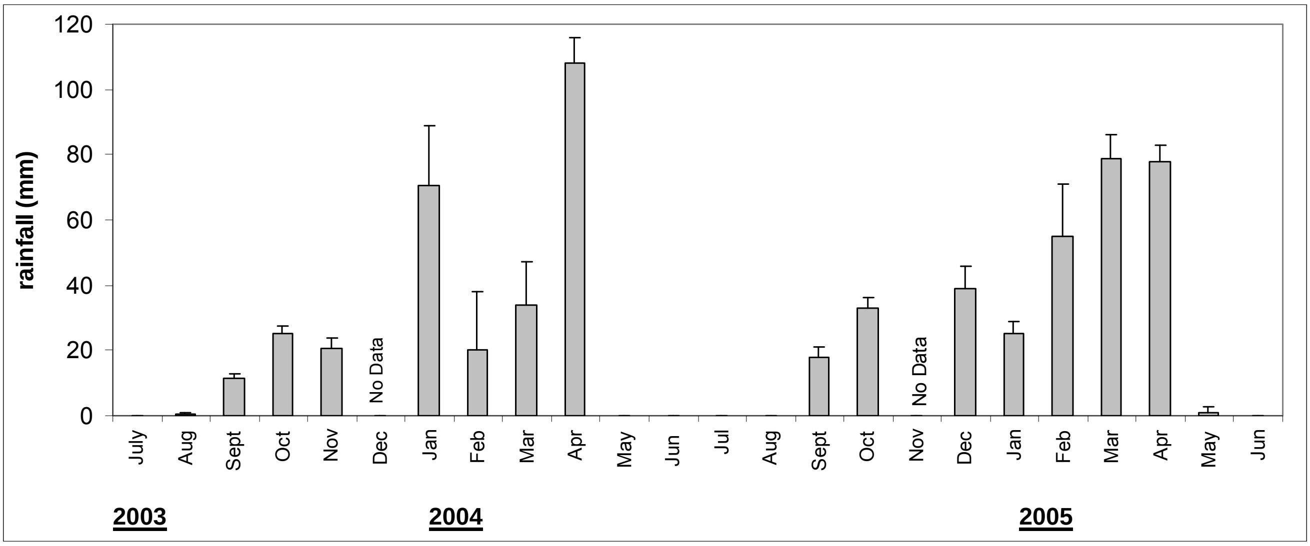


Figure 2.5 Mean monthly rainfall (with SD; n=6) on the farm Alpha in the southwestern Kalahari, over a span of two years (data supplied by Prof Anne Rasa).

2.3 GEOLOGY AND SOILS

Geologically, the area covered by Kalahari sands, extends over some 2.5 million km² of the interior of central southern Africa (Thomas & Shaw, 1991; van Rooyen, 2001) (Figure 2.1). Large deserts are primarily the result of hemispheric wind patterns. In the Pliocene era (2-7 million years ago) a semi-permanent ridge of high pressure in the Atlantic Ocean gave rise to incredibly strong north and northeastern winds. The thick mantle of sand of the Kalahari was formed in this way over a vast post-Karoo basin as sand was transported over great distances and redistributed to this area (van der Walt & le Riche, 1999). The windblown sands of the Kalahari are said to be the largest continuous stretch of sand in the world.

The present dunefield in the southwestern Kalahari (Figure 2.2) is thought to have developed about 19 000 – 16 000 years ago. This area in the southwestern Kalahari includes the vast sheet of aeolian sand of the central, southern and western border of Botswana, together with adjacent areas in Namibia and South Africa (van Rooyen & van Rooyen, 1998). The large area of aeolian sand in the southwestern Kalahari is of presumed Pleistocene age, but variation in the sandy soil types does occur. The aeolian sand covers over 95% of the southwestern Kalahari, and is largely piled into northwest to southeast-running stabilised dunes which are usually about 10 m high and have relatively flat tops often up to 9 m wide (Figure 2.1 and Figure 2.5). The dunes are separated by wide valleys (Werger, 1978). Drifting sand occurs where overgrazing and trampling have been too severe for a long period of time and have destroyed the vegetation. Such destruction is easily produced as the grazing capacity of the veld is very low and the veld is often overstocked (Werger, 1978; van Rooyen, 1998).

Vegetation types within the Kalahari are overridingly controlled by soil types (Leistner, 1967; van Rooyen & van Rooyen, 1998). The southwestern Kalahari is a vast region consisting predominantly of red sand overlying a calcareous sandstone layer. More than 95% of the soils in this area are either red or pink in colour (Werger, 1978). The red sandy soils are notably infertile, being relatively free of soluble salts and low in exchangeable cations, and produce poor quality vegetation (Stapelberg *et al.*, in press). The Kalahari therefore differs from most other arid regions because, in general the soils of arid to semi-arid regions are well supplied with most of the essential plant nutrients, since they suffer little loss of solubilised nutrient compounds through leaching (van Rooyen & van Rooyen, 1998). In those areas where the calcrete stratum is near the surface, the colour becomes more pinkish. Calcrete is often exposed within the pans and dry riverbeds. The resulting sand is white and more fertile, giving rise to vegetation of a better nutritional quality (Knight *et al.,* 1988). The riverbed soils are either silty, rocky or sandy. They are compact and poorly drained and rich in nutrients while pan soils are mostly clays or sandy clays that are also rich in minerals (Werger, 1978).

The colour and fertility of the sand in the Kalahari duneveld is also dependent on the rainfall of an area. The red colour can fade to pink or grey, depending on how much water is available to leach out the iron oxide coating the sand. For example, the white sand found beside rivers and in pans, is due to this process (Werger, 1978; van der Walt & le Riche, 1999).

2.4 VEGETATION

The vegetation of the Kalahari ecosystem is poor as far as species richness is concerned, but contains a variety of growth forms (van der Walt & le Riche, 1999). A feature that greatly affects the vegetation in the Kalahari is the variability and unreliability of the rainfall. Depending on the time of year and the amount of rainfall, different species grow and germinate in the Kalahari. Early summer rains promote growth of perennial grass species and late summer rains benefit the woody plants (Leistner, 1967). Also, during drought periods annuals are very scarce while in very wet seasons numerous species, which are normally rare, occur in great profusion (van Rooyen *et al*., 1984)

According to van Rooyen *et al*. (1984) the vegetation structure in parts of the southern Kalahari can be described as savanna or ‘bushveld’ and occurs on dunes and sandy plains (Figure 2.6). A key feature of all savannas in the world is that they occur in a climate that has a hot, wet season of four- to eight month duration and a warm, dry season for the rest of the year (Scholes, 1997). The savannas in southern Africa can be divided into arid and moist savannas based on differences in water availability, nutrient status of the soil and biological processes of nutrient release (Figure 2.7). Arid savannas, such as found in the southwestern Kalahari, are the spinescent, usually microphyllous wooded grasslands and thickets of base-rich substrates in hot, dry lowland regions with fire being uncommon (Scholes, 1997; van Rooyen & van Rooyen, 1998).

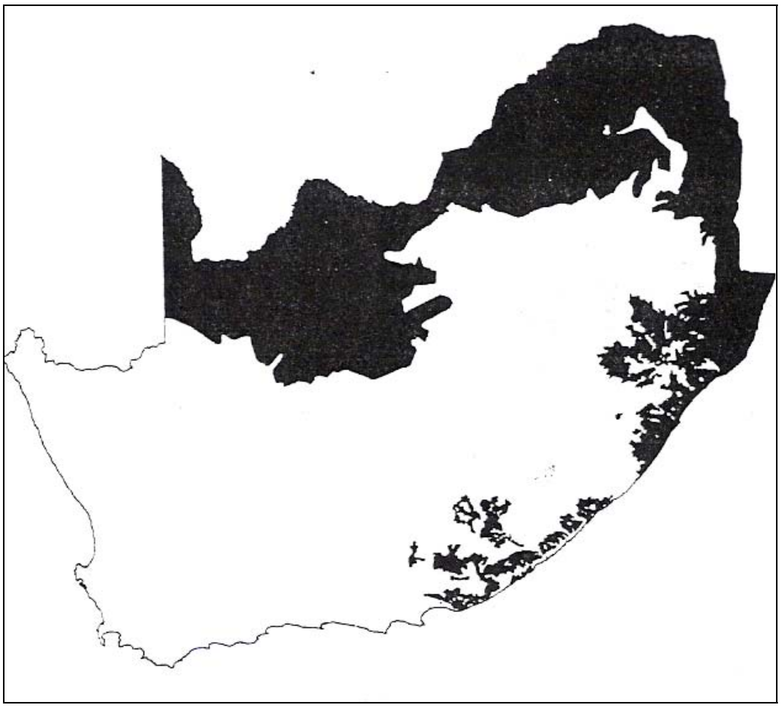


Figure 2.6 Extent of the Savanna Biome in South Africa (Low & Rebelo, 1998).

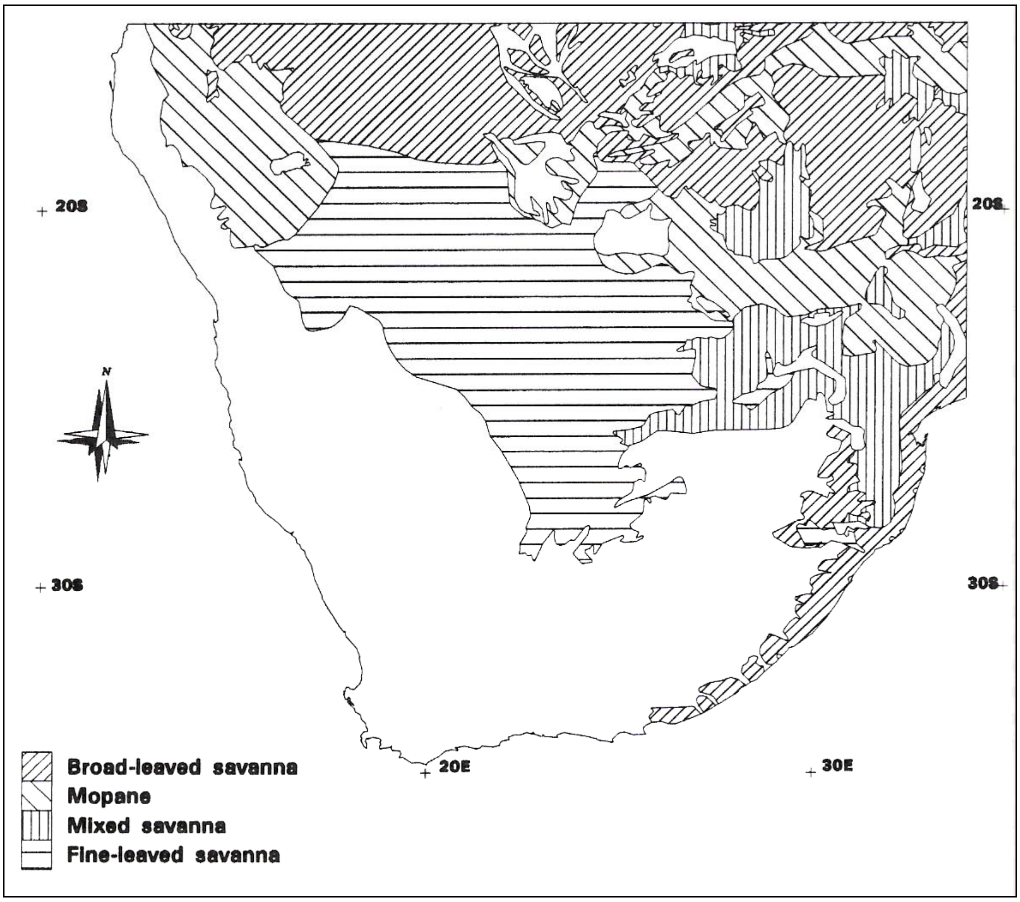


Figure 2.7 Distribution of four broad classes of savanna in southern Africa (Scholes, 1997).

According to Leistner (1967) the Kalahari Thornveld constitutes the southern portion of the arid or fine-leaved savanna on Kalahari sand (Figure 2.7). The different plant communities within this vegetation type are grouped according to habitat, namely on sand, calcrete outcrops, in pans and riverbeds (Werger, 1978; van Rooyen *et al*., 1984). According to Acocks' classification (1988), the Kalahari Thornveld region can be subdivided into two major subdivisions: Kalahari Thornveld proper and Vryburg Shrub Bushveld, each with different forms. The region in which the present study was conducted falls into the western form of the Kalahari Thornveld proper as described by Acocks (1988). According to Low and Rebelo's classification (1998), the Kalahari region in South Africa forms part of the Savanna Biome. More specifically, their classification of the Kalahari region or Kalahari Thornveld is divided into seven different vegetation types. The vegetation type in which the current research was conducted falls within the Thorny Kalahari Dune Bushveld which occurs on deep sand where parallel dunes with dune valleys occur. Further north into the Kgalagadi Transfrontier Park and east into the Gordonia region of South Africa, the vegetation is described as Shrubby Kalahari Dune Bushveld, where the dunes are more gently undulating and less distinct (van Rooyen, 2001). According to the latest vegetation classification of South Africa, the study area falls in the Gordonia Duneveld and the Nossob riverbed forms part of the Southern Kalahari Mekgacha (Mucina & Rutherford, 2006).

2.5 THE EFFECT OF ARTIFICIAL WATER SUPPLY ON THE SOUTHWESTERN KALAHARI ECOSYSTEM

2.5.1 Introduction

The Kalahari ecosystem evolved under conditions of edaphic drought, prior to the introduction of heavy livestock grazing and intense human settlements (Moleele & Mainah, 2003). No natural permanent water is present in the southwestern Kalahari region. The only surface water available to wildlife, before underground sources were tapped, were temporary pools in depressions in the riverbeds and in some pans after sporadic heavy rainstorms (Child *et al*., 1971; Moleele & Mainah, 2003). Agricultural utilization of arid and semi-arid environments in Africa used to be restricted but the supply of artificial watering points was necessitated by the introduction of cattle in the arid Kalahari since the 1930s. From the 1950s onwards the Kalahari was viewed as a large, virtually untapped grazing resource (Perkins, 1996; Verlinden *et al*., 1998). Exploitation of this resource has been made possible by the sinking of boreholes to tap groundwater permitting year-round grazing (Cooke, 1985). Livestock and human populations increased and became sedentarised, consequently pushing the Kalahari ecosystem into resource-use pressure and conflicts (Moleele & Mainah, 2003). The enormous increase of cattle herds has deteriorated the Kalahari sandveld and caused a change in vegetation composition (Martens, 1971; Tolsma *et al*., 1987; van Rooyen, 1998). The veld surrounding the borehole watering points is subjected to more or less continuous use by livestock (Martens, 1971) as opposed to seasonal migratory use. Thus the most notable effect on the vegetation is in the vicinity immediately surrounding the permanent water stations where herbaceous vegetation becomes degraded and bush encroachment occurs (Perkins, 1996; Chanda *et al*., 2003).

2.5.2 Boreholes in conservation areas

Conservation areas in the southern Kalahari are also affected by the drilling of boreholes. The South African part of the Kgalagadi Transfrontier Park (known as the Kalahari Gemsbok National Park) makes up a large section of state owned land which is set aside for the conservation of wildlife. The indigenous Kalahari ungulates are generally able to survive without drinking water because of their behavioural and physiological adaptations. However, due to the restriction of the ranges occupied by Kalahari wildlife, it was considered necessary to supply drinking water within conservation areas (Knight *et al*., 1988). Thus artificial watering points were erected in the Kalahari Gemsbok National Park since the 1930s. Authorities argued that the water sources were needed for the following reasons: to preserve the full spectrum of natural fauna; to sustain migratory herds throughout the relatively long dry season; to bring about more effective utilization of the available grazing; to prevent interference with farming and to utilize the tourist potential of the area (van Rooyen *et al*., 1994). A similar scenario took place at that time on the Botswana side of the border. The Government of Botswana started supplying water to wildlife through a borehole scheme to remedy the massive mortality of migratory populations of wildebeest and hartebeest (Perkins, 1996). These animals had historically moved seasonally between the Kalahari pan system, which has no water during the dry season; and the eastern and northern lakes of Botswana, which have a perennial water supply (Kalikawe, 1990).

CHAPTER 3

LITERATURE BACKGROUND ON SOIL SEED BANKS

3.1 INTRODUCTION

Soil seed banks are pools of viable seeds in the soil and on its surface in which seeds may persist for brief or extended periods of time (Thompson & Grime, 1979; Fenner, 1985; Kinucan & Smeins, 1992; Fenner & Thompson, 2005). After dispersal most seeds undergo a period of dormancy as they are incorporated into the soil and become part of a store or 'bank' of seeds which can be drawn upon to replenish the aboveground vegetation. The seed bank partly reflects the history of the vegetation, and is also likely to contribute to its future (Fenner, 1985). Seed banks are in a state of constant flux: seed rain adds seed to the seed bank, while death, decay, granivory, germination and dispersal remove seed from the seed bank. This constant flux may give an impression of randomness but subtle changes in subsequent seed bank structure influence the emergent plant community (Fenner, 1985; Lortie & Turkington, 2002). A complete description of a plant community should include the buried viable seeds, because they are as much part of the species composition as the above ground components (Major & Pyott, 1966).

3.2 SEED BANKS IN ARID REGIONS

Seeds are a crucial and integral part of arid ecosystems (Kemp, 1989; van Rooyen, 1999). Soil seeds can be the most prevalent or only viable form of many desert plants for several years (Pake & Venable, 1996; Guo *et al*., 1999; Cabin & Marshall, 2000; Kinloch & Friedel, 2005). Plant communities of arid and semi-arid regions have seed banks that are large and species rich, despite the sparse and usually patchy structure of the aboveground biomass and cover of these ecosystems (Caballero *et al.*, 2003). Seeds in desert soils are distributed mostly near the surface, and it is these seeds that form the seed bank. From 80-90% of soil seeds are in the upper 2 cm of soil, and most of those seeds are found in the litter (Guo *et al*., 1998). The seeds of many desert annuals cannot germinate or emerge from below about 10 mm and seeds of desert shrubs cannot emerge from below 40 mm soil depth (Kemp, 1989).

The desert climate governs life-form distributions and productivity, which in turn affects seed production and consequently seed bank size. Water availability is considered the main driving force for germination, growth and productivity of herbaceous plants and shrubs in arid ecosystems, but it is highly variable in time and space (Pake & Venable, 1996; Gutierrez *et al*., 2000). Thus desert seed banks are characterized by high temporal and spatial variability in seed density (Kemp, 1989; van Rooyen, 1999; Gutierrez *et al*., 2000; Lopez, 2003; Caballero *et al*., 2005). Annuals may comprise up to 40% of the desert flora, and during a drought seeds may be the only form of annuals for several years (Kemp, 1989; Lopez, 2003). Annuals have species specific requirements with regard to the water threshold required to germinate. This strategy prevents emergence in response to a rain pulse which provides insufficient moisture to complete the plant's life cycle (Freas & Kemp, 1983; Pake & Venable, 1996; Gutierrez *et al*., 2000). In many arid regions worldwide, drought years are followed by one or two years of above-average precipitation (van der Walt & le Riche, 1999; Guiterrez *et al*., 2000). In their study in North-central Chile, Gutierrez *et al*. (2000) found that soil seed densities and number of species recorded were markedly higher in the year following above-average rainfall year compared to the preceding drought year. They even found that some species that were absent or rare during the drought year, dominated in the following wet year. Thus annuals that respond strongly to infrequent rainfall apparently buffer the absence of sufficient water by having high productivity in favourable years thus assuring a large seed output. Their study suggests that species responding to the large infrequent bouts of rainfall, leave large seed reserves in this favorable 'window' to allow the seeds to persist in the system. Temporal changes of seed bank density in arid and semi-arid areas differ not only between years, but also between seasons (Freas & Kemp, 1983; Coffin & Lauenroth, 1989; De Villiers *et al*., 2002).

In deserts, seed banks tend to be spatially more patchy than surface plant distributions. Highly clumped distribution of seeds in soil are common for desert seed banks (Reichman, 1984; Henderson *et al*., 1988; Kemp, 1989; Pake & Venable, 1996; Gutierrez *et al*., 2000; Cabin & Marshall, 2000; Lortie & Turkington, 2002; Lopez, 2003). In North American deserts, the adult populations of annual species often display a clumped distribution related to shrub distribution or edaphic factors (Kemp, 1989). Seed distribution can also appear as clumped due to lack of specialised dispersal mechanisms. Desert seed banks are usually composed of very small seeds that lack dispersal structures (Fenner, 1985; Lopez, 2003). However, in general, dispersal is over relatively short distances (Van Rheede *et al*., 1999). In deserts, wind, sheet flooding, seed-eating animals, and soil surface microtopography are major factors affecting seed dispersal and distribution (Guo *et al*., 1998). The seeds that are distributed by wind or water, tend to accumulate in depressions or the wind shadows of obstructions. Seeds dispersed by granivores are likely to be clumped in unrecovered caches. However, after dispersal the seed distribution is dependent on other factors such as predation, germination, local decay and seed movement in the soil (Guo *et al*., 1998).

3.3 THE IMPORTANCE OF SEED BANKS IN RESTORATION AND CONSERVATION

3.3.1 Introduction

There is hardly a single area of modern plant ecology in which seed banks are not implicated, many of them with direct relevance to restoration ecology (e.g. recolonization after fire or volcanic eruption, prediction of marsh vegetation after drainage, succession, vegetation conservation and invasion by alien species) (Bakker *et al*., 1996). An understanding of the population dynamics of buried viable seeds is of some practical importance to agriculture, forestry and conservation (Fenner, 1985; Fenner & Thompson, 2005). If the species composition of the seed bank of an arable land is determined, a knowledge of the long-term viability of the species involved is clearly of value in providing a basis for control techniques (Fenner, 1985). The re-appearance of plant species after disturbance to vegetation often depends on the persistence of seeds in the soil forming a ‘memory’ of the original plant community (Bakker *et al*., 1996). A seed bank can be described as a ‘seed reservoir’ which has the function of replacing adult plants which are removed due to natural or unnatural death (Bakker, 1989). Seed banks enable plant populations to maintain their genetic variability, withstand adverse periods and persist through time (Caballero *et al*., 2003). Thus the seed bank is an indicator of the history of the vegetation in an area, but also a contributor to its future community structure and dynamics (Fenner, 1985; Guo *et al*., 1999). Shaukat & Siddiqui (2004) state that: ‘an understanding of the population dynamics of buried viable seeds is of considerable practical significance. The determination of the composition of the seed bank and spatial pattern of seeds in the light of the knowledge of the long-term viability of the species involved is clearly of great value in providing a basis for management and control strategy.’

3.3.2. The effects of grazing on soil seed banks

According to Chang *et al.* (2001) regeneration strategies of plants are shaped by patterns of disturbance and stress. These act as selective forces over evolutionary time. Seeds frequently persist in the soil as they are more tolerant of adverse conditions than their adult counterparts and once buried in soil, they may escape from agents of disturbance and predation (such as grazing by large herbivores). The presence of seeds in disturbed habitats is determined by the relationship between the original plant assemblages, the amount of propagule production and the capacity to build up seed reserves in the soil (Kinucan & Smeins, 1992; Chang *et al*., 2001). All these factors will be affected by disturbance and the seed bank will decline as a function of the time that has lapsed since the vegetation was destroyed (Chang *et al*. 2001). Grazing by large herbivores has been shown to alter composition and density of the seed bank by altering species composition and abundance relationships of the plant community, and subsequent seed output of each community component (Kinucan & Smeins, 1992; O'Connor & Pickett, 1992; Mayor *et al*., 2003; Kinloch & Friedel, 2005). Thus herbivory can modify successional processes over long-term grazing regimes.

The type of seed bank will often determine how a plant community will react to disturbance. The proportion of persistent and transient seeds within a seed bank can have important implications for the reaction to disturbance (Kinucan & Smeins, 1992). O'Connor & Pickett (1992) studied the influence of grazing on an African savanna grassland. They found that variation in species composition of a grassland reflects grazing history. They also found that seeds of perennial species germinate readily and have limited survival when in secondary dormancy. Consequently seed banks of perennial grasse species were poorly represented or absent on heavily grazed sites (Bertiller, 1992; O'Connor & Pickett, 1992; Mayor *et al*., 2003). In an Argentinian rangeland, Mayor *et al*. (2003) found that grazed sites usually show an increase in seeds of forbs and annual species and a decrease in seeds of perennial grasses as compared to ungrazed sites. They also found that the seed banks of perennial grasses which usually produce small numbers of seeds, can easily be eliminated by sustained grazing. Bertiller (1992) made similar conclusions for her study in a semiarid Patagonian grassland. Perennial grasses are extremely dependent on seed production and seed rain for the yearly replenishment of the soil seed bank (Bertiller, 1992; Peco *et al*., 1998). Annual grass species that are obligate seed reproducers are least vulnerable to grazing as sufficient seed will always be incorporated into the seed bank (Bertiller, 1992; O'Connor & Pickett, 1992) and they thus have a competitive advantage over perennial grasse species (Navie & Rogers, 1997). If perennial forage grass seed numbers are lowered in the seed bank due to the action of grazing this can imply a slow recovery of the rangeland from overgrazing (Mayor *et al*., 2003). The capacity to form persistent seed banks allows species to survive episodes of disturbance and destruction

(Cabin & Marshall, 2000). Thus an understanding of persistent seed banks is the key to many aspects of practical management of agriculture and conservation (Jalili *et al*., 2003).

3.3.3. Differences between the seed bank and aboveground floras

The growing literature on seed bank studies reflects an increased awareness of and interest in the role that seed banks play in influencing the colonization and structure of plant communities (Cabin & Marshall, 2000). Despite the growing awareness of the ecological and evolutionary importance of seed banks, in most ecosystems all that is known about them is their density, as measured at a single point in time in space. These 'snapshot' studies, argue Cabin and Marshall (2000), may give a distorted view of real soil seed distributions, as most seed banks are patchy in space and time. Thus while a static picture of the size of seed banks is starting to develop, the ecological dynamics of the relationship between soil seeds and surface plants remain poorly studied and understood. It is important to understand the dynamic relationship between vegetation and seed bank because in many habitats seed banks are of interest to scientists due to the potential of a seed bank to alter vegetation composition and productivity (Peco *et al*. 1998; Cabin & Marshall, 2000).

Some studies, which focus on the relationship between soil seed banks and vegetation, have been done in coastal marshes (Egan & Ungar, 2000; Chang *et al.,* 2001; Jutila, 2003). Such studies are scientifically interesting in that they not only look at habitat degradation and its impact on the resident flora but also include the facet of soil salinity and the effect it has on species composition within the seed bank and the aboveground vegetation. However, most other studies done to assess differences between soil seed bank and aboveground vegetation are done to see what impact management regimes alone have on plant communities (Milberg & Hansson, 1993; Bertiller, 1996; Peco *et al*., 1998; Lopez-Marino *et al*., 2000; Carter & Ungar, 2002; Touzard *et al*., 2002; Amiaud & Touzard, 2004; Kinloch & Friedel, 2005).

Differences between the floristic composition of a plant community and its soil seed bank are often due to the germination biology differing among species. Milberg and Hansson (1993) hypothesized that species with a high turnover would be relatively more frequent in the seed bank than species with a more constant occurrence in the vegetation. Since annuals depend on frequent regeneration from seed, they expected annuals to be more frequent in the seed bank than in the vegetation. They did indeed find that annuals (therophytes) were over-represented in the persistent seed bank. They suggest that short-lived species, which depend on seed regeneration, accumulate in persistent seed banks. The absence from the seed bank of several species which dominate the vegetation has been reported for many grasslands. Milberg and Hansson (1993), suggest that it is possible that the germination biology of these species prevents accumulation in the seed bank.

Similarities or differences between seed bank and established vegetation give a good estimate of the type of seed bank present and gives a clue as to the management history of a piece of land and also the life-history strategies of plants occupying a particular piece of land (Lopez & Marino *et al*., 2000). In frequently disturbed habitats the species composition of the seed bank and the vegetation is usually similar, but as the vegetation matures the disparity between the two increases (Fenner, 1985). The divergence of species composition of surface vegetation and buried seeds has often been noted in older aged stands of successional sites. The presence of these species as seeds in the soil is important to the recovery of vegetation following disturbance (Roach, 1993)

3.4 SEED BANK CLASSIFICATION

According to Csontos and Tamas (2003), a comparative understanding of different seed bank classification systems can facilitate choosing an appropriate system for specific research objectives. Charles Darwin seems to have been the first person to make scientific observations of seed banks in 1859 (Bakker *et al*., 1996). Since 1969, ten soil seed bank classification systems have been published (Csontos & Tamas, 2003). The following section is based on a review article by Csontos and Tamas (2003) on published work on soil seed bank classification.

The earliest soil seed bank classification system, was proposed by Schafer and Chilcote (1969). They divided all the seeds in the soil into four general categories namely:

1) seeds that are dormant due to exogenic (environmental) causes;
2) seeds that are dormant due to endogenic causes (innate dormancy);
3) seeds capable of germinating under current conditions; and
4) the non-viable seeds in the soil.

The first soil seed bank classification with an ecological approach, was proposed by Thompson and Grime (1979). These authors defined four soil seed bank types. Their system is hierarchical where the two main groups of classification are created by separating transient and persistent seed types. They consider a soil seed bank to be transient when the dispersed seeds remain viable for less than a year. In the persistent soil seed bank, a portion of the seeds remain dormant in the soil for more than a year. Till recently, this system has been the most commonly used reference in seed bank studies (Bakker *et al*., 1996).

Grime and Hillier (1981) and Grime (1981) tried to refine Thompson and Grime's (1979) system. They developed a key, based on laboratory characteristics of seeds, to predict seed bank types. However, their key was compiled for the northwest European region, and modifications may be necessary for its successful use in other regions, especially as more than four seed bank strategies have already been reported for soil seed banks of other regions (De Villiers *et al*., 2002). Japanese ecologists (Nakagoshi, 1985) have also modified the Thompson and Grime (1979) system in the past few decades by combining it with three main life-form categories (herbaceous plants, shrubs and trees). This resulted in twelve seed bank categories.

Grubb (1988) differentiated three types of seed bank according to environmental effects (disturbance) and the characteristics of the related soil seed bank activation (recruitment). The strength of this classification is that the role of seed banks in the life of populations is closely connected with the reaction to disturbance. Grubb's three seed bank types based on reaction to disturbance are as follows:

1) Pioneer species or the 'disturbance broken' soil seed bank type, reacts to disturbances quickly and almost completely.
2) Species with the 'risk spreading' seed bank type retain a certain percentage of their soil seed bank even under favourable conditions because of the innate dormancy of the seeds.
3) The seeds of the 'weather-dependent' seed bank type, await a special signal from the environment.

Garwood (1989) proposed a classification of five categories, based on research done in equatorial rainforests. However, this classification system is not intended to be universal and is a modification of Thompson and Grime's (1979) system which is based on site-specific research (Csontos & Tamas, 2003).

Bakker (1989) revised Thompson and Grime's (1979) system by subdividing the persistent seed bank into two groups. Bakker (1989) found that some seeds are present in the top layer of soil in larger amounts than in deeper layers, while seeds of other species are more abundant in the deeper layers of soil compared to the top layer. He tried to revise the system because he realized that the population dynamics of these two groups are different and that their importance in rehabilitation ecology is not the same.

A three-category system was published by Thompson in 1993:

1) Transient seed banks contain seeds that are viable for a maximum of 1 year
2) Short-term persistent seed banks contain seeds with a viability longer than 1 year but less than 5 years
3) Long-term persistent seed banks contain seeds with a viability of at least three years.

This classification system was modified by Poschlod (1993) for habitat conservation purposes, for possible use in retoration ecology and for possible application to 'red data' species. This modified version consists of five categories based on seed persistence in the soil. This system is based on seed bank dynamics of calcareous grassland plants.

A further four-category system with subcategories was proposed by Poschlod and Jaeckel (1993). This classification highlights the dynamics of the seed bank and seed rain i.e. the survival period of the seeds (Bakker *et al*., 1996; De Villiers *et al*., 2002; Csontos & Tamas, 2003). This classification system is summarised in Bakker *et al*. (1996).

i) Transient seed bank with seeds that are confined to the upper soil layer and are only present for a short period after the seed rain (persistent for <1 year).
ii) Transient seedbank with seeds present in the upper soil layer all year round but with a peak after the seed rain. Some seeds are found in the lower soil layer which persist for 1-2 years.
iii) Persistent seed bank with many seeds are in the soil surface with some in the lower layer all year round. The upper layer has a distinct peak after the seed rain while the lower layer has a small peak after the seed rain. Seeds persist for some years to some decades.

iv) Persistent seed bank with at least as many seeds in the lower layer as in the upper soil layer all year round and no distinct peak after the seed rain. Seeds persist for several decades.

This classification combines seasonal behaviour and depth distribution which makes it more refined than other classifications. The drawback with this classification is the amount and type of data needed for each species in order to use the classification. This key requires the knowledge of when a species was last present at a study site and often such data are not available (De Villiers *et al*., 2002).

CHAPTER 4

MATERIALS AND METHODS

4.1 SAMPLING TECHNIQUES

4.1.1 Habitats

Sampling was conducted on the farm Alpha, in the southwestern Kalahari, South Africa. Five habitat types that are represented within the Kalahari duneveld were selected for this study. The habitat types included dune crests (Figure 4.1), dune slopes (Figure 4.2), dune streets (Figure 4.3), a calcrete outcrop (Figure 4.4) and a riverbed (Figure 4.5). Another habitat type, the salt pan, also occurs within the duneveld area of the southwestern Kalahari but this habitat type is not represented on the farm Alpha.

Four sites were randomly selected in each habitat type to sample the floristic composition and seed bank composition for that habitat. Each sampling plot was laid out as a 10 m by 20 m sample plot. During each season (namely spring, summer, autumn and winter), a Braun-Blanquet vegetation survey (Werger, 1974) was done in each sampling plot in each habitat to determine the floristic composition of that habitat. Simultaneously, soil samples were taken in each of the four sites used to represent each habitat type. Fifteen soil samples were taken randomly within each sampling plot. This resulted in a total of 60 soil samples for each habitat type per season.

Each soil sample was composed of two soil cores that were put into a common soil bag. Each soil core was taken with a soil auger with a diameter of 60 mm, and to a depth of 50 mm. The depth of 50 mm was chosen as previous studies suggest that desert soil seed banks are shallow and rarely occur below the top 50 mm of the soil in general. (Reichman, 1984; Guo *et al*., 1998; Pake & Venable, 1996; Lortie & Turkington, 2002).

4.1.2 Transect

A transect was laid out from a watering point in a northwesterly direction along a dune street (Figure 4.6). This was done to determine the impact of grazing on the vegetation composition as a function of distance from a watering point (Child *et al*., 1971; van Rooyen *et al*., 1990; Navie *et al*., 1996; Moleele & Perkins, 1998). The transect was divided into six major partitions in relation to distance from the watering point. A GPS was used to determine the direction of sampling while a measuring tape of 30 m was used to measure out the length of each partition. The major partitions were marked out for the duration of the study by hammering metal rods into the sand. In each major partition, twenty four, 25 m² (5m x 5m) sampling plots were placed out.

Within each 25 m² plot, a Braun-Blanquet vegetation survey (Werger, 1974) was done in each season to determine the floristic composition of the aboveground vegetation. Simultaneously, four random soil samples were taken to a depth of 50 mm with a soil auger of 60 mm diameter within each 25 m² plot. The four random samples from each plot were placed into a common soil bag to form one soil sample. Studies suggest that a large number of smaller soil samples give a better estimate of the soil seed bank than a single large sample of the same volume (Bigwood & Inouye, 1988).

The first partition of the transect included a 30 m circumference around the watering point. The individual sample plots along the length of the tape were marked out at 5 m intervals. Within the 30 m circumference, the transect was divided into four sections pointing northwest, northeast, southwest and southeast. Thus each 30 m section was divided into six consecutive sampling plots of 25 m² each. The next section of the transect was divided into two sections which ran in a northwest and southeast direction in the centre of the dune street from >30 – 90 m from the watering point. Each section was 60 m in length and was divided into 12 consecutive 25 m² sample plots.

The rest of the transect was sampled in the northwesterly direction only, along the dune street away from the watering point. In the third section from >90 – 210 m, the 24 sampling plots were placed consecutively to form a transect section which was 120 m in length. The fourth section of the transect from >210 – 450 m, had its 24 sampling plots spread over a length of 240 m, with each sampling plot placed at 5 m intervals. The fifth section of the transect from >450 – 810 m, was laid out over 360 m, with the sampling plots placed at 10 m intervals. The last section of the transect from > 810 – 1530 m, ran over a length of 720 m, with plots spaced at 25 m intervals.

4.2 THE USE OF THE SEEDLING EMERGENCE AND THE SEED EXTRACTION METHOD IN THE STUDY

All soil samples collected during the study were analysed using the seedling emergence method. To get a good estimate of seed bank size and composition, various authors have used different methods in their studies (Gross, 1990; Manders, 1990; Brown, 1992; De Villiers *et al*., 1994; Barberi *et al*., 1998). Soil samples that were collected along the transect during spring, were also analysed using the seed extraction method (Janse van Rensburg, 1992) in order to make a comparison with the seedling emergence results for spring. Physical extraction of seed from the soil overestimates the seed bank as many unviable seeds are counted. Emergence of seedlings will underestimate the seed bank as only the readily germinable seeds are counted while dormant seeds go unnoticed (Brown, 1992). Seed extraction methods are very effective in finding large seeded species, but these methods are very time-consuming and ineffective for finding small-seeded species, especially in large-scale studies (ter Heerdt *et al*., 1996) and desert seed banks are usually made up mostly of small seeds (Leck *et al.,* 1989). Thus the seedling emergence method was mainly used in this study as the Kalahari vegetation is expected to have a desert-type seed bank.

4.2.1 Flotation

The flotation method used in this study was a modification of Janse van Rensburg (1982) to meet the needs of the present study. Instead of using a glass column, conical flasks were used. A glass column could not be used for this study as the fine Kalahari sand made a dense cake which remained stuck and could not be poured out. Soil samples that were collected along the transect during the month of October (spring) 2004, were analysed to count the number of seeds present in the soil sample. A 100 ml sample of each soil sample was used. A saturated solution of potassium carbonate was poured into a medium sized conical flask (330 ml) until it was 2/3 full. The soil was added to the liquid and stirred with a glass rod. The mixture was not swivelled, only stirred to ensure that the organic matter was not re-trapped under the dense layer of fine Kalahari sand which settled at the bottom of the flask. The solution was left to stand for fifteen minutes allowing the sand to settle at the bottom of the flask and all the organic matter to rise to the top of the flask. The conical flask was tilted over an extremely fine sieve (53 micrometer) and carefully rotated while pouring to ensure that all the organic matter was poured into the sieve while the sand remained in the bottom of the flask. The organic matter in the sieve was rinsed with water from a rubber tube attached to a tap. A weak stream of water from the rubber tube was used to wash the organic matter into a corner of the sieve from where it was rinsed out of the sieve into a Buechner filter lined with Whatman no.1 filter paper. Once the excess water had been removed, the filter paper was taken out and placed into a Petri dish and left to dry at room temperature.

A stereomicroscope was used to analyse the organic matter removed from each soil sample. The number of seeds for each species that could be identified, were counted. If a seed could not be identified to species level, it was counted and added to a genus or life-form category.

4.2.2 Seedling emergence

In seedling emergence methods, the soil samples are usually spread in trays in a greenhouse and kept under those conditions known to promote the germination of as many species and individuals as possible (Manders, 1990; Bakker *et al*., 1996; ter Heerdt *et al*., 1996; Kellerman, 2004). The seedling emergence analyses were carried out at the University of Pretoria. For the analysis, 100 ml soil from each sample was spread out onto a pot filled with fine quartz sand within two weeks after collecting the soil. The remaining soil was stored at room temperature until further use. The results of these trials, conducted directly after collection, will be referred to as the readily germinable seed bank or direct seedling emergence method. In the present study, pots were placed outside in full sunlight. The soil was watered once a day with tap water. During times of rain the soil samples in the pots were not watered.

Hoagland’s complete nutrient solution was used approximately once a week to provide the seedlings with essential nutrients (Machilis & Torrey, 1956). Pots were checked once a day and a record was kept of germinated seeds using toothpicks to mark each space where a seedling appeared. Once a seedling could be identified, a record was made and it was removed to prevent competitive effects as well as re-seeding. A record was also kept of the number of seedlings that died before they could be identified.

One third of the number of soil samples that were collected in autumn, winter and spring (i.e. not collected during the optimum growth season in the Kalahari), were examined again in January 2005. One hundred ml from each soil sample of these collections were placed out again to germinate in summer (January) 2005. Each 100 ml was placed into a pot filled with fine quartz sand and watered and supplemented with Hoagland's complete nutrient solution in the same way as the initial investigation was done. Once again, a record was kept of the number of seedlings and the species that germinated. Herbarium specimens were made of plants which had to be identified in the herbarium. These specimens are kept in the H.G.W.J. Schweickerdt Herbarium of the University of Pretoria (PRU).

4.3 STATISTICS AND DATA ANALYSIS

The STATISTICA program (Version 8, StaSoft Inc., Tulsa, OK) was used to do an analysis of variance (one-way ANOVA) to compare the direct and the re-examination seedling emergence results from the habitats. The direct seedling emergence, re-examination and flotation methods were compared with data from the transect. Also seed bank size between the transect sections was compared using the post-hoc Fischer tests with $p \leq 0.05$.

Data collected using the Braun-Blanquet method of vegetation analysis, were captured with the TURBOVEG software and the classification of the data was done with the aid of MEGATAB (Hennekens & Schaminée 2001). A Canonical Correspondence Analysis (CCA) was done with the program CANOCO (Version 4.5, Microcomputer Power, Ithaca, New York) to create ordinations for the direct germination data of each habitat, to compare the germinability of species over four seasons, for each habitat.

Figure 4.1 A dune crest habitat on the farm Alpha in the southwestern Kalahari (Photo: A. Johannsmeier 2004)

Figure 4.2 A dune slope habitat on the farm Alpha in the southwestern Kalahari (Photo: Anne Johannsmeier 2004)

Figure 4.3 A dune street habitat on the farm Alpha in the southwestern Kalahari (Photo: Anne Johannsmeier 2004)

Figure 4.4 A calcrete outcrop habitat on the farm Alpha in the southwestern Kalahari (Photo: Anne Johannsmeier 2004)

Figure 4.5 A riverbed habitat on the farm Alpha in the southwestern Kalahari (Photo: Conrad Geldenhuys 2004)

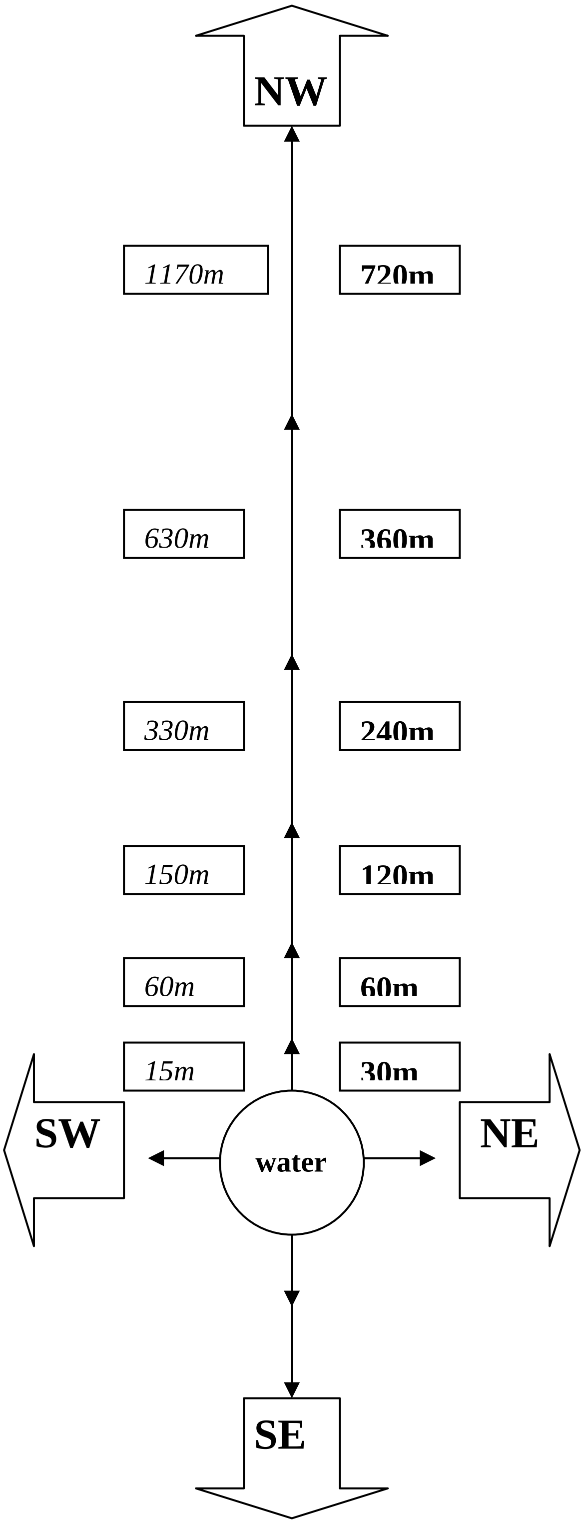


Figure 4.6 Diagrammatic representation (not to scale) of the layout of the transect along a dune street from the watering point. Each subdivision (boxes with bold type represent the length of each section) around the circumference of the watering point has twenty-four sample plots. The midpoint within each subdivision/section is indicated on the left (boxes with italics).

CHAPTER 5

PIOSPHERE EFFECTS ON A KALAHARI SOIL SEED BANK

5.1 INTRODUCTION

Provision of artificial watering points through sinking of boreholes in arid areas, is often used to increase year-round grazing by livestock and wildlife. Gradients of animal impact known as piospheres tend to develop around artificial watering points, particularly in arid zones (Todd, 2006). Watering points promote heavy concentrations of livestock and wildlife causing heavy trampling and overgrazing (Nangula & Oba, 2004). Such disturbances can result in lower production and turnover of seeds (Solomon *et al*., 2006). Furthermore, cattle grazing in the southwestern Kalahari and other arid and semi-arid savannas, is known to lead to bush encroachment (Jeltsch *et al*., 1997). Gradients of grazing over increasing distances from watering points have been used extensively in rangeland research to investigate the impact of livestock on rangeland vegetation (Smet & Ward, 2006; Solomon *et al*., 2006). Grazing gradients represent a potential opportunity for differentiating the long-term effects of livestock activity from other environmental patterns (Todd, 2006).

In this chapter the effects of the grazing gradient around artificial watering points on the seed bank are investigated in three different ways. In Section 5.2, three techniques which can be used to estimate seed bank size and composition, are compared. The benefits of each technique are explored, in context of a degradation gradient. Two out of the three techniques were applied to seed bank samples once in each season, to explore effects of seasonal changes on the composition and size of the readily germinable seed bank along a degradation gradient. In Section 5.3, the differences between the aboveground and seed bank (belowground) floras are studied along a degradation gradient. Seasonal changes in species richness of the aboveground vegetation and belowground flora are compared and discussed. In Section 5.4, species are grouped into seed bank classes or SBFTs (seed bank functional types; after Bertiller & Aloia, 1997), depending on their germination behaviour across four seasons, as well as their life history and growth-form characteristics.

5.2 COMPARISON OF THE SEEDLING EMERGENCE (WITH A RE-EXAMINATION) AND FLOTATION TECHNIQUES

5.2.1 Introduction

Extracting seeds from the soil is time-consuming and results are influenced by the time of year, methods used to take soil samples, as well as methods used to determine seed numbers (Bigwood & Inouye, 1988). Several studies have noted that sampling time and testing method can influence the species that emerge from the samples (Gross, 1990). Comparative studies of seed banks in various communities have been limited by the difficulty of accurately determining the numbers of seeds and species present (Gross, 1990). Therefore, in recent years, researchers have often relied on two methods to determine seed numbers, to get a more accurate estimate of seed bank size for a specific area (Manders, 1990; Brown, 1992; De Villiers *et al*., 1994; Barberi *et al*., 1998; Kellerman & Van Rooyen, 2007). One method, referred to here as the seedling emergence method, estimates the size of the viable seed bank by placing soil samples under conditions suitable for seed germination. This method underestimates the seed bank as it only traces the readily germinable fraction of the seed bank. The second method, referred to here as the flotation technique, relies on physical extraction of seeds from the soil. This method often overestimates the seed bank as it detects many unviable seeds.

In the present study, the accuracy of the seedling emergence method was tested by doing duplicate experiments of soil samples collected in previous seasons, in the main germination/growing season (summer), referred to here as the re-examinations. Seed bank size and composition estimated by the examination of samples directly after collection and the re-examination in the main growing season were compared for the autumn, winter and spring seasons.

Soil samples that were collected during spring were subjected to three seed bank estimation techniques namely the direct seedling emergence technique, the seedling emergence re-examination and the flotation technique. Results were compared and analysed.

5.2.2 Results

5.2.2.1 Seedling emergence: Direct and re-examination

The results in Figure 5.1 showed clear temporal as well as spatial variation of seed bank size across the transect Standard deviations were not added to Figure 5.1 as the standard deviations were too small to be seen on the graphs. During summer, when duplicate samples were placed out, the readily germinable seed banks of the autumn-, winter- and spring-collected samples were notably larger in all sections of the transect. The spring-collected samples had much greater spatial variation in the seed bank sizes along the transect, for the direct and re-examination than the other seasons. However, when the *Schmidtia kalahariensis* data were removed, the difference in seed bank size between the direct and re-examinations was less apparent.

The re-examinations of the seed banks of the autumn- and winter-collected samples over the first (30 m) section, showed an almost four-fold increase in size. The autumn-collected seed bank increased from a seasonally germinable seed bank of 1 916 seeds/m² to a readily germinable seed bank of 7 750 seeds/m² when examinedin summer, whereas the winter-collected seed bank increased form a seasonally germinable seed bank of 2 041 seeds/m² to a readily germinable seed bank of 7 625 seeds/m² in summer. The spring-collected samples, showed a two-fold increase in seed bank size upon re-examination (from 10 416 seeds/m² − 21 000 seeds/m²). Over the first 30 m from the watering point, the vegetation experienced the greatest degradation. When the *Schmidtia kalahariensis* data were removed, the original estimate of seed bank size in this section of the transect decreased drastically in all seasons, but especially in spring.

Similar, but not as dramatic increases in the size of the readily germinable seed bank were seen for samples collected during autumn, winter and spring in the second section of the transect at a mean distance of 60 m from the watering point where the vegetation was also severely degraded. The autumn-, winter- and spring-collected seed banks showed an approximately 3-fold increase in seed bank size, in each case, when re-examinations were done. When the *Schmidtia kalahariensis* seed bank data were removed, the contrast between the seed bank size estimate of the direct and re-examination method, was not as obvious.

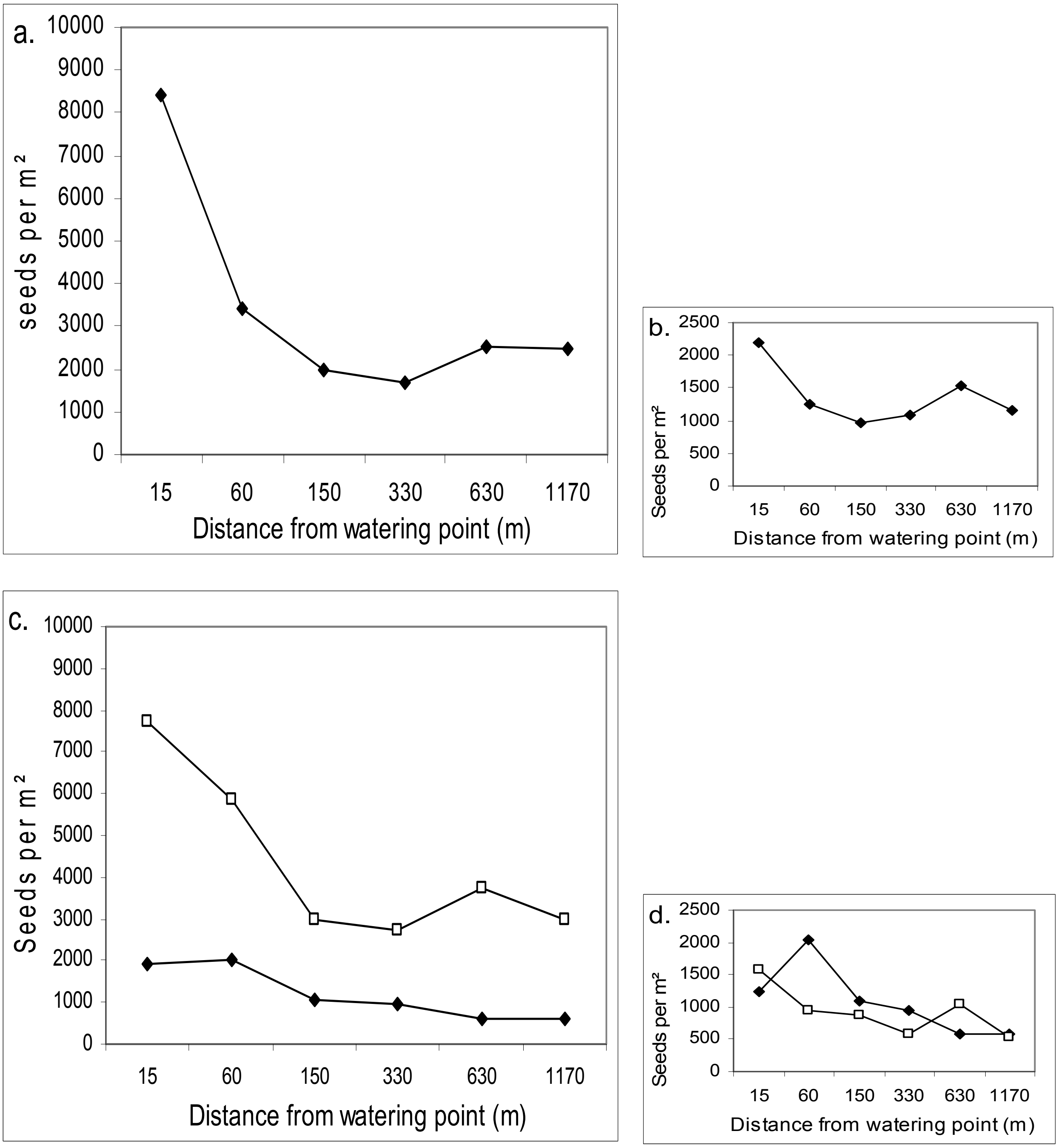


Figure 5.1 Seasonal changes in seed bank size along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld. a. Direct examination of the summer seed bank; b. direct examination of the summer seed bank without *Schmidtia kalahariensis* data; c. direct and re-examination of the autumn seed bank; d. direct and re-examination of the autumn seed bank without *Schmidtia kalahariensis* data (diamonds=direct germination; squares=re-examination).

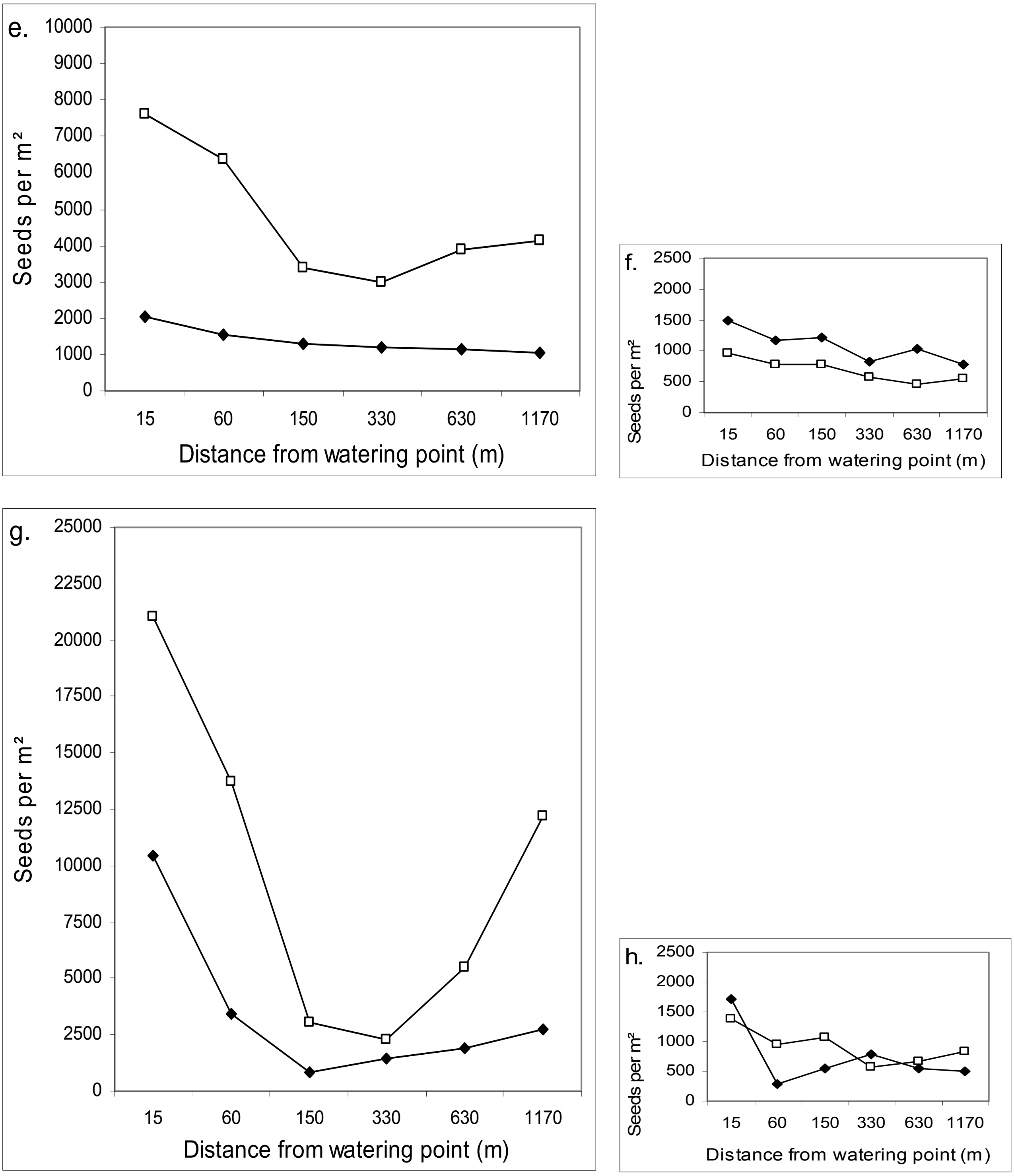


Figure 5.1 (cont.) Seasonal changes in seed bank size along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld. e. Direct and re-examination of the winter seed bank; f. direct and re-examination of the winter seed bank without *Schmidtia kalahariensis* data; g. direct and re-examination of the spring seed bank; h. direct and re-examination of the spring seed bank without *Schmidtia kalahariensis* data (diamonds=direct germination; squares=re-examinations).

At mean distances of 150 m and a mean distance of 330 m (the third and fourth sections which were expected to experience significantly less degradation by trampling), the size of the readily germinable seed banks did not increase to a such a great degree in the re-examinations as they did in the other sections. The autumn-collected seed bank at 150 m increased from 1 083 – 3 000 seeds/m² when re-examined in summer, while at a mean distance of 330 m it increased from 958 – 2 750 seeds/m². The winter-collected seed bank showed a very similar pattern. The spring-collected seed bank increased from 833 – 3 041 seeds/m² in summer at a mean distance of 150 m. At a mean distance of 330 m, it only increased from1 416 seeds/m² in winter to 2 291 seeds/m² in summer. When the *Schmidtia kalahariensis* data were removed, the direct and re-examinations showed similar patterns.

The direct seedling emergence experiments for the autumn-and winter-collected samples, showed a general decrease in seed bank size at a mean distance of 60 m through to a mean distance of 1170 m. The re-examination experiments however, showed that seed banks were larger at a mean distance of 630 m and 1 170 m (the section which experiences fence effects).

The spring-collected samples showed a similar trend over the whole transect for both the direct and repeat experiments. Seed bank size was largest at a mean distance of 15 m, while it was smallest from a mean distance of 150 – 330 m. It was also noticeable that the 15 m seed bank of the spring-collected samples was much larger than the 15 m's direct and re-examination of the autumn and winter samples. In contrast the seed bank values at a mean distance of 150 – 330 m for the spring-collected samples were not very different to the winter- and autumn-collected values. However, when the *Schmidtia kalahariensis* data were removed, the patterns of the direct and re-examination results differed markedly. There was no longer such a marked contrast between the seed bank size estimated for the direct and re-examination seed bank trials. Also, the estimation of seed bank size over all transect sections and over all seasons was smaller.

Main-effects ANOVA tests showed that when comparing the direct seedling emergence method and the re-examination with each other in each season (including all species), the results of the techniques are only significantly ($p<0.000$) different for the spring data (Figure 5.1g) while in autumn (Figure 5.1c) and winter (Figure 5.1e) no significant differences in results could be detected for the two methods ($p>0.05$).

5.2.2.2 Flotation experiments

Figure 5.2a shows the size of the seed bank of each section of the transect, estimated by three methods for spring-collected samples. It is clear that the direct seedling emergence method, which estimates the seasonally germinable seed bank, gives the smallest result for the seed bank size in spring. It is also clear that the re-examination, which estimates the readily germinable seed bank, gives a larger seed bank size. The most noticeable feature of the graph is that the flotation, or physical seed extraction method gives a markedly larger seed bank size than the other two methods.

The largest seed bank estimation was by the flotation method at a mean distance of 1 170 m (177 041 seeds/m²). The estimation of seed bank at 1 170 m by the re-examination was about a fourteenth of the size (12 208 seeds/m²) of that estimated by the flotation method. The direct seedling emergence method estimated a seed bank size at 1 170 m (2 750 seeds/m²) which was about a fourth the size estimated by the re-examination and a sixty-fourth of the size estimated by the flotation method.

The contrast between the results of the three methods was also great at a mean distance of 60 m where there was a 45-fold difference between the flotation (156 916 seeds/m²) and the direct germination (3 458 seeds/m²) results. The contrast between the results of the three methods was most visible on the graph at mean distances of 150 m and 330 m. The results of the flotation technique at 150 m were 95 times bigger than the results estimated by the direct seedling emergence method, and 85 times bigger than the direct germination result at 330 m.

The seed bank size estimated by the direct and repeat methods increased incrementally towards the end of the transect. The direct method estimated an increase from 1 416 seeds/m² to 1 875 seeds/m² to 2 750 seeds/m² over the last three sections of the transect. The re-examination estimated an increase from 2 291 seeds/m² to 5 500 seeds/m² to 12 208 seeds/m² over the last three sections of the transect. The flotation estimated a seed bank of an average of about 120 000 seeds/m² for the fourth and fifth sections of the transect with the seed bank size of the last section being much larger.

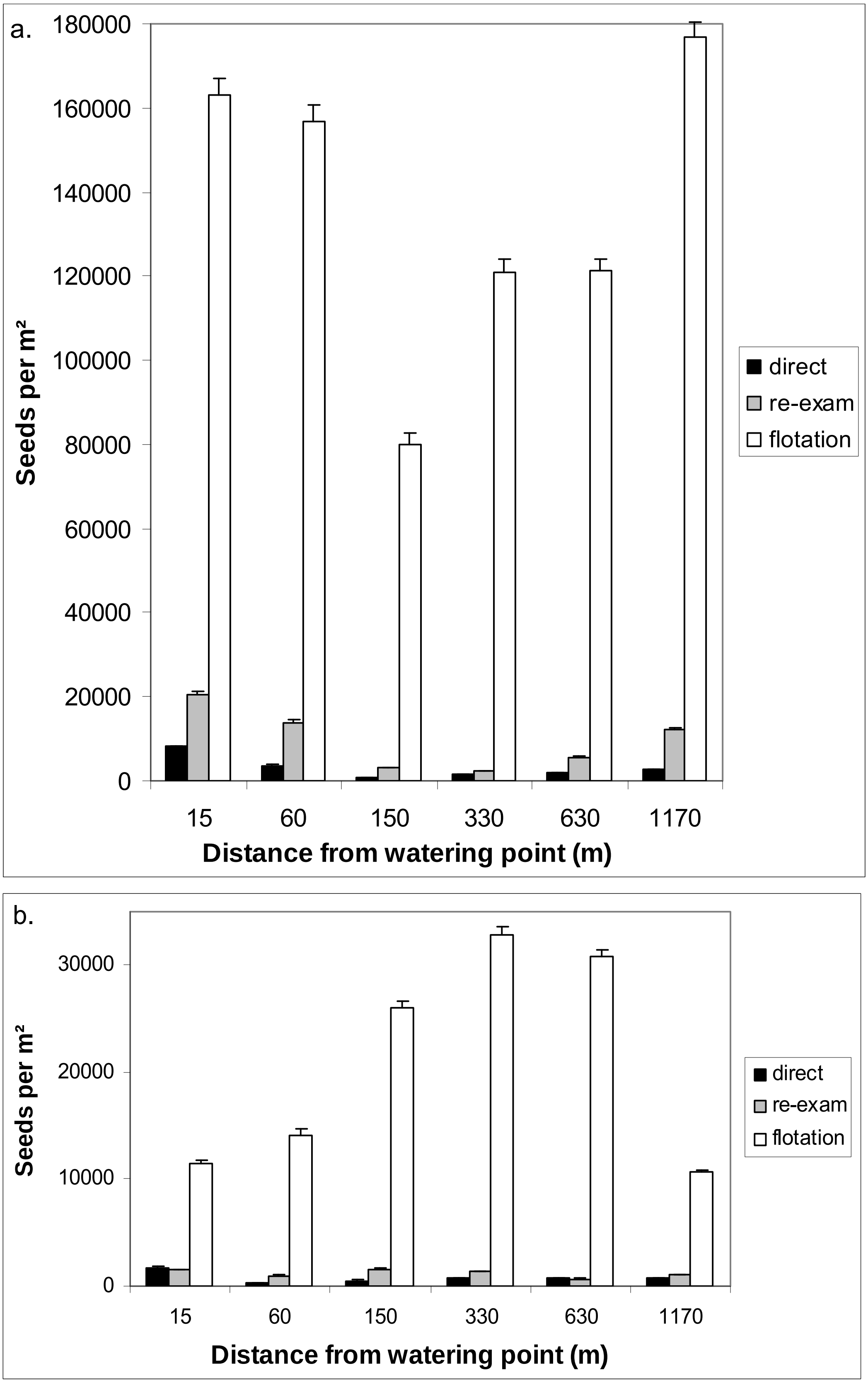


Figure 5.2 Comparison of three methods to determine seed bank size along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld. a. Spring seed bank size including all species; b. spring seed bank size without *Schmidtia kalahariensis* data.

Figure 5.2b shows how the results of seed bank size can be affected by one species, namely *Schmidtia kalahariensis.* Figure 5.2b differs noticeably from Figure 5.2a. Firstly, the flotation data showed a very different pattern. Without the *Schmidtia kalahariensis* data, the flotation method estimated the smallest seed bank to occur in the most degraded areas, and the largest seed bank in the areas under least grazing pressure and trampling. Instead of the largest seed bank size estimate being at a mean distance of 15 m, it was at a mean distance of 330 m (33 083 seeds/m²). Another change which could be observed, was that the values were much smaller. For example, at a mean distance of 630 m the seed bank size estimates for the direct examination, changed from 1 875 - 542 seeds/m², for the re-examination from 5 500 - 667 seeds/m² and for the flotation experiments from 48 708 - 30 708 seeds/m².

One-way ANOVA tests were done for each method in Figure 5.2, to detect the effects of *Schmidtia kalahariensis* significantly influenced the spring data (Figure 5.2a vs Figure 5.2b). The data which included *Schmidtia kalahariensis* and the data which excluded it, were compared to each other separately for each method. *Schmidtia kalahariensis* was deemed as a significant factor in influencing results, where $p<0.000$ for all three methods respectively.

Figure 5.3 and Figure 5.4 illustrate the effect that a grazing gradient has on seed bank size. A one-way ANOVA with post-hoc Fischer tests, highlights significant differences between the transect sections estimated by each method. Significant differences between transect sections were shown by all three seed bank estimation techniques. In Figure 5.3 *Schmidtia kalahariensis* data were included and all three techniques estimate that the first two transect sections were significantly larger than the following three sections. In Figure 5.4 where *S. kalahariensis* data were removed, the three techniques do not show such similarities in their results as in Figure 5.3. Once the *S. kalahariensis* data were no longer dominating the results, each technique probably picked up data for different species, illustrating a grazing gradient in different ways. The direct seedling emergence technique picked up the most seeds for species at the average distance of 15 m and a slight gradient can be observed for the rest of the transect. The results of the re-examination technique do not highlight any gradient along the transect. The flotation technique detected fewer seeds in the highly trampled areas close to the watering point and close to the fence.

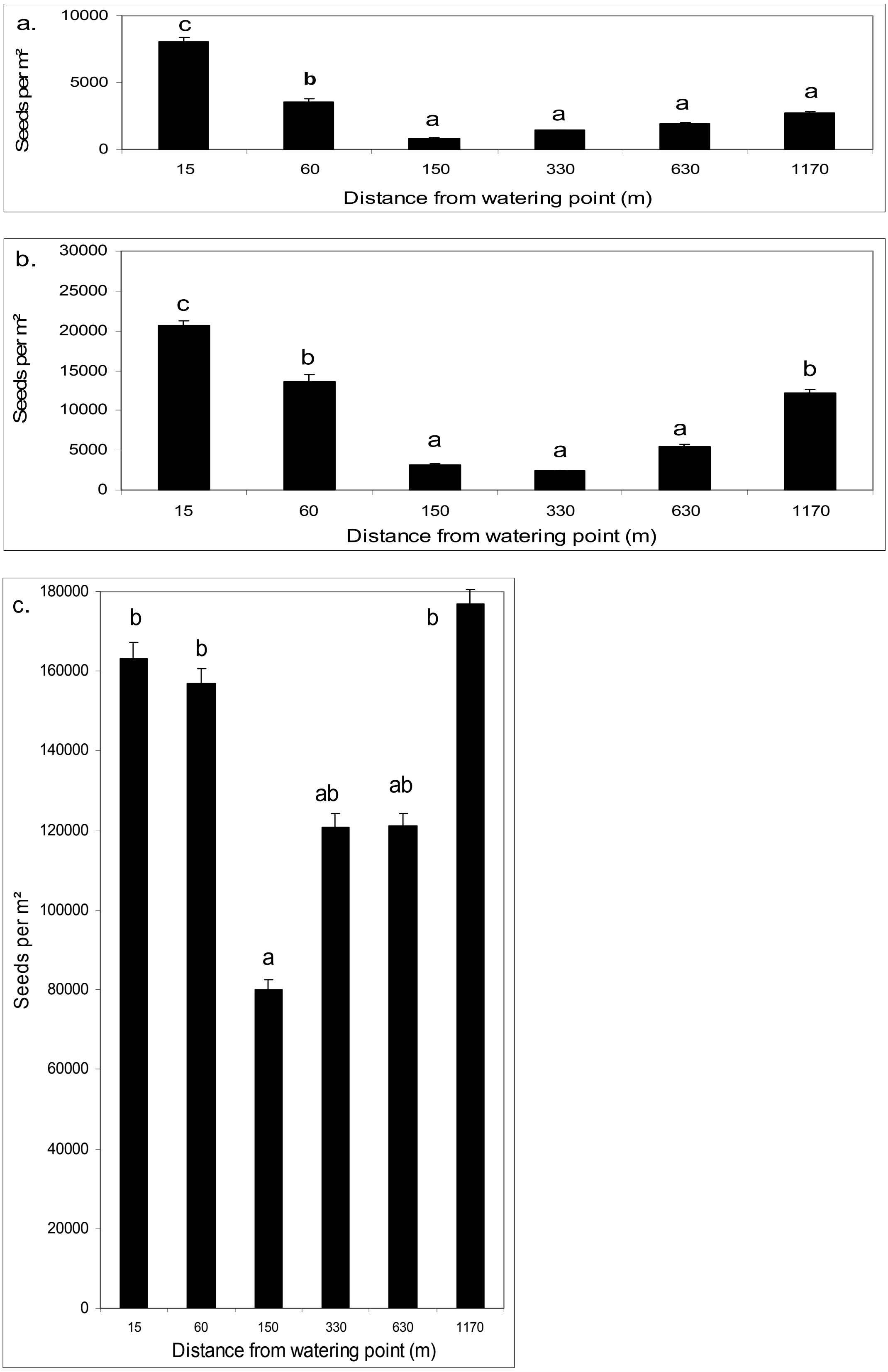


Figure 5.3 Comparison of mean seed bank size (with SD) along a grazing gradient in spring, using three methods (including all species) on the farm Alpha in the Kalahari duneveld. a. Direct seedling emergence method; b. re-examination method; and c. flotation method. Bars with the same letter do not differ significantly at $p < 0.05$.

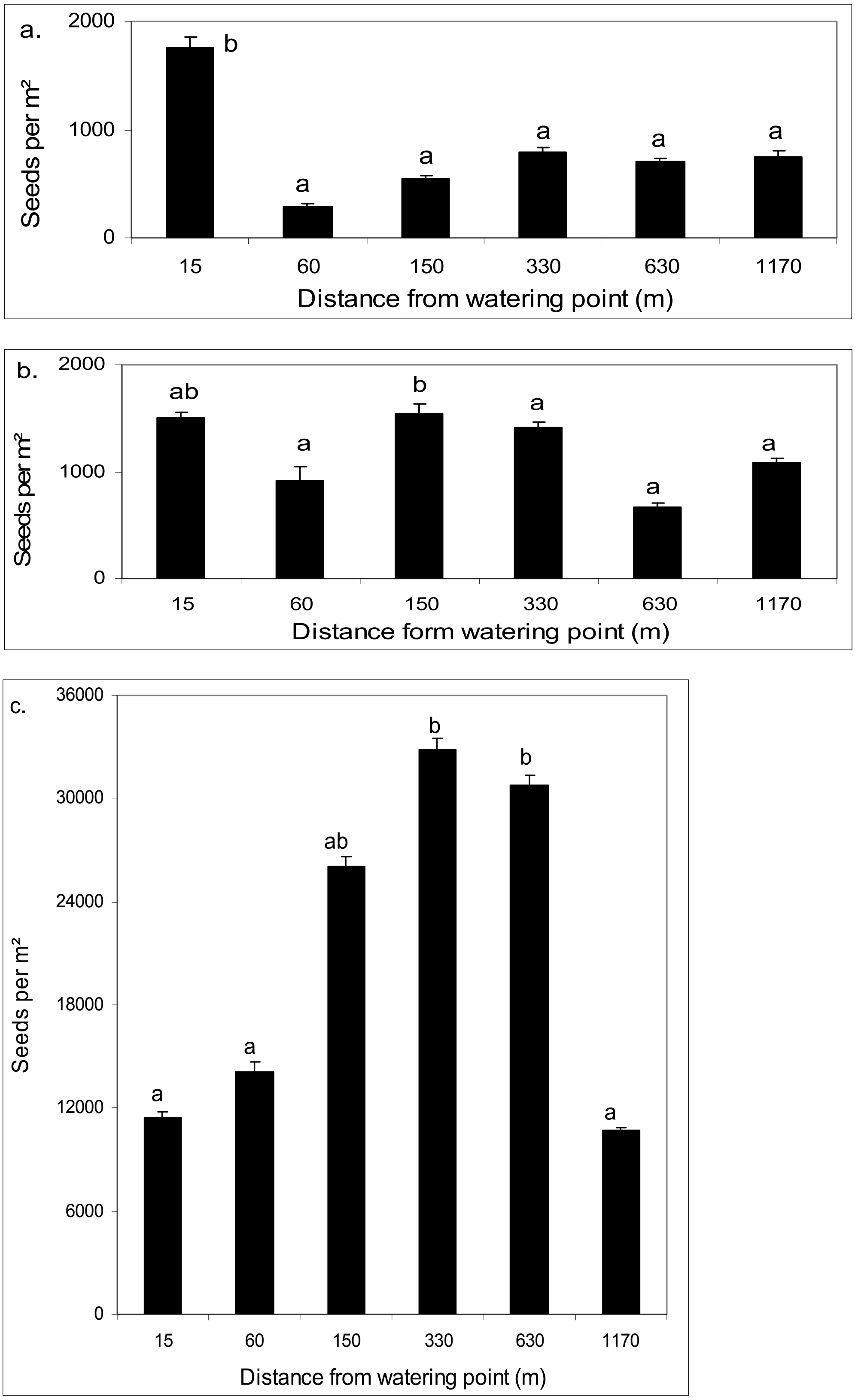


Figure 5.4 Comparison of mean seed bank size (with SD) along a grazing gradient in spring, using three methods (excluding *Schmidtia kalahariensis*) on the farm Alpha in the Kalahari duneveld. a. Direct seedling emergence method; b. re-examination method; and c. flotation method. Bars with the same letter do not differ significantly at $p < 0.05$.

Table 5.1 Comparison of three methods to determine seed bank size of some plant species along a grazing gradient from a watering point in the spring of 2004 on the farm Alpha in the Kalahari duneveld

		Seed bank size (seeds/m²) at different distances from a watering point (midpoint of section given in m from watering point)					
		15	**60**	**150**	**330**	**630**	**1170**
Schmidtia kalahariensis							
	Direct examination	8 708	3 166	291	625	1 333	2 250
	Re-examination	19 625	12 791	1 958	1 041	4 833	11 166
	Flotation	163 125	156 916	79 958	120 833	121 250	177 041
Tribulus zeyheri							
	Direct examination			41			
	Re-examination	41	41			41	41
	Flotation	2 041	2 541	1 208	1 208	2 333	1 458
Limeum spp.							
	Direct examination						
	Re-examination	83			125		
	Flotation	667	6 041	13 791	19 667	16 458	833
Indigofera alternans							
	Direct examination					1708	
	Re-examination						
	Flotation	5 208	4 750	3 250	3 916	4 250	1 125
Amaranthus spp.							
	Direct examination	1 166	41	41			
	Re-examination	791	41				
	Flotation	6 375	1 125	1 083	1 000	875	875
Dipcadi glaucum							
	Direct examination						
	Re-examination				41	83	41
	Flotation			125	125	1 708	
All other grass spp.							
	Direct examination			166	250	5 208	208
	Re-examination	208	208	500	708	166	458
	Flotation		1 000	2 500	3 583	2 291	2 416
All other forb spp.							
	Direct examination	166	166	250	375	333	125
	Re-examination	250	667	583	458	458	541
	Flotation	2 166	2 750	4 125	3 583	708	3 916

By using the flotation method to estimate seed numbers in the soil, one is able to find large, hard-seeded species which would generally not be found in the readily germinable seed bank. Several species were recorded in the seed bank by the flotation method, which were not found (or seldom found) by the seedling emergence method. These large-seeded/hard-seeded species include *Tribulus zeyheri*, several *Limeum* species, *Indigofera alternans* and *Amaranthus* species (Table 5.1).

Tribulus zeyheri was found to be present in most parts of the transect, when using the direct germination and re-examination seedling emergence methods. However, the flotation method revealed that many more seeds were present in the soil throughout the transect. For example, at a mean distance of 60 m, the re-examination method estimated 41 seeds/m², the direct method estimated 0 seeds/m² and the flotation method estimated 2 541 seeds/m². A similar pattern was observed across the whole transect for *Tribulus zeyheri*.

The *Limeum* species are also hard-seeded and were easy to detect in the samples. No *Limeum* spp. seeds germinated during the direct emergence investigation. Some seeds germinated in the re-examinations from soil collected at mean distances of 15 m and 330 m in the transect. Many seeds were detected in samples from all sections in the transect, using the flotation method. The biggest *Limeum* spp. seed bank was estimated at a mean distance of 330 m (19 667 seeds/m²) and the smallest at 15 m (667 seeds/m²).

The flotation method estimated large seed banks for *Indigofera alternans* throughout the transect. The largest seed bank was estimated at a mean distance of 15 m (5 208 seeds/m²) and the smallest seed bank at a mean distance of 150 m (250 seeds/m²). The direct germination method only recorded seeds at a mean distance of 630 m (1 708 seeds/m²). The re-examination did not give any results for this species.

Seeds of *Amaranthus* species were only recorded by the seedling emergence methods in the first three sections of the transect, where they were abundant. The flotation method provided estimates for all sections of the transect. For example, at a mean distance of 60 m, the direct and re-examinations both estimated a seed bank size of 41 seeds/m² while the flotation method estimated a seed bank size of 1 125 seeds/m².

While *Amaranthus* species were most abundant in the first few sections of the transect, *Dipcadi glaucum* was most abundant and only present in the last few sections of the transect. *Dipcadi glaucum* seedlings were not present in any of the direct seedling emergence results. However, the re-examination estimated seed banks for this species, for three sections of the transect. The biggest seed bank recorded by the re-examination was at a mean distance of 630 m, at 83 seeds/m². For this section the flotation method estimated a seed bank of 1 708 seeds/m².

5.2.2.3 Species richness

The direct seedling emergence method detected the greatest number of species in each transect section in summer (from six species to 13 species), with the winter readily germinable seed bank having the smallest number of species (from two species to three species) across the transect (Table 5.2).

The duplicate seedling emergence trials always detected more species in each section of the transect than the direct seedling emergence trials (except at a mean distance of 60 m in autumn). The re-examination detected the most species in spring (from seven species to ten species), the second largest number of species in autumn (from five species to eight species) and the smallest number of species in winter (from three species to six species).

The direct seedling emergence investigation detected some species which the re-examination did not detect, and likewise the re-examination detected some species which the direct examination did not detect. For example, at a mean distance of 150 m, direct trials done in spring yielded seven species and the duplicate trials also yielded seven species. However, only four of the species were common in both examinations. This means that three species exclusively germinated during the direct trials and another three species germinated exclusively during the re-examination trials.

Table 5.2 Comparison of species richness by the direct and re-examination seedling emergence methods along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld.

Mean distance from the watering point (m)		**Species richness (number of species)**			
		SUMMER	**AUTUMN**	**WINTER**	**SPRING**
15	Direct examination	6	5	3	4
	Re-examination		7	4	8
	Species in common	N/A	4	3	3
60	Direct examination	7	7	3	4
	Re-examination		5	5	7
	Species in common	N/A	2	3	4
150	Direct examination	9	3	2	7
	Re-examination		6	5	7
	Species in common	N/A	3	2	4
330	Direct examination	13	4	2	6
	Re-examination		5	6	10
	Species in common	N/A	3	2	3
630	Direct examination	7	3	2	5
	Re-examination		8	3	10
	Species in common	N/A	2	2	3
1170	Direct examination	6	3	2	5
	Re-examination		7	3	9
	Species in common	N/A	3	2	3

5.2.3 Discussion

5.2.3.1 Seedling emergence: Direct and re-examination

Schmidtia kalahariensis is an annual, unpalatable grass species which grows especially well in degraded and trampled areas. Its seeds form an abnormally large part of the total seed bank over all seasons, and especially in the areas most prone to trampling (near the waterhole and along the fence). The contribution of *Schmidtia kalahariensis* seeds to the seed bank should be taken into account when making inferences about the effect of grazing.

Various authors have noted that seed bank size tends to increase in arid/semi-arid areas when stocking pressure is high (Russi *et al*., 1992; Navie *et al*., 1996; Snyman, 2004).
Navie *et al*. (1996) proposed that heavy grazing led to an increase in the size of the seed bank as a result of an increase in annual species that possess large and persistent seed banks. This grazing effect may explain the larger than expected seed densities found near a waterpoint (Navie *et al*., 1996). Also, according to Russi *et al*. (1992), studies in Mediterranean grassland communities showed that there was a tendency for all species to set more seeds per plant under high stocking densities rather than at lower densities. Greater seedling establishment also seemed to occur in more degraded areas of rangelands (Snyman, 2004). According to Snyman (2004) the short lifespan of the pioneer grass species, associated with greater seed production, was an important factor that could contribute towards greater seedling establishment in rangeland in poor condition. But he also mentioned that although seed bank size for grasses was larger for the poor rangeland, its species richness was the smallest (Snyman, 2004) with no climax grass seeds present in the rangeland in poor condition. Despite this fact, annual plant species constitute an important proportion of the biodiversity of arid land vegetation (Meissner & Facelli, 1999). They are an important functional part of arid ecosystems, using resources not available to perennial plants and providing temporary ground cover. Grazing by domestic stock is one of the main factors that currently determines the structure of annual plant communities in most arid lands (Meissner & Facelli, 1999).

Many species exhibit distinct seasonal patterns in emergence from the persistent seed bank which may be associated with cyclic changes in the germination requirements of the buried seeds (Roberts, 1986). The most obvious pattern that could be observed, was that

Schmidtia kalahariensis was mainly a spring and summer germinator with its readily germinable seed bank being biggest in spring for both the direct germination and the re-examination seedling emergence trials. The most degraded areas of the transect could easily be distinguished as peaks in the graph (Figure 5.1). These results were similar to those observed by Jones and Esler (2004) who found a two-fold increase in the average number of seedlings germinating in spring (October) sampling, compared with autumn (April) in the Nama Karoo. They also found that annual grasses constituted a higher percentage of total germination from spring than from autumn sampling (Jones & Esler, 2004).

However, these results differed from those observed by Snyman (2004) in the Orange Free State province, South Africa. He found that in April (autumn) the highest emergence of grass seedlings occurred in the rangelands for all states of degradation compared to the other seasons. In January (summer), the seed bank size for grasses was the smallest compared to other seasons, although the rangeland in poor condition had the largest grass seed bank. In the Kalahari the largest grass seed bank was in spring but only because of one species (*Schmidtia kalahariensis*). This species may not only contribute such a large proportion of seeds to the seed bank because it is an annual, but perhaps also due to its unpalatability and its acidic/irritant exuviate which discourages wildlife/livestock from trampling it (personal observation) and thus ensuring a larger seed set.

5.2.3.2 Flotation experiments

The flotation method provided larger seed bank sizes in all sections of the transect, than those by the seedling emergence trials. Other authors have reported similar trends (Gross, 1990; Manders 1990). The flotation method may overestimate the frequency and density of a species if unviable seeds are present in the samples (Gross, 1990). The viability of the seeds extracted by flotation was not determined in the present study and the reported values may therefore overestimate the true seed bank size. Differences in the estimated number of species per sample, among germination and flotation samples may also be due to failure of some species to emerge in the germination tests because specific germination cues were not met (Gross, 1990; De Villiers *et al*., 2004).

Figure 5.2a & b demonstrated the ability of the flotation method to detect seeds which were either dormant or unviable, as the estimated seed bank size was notably larger in all sections using this method. Figure 5.2a highlighted the large contribution of the seeds of a single annual grass species to the soil seed bank. In this figure all three methods estimated the largest seed banks to be in the transect sections experiencing the greatest grazing/trampling pressure. This effect was due to the contribution of *Schmidtia kalahariensis* seeds. *Schmidtia kalahariensis* seeds are light and were easily separated from the soil particles during the flotation process. Also, the seeds were easy to detect under a stereomicroscope and thus all seeds should be detected and counted when using the flotation method. The seeds of this species also germinated readily, making it easy to detect the seedlings by the seedling emergence method.

Another observation which could be made was that the flotation results without *Schmidtia kalahariensis* data (Figure 5.2b) highlighted the effects of the grazing gradient. The largest seed banks were estimated from areas furthest from the points of disturbance and the smallest seed banks were estimated from areas closest to the watering point as well as closest to the fence (fence effect). The grazing effect could not be detected by the seedling emergence results in Figure 5.2a because *Schmidtia kalahariensis* masked the trend that many other species followed along the grazing gradient. There was no notable difference between the seed bank size estimated by the direct and the re-examination seedling emergence methods, once the *Schmidtia kalahariensis* data were removed.

The seedling emergence study provides an estimate of the readily germinable fraction of the seed bank (Brown, 1992) and the conditions in the 'greenhouse' are seldom favourable to stimulate the germination of all viable seeds (De Villiers *et al*., 1994). However, it can give a good estimate when comparing seed bank sizes between sections along a grazing gradient. Thus the absolute number of seeds per m² may not be as important as the differences in seed bank size from one section to another. Manders (1990), suggests that more information can be revealed by combining the results from both techniques and adopting the greater estimate of the two techniques, than by relying on one technique alone. Also, the value of such information does not lie in its estimation of viable seed stores, but in allowing comparison among sites or identification of changes with time (Manders, 1990). When a study is conducted for comparative purposes (where relative differences are the concern), the ability of the method to distinguish between different conditions may be more desirable, than providing an unbiased estimate (Brown, 1992). In these situations both methods have a similar ability to detect differences (Brown, 1992). Comparisons of methods to determine soil seed bank density/composition are necessary to determine the relative accuracy of different methods for estimating specific characteristics of the soil seed bank (De Villiers *et al*., 1994).

Four duneveld species and two genera were identified in the soil seed bank by using the flotation method (Table 5.1). The seedling emergence method, on average, detected more species in the soil seed bank than the flotation method and this suggests that germination methods may provide a more reliable method for determining the species composition of the seed bank of a plant community than flotation. The difficulty in distinguishing among species with similar seeds, and detecting species with small seeds, results in an underestimate of species composition in flotation results. Furthermore, flotation methods are extremely laborious and impractical for large-scale studies, especially those involving small-seeded species from arid areas (De Villiers *et al*., 1994) as in this case. If the majority of seeds in samples are small, then this complicates seed isolation, identification and determination of viability after flotation has been completed (De Villiers *et al*., 1994). Another factor is that the large number of unviable seeds in the flotation results can result in an overestimate of seed density (Gross, 1990).

Physical separation is more successful for large seeds than for small seeds (Manders, 1990) and in this study only species with relatively large seeds could be identified when using this method. Most of the species detected by the flotation method, in this study, were not detected or underrepresented by the seedling emergence method. For example, *Tribulus zeyheri, Limeum* species and *Indigofera alternans* all form a large part of the seed bank as shown by the flotation results. However the seedling emergence method hardly detected any seedlings of these species. The seeds of these species are all relatively large (in desert seed bank terms) and are all covered in a very thick and hard testa. *Indigofera alternans* is a legume, and legume species are generally known to be hard-seeded (Russi *et al.*, 1992) and to form a persistent seed bank due to an impermeable seed coat (Shaukat & Siddiqui, 2004).

Russi *et al*. (1992) found that in a Mediterranean grassland, the seed bank of legumes was greater at areas with a high stocking density than areas with a low stocking density. They also found that there were generally more legume seeds than grass seeds in the seed bank and that the total seed bank was usually greater at a high stocking density. A similar pattern was observed in the Kalahari, where *Indigofera alternans* seeds were most concentrated in the transect sections nearest to the watering point. This phenomenon could be due to several reasons: i) heavy grazing may reduce the perennial plant cover and thus allow annual species with high seed production to enter, ii) trampling increases the burial of seeds or iii) seeds passing through the alimentary canal are forced into dormancy (Russi *et al*., 1992). As far as legumes are concerned, seed burial generally exposes seeds to smaller amplitudes of diurnal temperature fluctuation than at the soil surface, resulting in dormancy not being broken (Russi *et al*., 1992). This abundance of the hard-seeded species showed the opposite pattern to the 'other grass' data, which represented all grass species in the seed bank excluding *Schmidtia kalahariensis*. The 'other grass' species were not present in the first section, and their concentration increased away from the watering point.

There is a substantial variation in the efficacy of the two techniques among species and seed types (Manders, 1990). Both techniques have limitations with regard to accuracy in assessing composition of soil seed banks, and both are very time-consuming (Manders, 1990). Researchers have found that the two methods could give contradictory results, both for species numbers and total seed bank size (Brown, 1992). Authors such as Barberi *et al*. (1998), found that the seedling emergence method provided a more accurate estimate of seed bank species composition than the seed extraction method. They also found that correlation between the two methods for seed bank analysis seemed to be higher when density of seeds/seedlings was higher (Barberi *et al*., 1998). The comparability between the seed extraction and seedling emergence methods seems to be partly dependent on sampling time (Barberi *et al*., 1998).

In this study, the seedling emergence re-examinations detected a greater number of species for the soil seed bank than the direct examinations. One could thus conclude that direct seedling emergence was not necessary, as the re-examinations detected a greater number of species for samples collected in each season. The species in the soil samples that were detected by the direct examinations were often also detected by the re-examinations done in January. However, this was not always the case. A portion of the species detected by the direct examinations were sometimes not detected in the re-examinations. This may be due to seasonal preferences in certain species for germination.

The soil seed bank was composed of a) a transient component, made up mostly of seeds at the surface that were capable of immediate germination, a few of which remained viable for more than a year, and b) a persistent component consisting of seeds that may have remained viable for several years (De Villiers *et al*., 1994).

During summer (the growing season) the most species were present in the readily germinable seed bank. Species that had after-ripened, those that had not entered dormancy yet and those that formed transient seed banks, probably contribute to the species richness of the readily germinable seed bank during this season.

During autumn and winter the number of species in the readily germinable seed banks was lowest. Thus species that were added to the seed bank during the summer season may have entered dormancy or already germinated (in the case of transient seed banks). When re-examinations were done it became clear that some species had viable seeds in the soil but that they did not germinate in autumn or winter, and could only be detected when they were put out to germinate in summer (the re-examination). Such species that were only detected in the re-examination thus had a persistent or partially persistent seed bank.

During spring more species could be detected than in autumn and winter with the direct seedling emergence trials. Thus some species present in the soil seed bank during spring, start to break out of dormancy. However, when re-examinations were done in summer, even more species could be detected form the spring soil seed bank. This indicated that although dormancy was broken for some species in spring, this only occurred in summer conditions for other species. The seed bank species richness was lowest in the sections nearest the watering point as well as the section nearest the fence. While the sections further away from the watering point tended to have a higher species richness in the soil seed bank. This effect could best be seen by investigating trends in seed bank species richness derived from the direct seedling emergence trial in the summer, as well as the re-examinations of the spring-collected soil samples.

Along a grazing gradient, one would expect the species richness to decrease with increasing grazing intensity. Snyman (2004) found a decrease in species richness of a seed bank, in southern Africa, within a more degraded semi-arid rangeland than a rangeland in good condition. The dynamics of savanna grasslands of southern Africa reflect the variability of the annual rainfall as well as changes in composition that occur in response to sustained mammalian grazing (O'Connor & Pickett, 1992). Studies have consistently shown that grazing changes the relative abundance of species in the seed bank, indicating that grazing caused a persistent change in the vegetation (Solomon *et al*., 2006). Solomon *et al*. (2006) also found that heavy grazing not only alters the aboveground species composition towards the abundance of less desirable species, but also changes the species composition of the seed bank in a similar direction. In Ethiopian rangelands, the size, species richness and species composition are important variables to reflect the past, current and the future conditions of the ecosystems and tend to have different structures to that of the aboveground plants (Solomon *et al*., 2006).

5.2.4 Conclusions on seed bank size and species richness

Extracting seeds form the soil is both time and labour consuming and the results are influenced by sampling techniques, the time of sampling and methods used to determine seed numbers (De Villiers *et al*., 1994). Thus the presence of large numbers of unviable seeds in soils makes it difficult to draw conclusions about seed densities from studies using seed counts from flotation samples only (Gross, 1990). The main advantages of the seedling emergence technique are that the effort required is spread over a period, each seedling represents a viable seed, and seedlings are usually easier to identify than seeds (Brown 1992, De Villiers *et al*., 1994). This method is therefore usually preferred for monitoring long-term experiments and for studying seasonal changes in the seed bank (De Villiers *et al*., 1994). Careful consideration should be given to both the objectives of the seed bank study and the relevant literature, prior to the selection of an appropriate method (Brown, 1992).

The direct seedling emergence method showed seasonal differences in the readily germinable seed bank of each section of the transect. The re-examination trials showed the considerable effect that *Schmidtia kalahariensis* had on seed bank size, especially in the more grazed/trampled areas of the transect. The flotation method gave considerably higher results for seed bank size than the seedling emergence and re-examination trials. Once the *Schmidtia kalahariensis* data were removed from the flotation results, a different picture emerged which clearly showed the effects of grazing over the transect. The flotation method detected species in the soil samples that the seedling emergence methods did not detect. These species were all hard-seeded and formed persistent seed banks. The flotation method thus detected species from the persistent seed bank, which were important to the understanding of the seed bank dynamics along the transect. The seedling emergence direct and re-examination trials detected species which were present in the readily germinable or partly-persistent component of the seed bank and the seedling emergence method detected more species in the seed bank than the flotation method.

5.3 COMPARISON OF THE ABOVEGROUND AND BELOWGROUND FLORAS

5.3.1 Introduction

Large variation in the similarity between the seed bank and standing vegetation usually occurs along environmental gradients (Osem *et al*., 2006). The similarity between a seed bank and its standing vegetation has been frequently studied in plant communities, in order to have a better understanding of the role of seed banks in regeneration processes. Low similarity usually occurs in plant communities dominated by perennial species while higher similarity is found in communities dominated by annuals. Perennial species generally have a low seed production because they often have the ability to alternate this type of reproduction with vegetative forms of reproduction and because their seeds have a short-term persistence in the soil (Peco *et al*., 1998). Annual species on the other hand form copious amounts of seed as this is their only reproductive strategy. Seed banks of most habitats contain both transient and persistent components (Shaukat & Siddiqui, 2004). The degree to which a seed bank is dominated by either type of component depends to a large extent on the patterns of disturbance and stress which a plant community experiences. There is a lack of correspondence between the composition of the seed bank and the vegetation for many perennial grasslands. Abundant perennial grass species may be absent form the seed bank, while annual species with abundant, persistent seed banks may be absent from the vegetation (O'Connor & Pickett, 1992).

In this section, the degree of correlation between the aboveground flora and the belowground flora, over the grazing gradient, was explored. Changes in species richness over four seasons and between the sections of the transect were recorded and analysed.

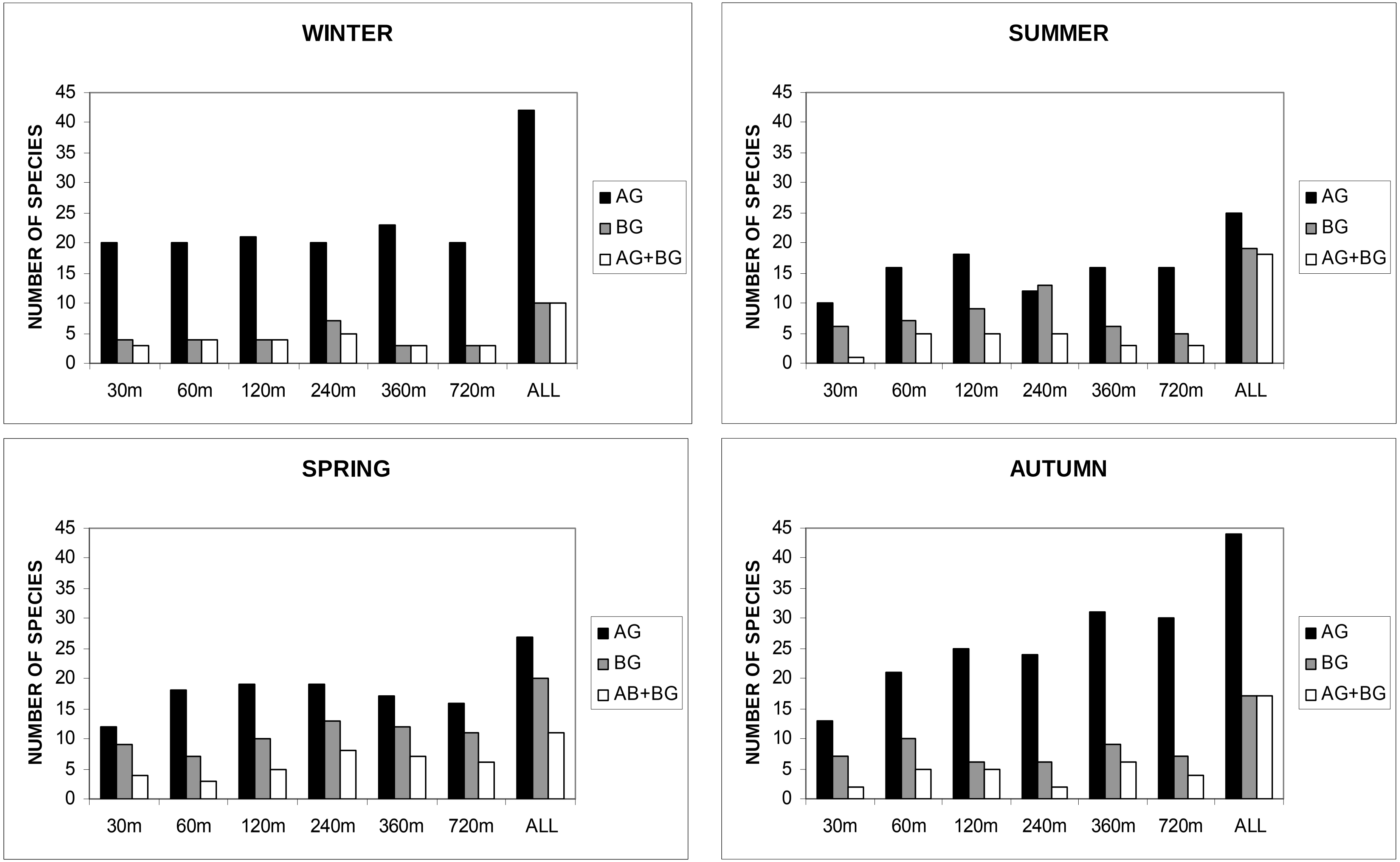


Figure 5.5 Seasonal comparisons of the aboveground (AG) and belowground (BG) floras and species common to both floras (AG + BG) along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld.

Table 5.3 The percentage of aboveground species which were also found in the readily germinable seed bank along the transect, over four seasons, on the farm Alpha in the Kalahari duneveld

	Similarity between aboveground flora and seed bank (%)			
Sections	**Summer**	**Autumn**	**Winter**	**Spring**
30 m	10	15	15	33
60 m	31	24	20	17
120 m	17	20	19	26
240 m	42	8	25	42
360 m	19	19	13	41
720 m	19	13	15	38
All sections	72	25	24	41

5.3.2 Results

The number of species in all sections of the transect occurring aboveground was always greater than the number of species occurring belowground (readily germinable seed bank), over all seasons (Figure 5.5). The combined aboveground species richness (‘ALL sections’) for the transect is much greater during autumn (44 species) and winter (42 species) than during summer (25 species) and spring (27 species). However, the combined belowground species richness (‘ALL sections’) of the transect is greatest in spring (20 species) and also large in summer (19 species) and autumn (17 species).

In all seasons, except spring, all the species that were found belowground, cumulatively over the entire transect, were also found aboveground in the transect (‘ALL sections’). In spring, many species that were found cumulatively belowground, were not represented aboveground. Twenty species were present belowground, while only 11 out of those species were present aboveground. Thus nine species were exclusive to the seed bank during this season. Over the entire spectrum of the transect, the aboveground vegetation was generally most species rich in autumn and most species poor in summer. The species richness of the belowground flora followed the opposite pattern being generally smallest in winter and largest in spring. During winter, nearly all transect sections had all species present in the seed bank, also present aboveground. However, during all other seasons the seed bank contained some species not shared in the aboveground (see AG+BG in all sections).

Table 5.3 highlights the percentage similarity between the standing vegetation the readily germinable seed bank in each season. During summer, the entire transect had 72% of species of the standing vegetation represented belowground as well, while in winter this dropped to 24%.

5.3.3 Discussion

The absence from the seed bank of several species dominating the vegetation has been reported for many grasslands (Milberg & Hansson, 1993). Usually, low similarity occurs between the species richness of the seed bank and vegetation, in grasslands dominated by perennial species, while higher similarity has been found in grasslands dominated by annuals, as in early successional stages and in Mediterranean grasslands (Peco *et al*.,1998; Osem *et al*., 2006). Most annual plant species in arid lands can only be found in the soil seed bank for most of the year (Meissner & Facelli, 1999). In general there is variable correspondence (or in some instances lack of correspondence) between species present in a seed bank and existing vegetation in habitats, especially those that are undisturbed. According to Milberg and Hansson (1993), the floristic similarity between the vegetation in the grazed plots and the seed bank was larger than the similarity between the vegetation and seed bank of the ungrazed plots in a Swedish calcareous grassland. In regularly disturbed habitats it has been noted that above- and belowground species composition is often similar (Jones & Esler, 2004).

Although the grass species in the Kalahari duneveld are mostly perennial species, degradation tends to favour annual grass species such as *Schmidtia kalahariensis*. Annual forbs are also more common and abundant near watering points where the greatest degradation occurs (Navie & Rogers, 1997). Many of the species may be perennial dicotyledons with persistent seed banks (such as *Hermannia tomentosa* and *Senna italica*) and which prefer disturbed areas to grow in.

The dominant species in the first section was *Schmidtia kalahariensis* which formed dense, homogenous stands (personal observation). Consequently this section had the fewest species aboveground throughout the year. Also, the similarity between the seed bank and the aboveground vegetation was smallest for all seasons compared to the rest of the transect. This is in contrast to the trends predicted in other studies. It would have been expected that the sacrifice zone would be dominated by annual species and that the seed bank and vegetation would be almost similar. However, according to Roberts (1986), disturbance or destruction of vegetation can result in the immediate disappearance of some species, whereas others might persist as seeds for at least several years.

The comparison between the aboveground and belowground floras, however, only compared species presence and not density, thus the comparison did not give information about the dominance or abundance of certain species. *Schmidtia kalahariensis* dominated the above- and belowground flora in the first section from the watering point. The results thus may indicate that certain species were present in the soil seed bank in small proportions, but that they never became established. Other species (such as *Indigofera alternans* and *Tribulus terrestris*) may be hard-seeded and thus may not contribute to the readily germinable seed bank but are visible in the aboveground vegetation. After disturbance, the vegetation that develops will depend, to a considerable extent, on which species were represented in the seed bank and whether their requirements for germination had been met (Roberts, 1986).

In the present study the grazing gradient was not clearly reflected in the species richness in either the aboveground or belowground flora. Species richness is a coarse measure of diversity and gives no information of the desirability or abundance of a species. Furthermore, the relationship between species richness and disturbance is complex (references).

Although species richness did not change markedly along the transect, species composition did differ between the sections of the transect. In his study, Snyman (2004) found that in a semi-arid rangeland in southern Africa, rangeland degradation was associated with a decrease in species richness in the seed bank and a decrease in grass species richness. He found that in the rangeland in good condition all eight grass species from the seed bank were also present in the standing vegetation with six extra grass species in the standing vegetation. However, in the rangeland in poor condition five grass species were present in both the seed bank and standing vegetation with six species only aboveground (Snyman 2004). He found no climax grass seedlings in rangeland in poor condition. In an Australian chenopod shrubland, the effects of grazing were not expressed in the same way in the growing vegetation and the soil seed bank (Meissner & Facelli, 1999). Meissner & Facelli (1999) found that grazing had a contrasting effect on the spatial heterogeneity of the soil seed bank and that of growing vegetation. In their study the heterogeneity of the soil seed bank was lower in less grazed areas and higher in more grazed areas, whereas grazed areas had a more homogenous vegetation.

5.3.4 Conclusions on comparisons between aboveground and belowground floras

In grasslands, the degree of similarity in species composition between the standing vegetation and the seed bank differs across habitats and environmental conditions, successional stages and type of disturbance (Osem *et al*., 2006). However, the processes by which abiotic stresses and resource availability interact with disturbances (e.g. grazing) in determining plant community dynamics and seed bank – vegetation similarity are not fully understood (Osem *et al*., 2006). Grazing was found to either increase, decrease or have no effect on seed bank – vegetation similarity. These contrasting patterns are probably due to differences in grazing regimes, environmental conditions and vegetation characteristics (Osem *et al*., 2006). Variation in seed bank – vegetation similarity along continuous productivity gradients, as well as the interactive effects of productivity and grazing on this similarity, have rarely been examined. These relationships are particularly important in semi-arid rangelands where factors constraining germination, establishment and plant survival, shift from soil, to canopy resources along productivity gradients. A better understanding of the processes shaping the relationships between seed bank and vegetation is needed for the establishment of adequate conservation and management policies for these regions (Osem *et al*., 2006).

In this study, changes in the species richness of the vegetation and of the soil seed bank could be observed over four seasons. In spring and summer the seed bank was most species rich along the entire transect. In autumn and winter the aboveground vegetation was most species rich along the entire transect.

A grazing gradient was not identifiable by changed species richness along the transect, although the ‘sacrifice zone’ did have fewer species above- and belowground than the other sections of the transect. The fence effect at the end of the transect as well as serious overgrazing by cattle in previous years, may also have obliterated any grazing gradient effects which could have been manifested along the transect. In this analysis the abundance of species found in each section was not incorporated and thus a grazing gradient might be identified by an ordination which includes species abundance.

5.4 SEED BANK TYPES AND GROWTH FORM

5.4.1 Introduction

Semi-arid seed banks show considerable spatial and temporal variation and determination of the size and composition of the seed banks is a complex problem (Navie *et al*., 1996). A simple approximation that is informative with respect to short-term vegetation response, however, is determination of the germinable seed bank (Navie *et al*., 1996). A study of germinable seed banks over distance, away from a water source, across an otherwise uniform landscape can therefore be assumed to be a study of soil seed banks across a stocking gradient (Navie *et al*., 1996).

Seed banks of most habitats contain both transient and persistent components. The transient component is composed of short-lived, non-dormant seeds that may be viable at the onset of the following growing season (Thompson & Grime, 1979; Shaukat & Siddiqui, 2004). The current year's seeds that remain viable at the onset of the following growing season, as well as viable seeds dispersed in previous years, constitute the persistent component of the seed bank (Thompson & Grime, 1979; Shaukat & Siddiqui, 2004). Understanding the seed bank ecology is a key to elucidating community development and its dynamics and may be useful in various practical aspects of management and conservation of natural and semi-natural ecosystems.

It is possible to identify seasonal patterns in seed bank composition. Seasonal germination strategies can then be described from the temporal distribution of abundances of different species (Lavorel *et al*., 1993). Germination strategies can be defined as response patterns of species (or groups of species) to sets of environmental conditions (Lavorel *et al*., 1993). Thompson and Grime (1979) have classified seed banks according to seasonal patterns of germination and especially according to the possibility of carry-over from one year to the next. The interaction of germination strategies with the temporal distribution of disturbances, determines the pattern of local and regional co-existence (Lavorel *et al.*, 1993).

In arid and semi-arid rangelands, there is usually a decline in the density and basal area of the perennial grasses, coupled with an increase in the population of winter and summer annuals and woody species, when grazing pressure is increased (O'Connor & Pickett, 1992). The effects of grazing on the seed bank are usually similar in different areas (Navie *et al*., 1996). The interaction of stocking pressure and soil seed bank composition is therefore of great importance in the ecology of grazed pastures where stock management is one of the few economically viable methods of pasture management (Navie *et al*., 1996).

5.4.2 Results

Based on the seasonal germination patterns observed in the seedling emergence trials the species were tentatively classified into the following categories:

Seed Bank Type I (transient)	Seed Bank Type II (short-term persistent)	Seed Bank Type III (long-term persistent)
Eragrostis lehmanniana	*Aristida adscensionis*	*Indigofera alternans*
Eragrostis porosa	*Amaranthus dinteri*	*Limeum arenicolum*
Stipagrostis ciliata	*Bulbostylis hispidula*	*Requienea sphaerosperma*
Stipagrostis obtusa	*Chamaesyce inaequilatera*	*Tribulus zeyheri*
Stipagrostis uniplumis	*Gisekia africana*	
	Helichrysum argyrosphaerum	
	Hermannia tomentosa	
	Hirpicium echinus	
	Manulea burchellii	
	Mollugo cerviana	
	Plinthus sp.	
	Schmidtia kalahariensis	

At a mean distance of 15 m from the watering point, three species with Type II seed banks, were dominant in the readily germinable seed bank throughout the four seasons, namely *Schmidtia kalahariensis, Amaranthus dinteri* and *Helichrysum argyrosphaerum* (Table 5.3). At a mean distance of 60 m from the watering point, these three species still dominated, but a few other species with other seed bank types were also present in the seasonally germinable seed banks. Five species with Type II seed bank (eg *Hermannia tomentosa, Bulbostylis hispidula*), two Species with Type I seed bank (*Eragrostis lehmanniana*, *Stipagrostis ciliata*) and one species with Type III seed bank (*Requenia sphaerosperma*) were present in small numbers in this section.

At a mean distance of 150 m from the watering point, *Schmidtia kalahariensis* and *Helichrysum argyrosphaerum* (Type II) were not as dominant as in the previous sections. There were two species with a Type I seed bank, which were well represented in the seasonally germinable seed bank (*Stipagrostis ciliata, Eragrostis lehmanniana*), one species with a Type III seed bank (*Tribulus zeyheri*) and one other species with a Type II seed bank.

At a mean distance of 330 m from the watering point, *Helichrysum argyrosphaerum* and *Schmidtia kalahariensis* (Type II) were still dominating the readily germinable seed bank but not as much as in the first two sections. However, in this section five species were present from the Type I seed bank (two *Eragrostis* and three *Stipagrostis* species), two species from the Type III seed bank (*Requenia sphaerosperma, Limeum arenicolum*) and another five species from the Type II seed bank.

At a mean distance of 630 m, *Helichrysum argyrosphaerum* and *Schmidtia kalahariensis* were still dominating the readily germinable seed bank. In this section three seed bank Type I species were more abundant than in the previous sections (*Eragrostis lehmanniana, Stipagrostis uniplumis, Eragrostis porosa*) and contributed to a large part of the total readily germinable seed bank. Five species with a Type II seed bank occurred in this section and one Type III species (*Indigofera alternans*).

At a mean distance of 1 170 m, *Schmidtia kalahariensis* dominated the readily germinable seed bank. *Helichrysum argyrosphaerum* also formed a large portion of the seed bank but was not as dominant as *Schmidtia kalahariensis*. In this section *Eragrostis lehmanniana* had the largest seed bank compared to the other transect sections. This section had four species with Type I seed banks and four species with Type II seed banks.

Table 5.3 gives a summary of seed bank density for each of the life forms in each transect section, as well as in each season. Figure 5.6 gives a summary of the dispersal of life forms along the transect over the entire year. By comparing Figure 5.6a and 5.6b, it is clear that perennial dicot species are poorly represented in the seed bank while annual dicot species are well represented in the seed bank. Figure 5.6 shows that the fewest species above- and belowground are found at a mean distance of 15 m from the watering point. The most species above- and belowground are found at an average distance of 330 m from the watering point. Table 5.4 gives a good visual overview of species behaviour along the grazing gradient during the course of one year.

Table 5.3 Seed densities (seeds/m²) in the seasonally germinable seed bank (direct examinations) along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld

SUMMER		Seed density (seeds/m²) at different distances from a watering point (midpoint of section given in m from watering point)					
SPECIES	**LIFE FORM**	**15**	**60**	**150**	**330**	**630**	**1170**
Amaranthus dinteri	Annual Dicot	958	416		41		
Bulbostylis hispidula	Annual Dicot			125		83	
Chamaesyce inaequilatera	Annual Dicot				41		
Eragrostis lehmanniana	Perennial grass		83	250	83	416	500
Gisekia africana	Annual Dicot						41
Helichrysum argyrosphaerum	Annual Dicot	875	333	291	291	375	375
Hermannia tomentosa	Perennial Dicot		41				
Hermbstaetia fleckii	Annual Dicot				41		
Hirpicium gazanoides	Annual Dicot			41			
Limeum arenicolum	Annual Dicot				41		
Manulea burchellii	Annual Dicot				41		
Mollugo cerviana	Annual Dicot	41		41	41	41	41
Pharnaceum sp.	Annual Dicot			41			
Plinthus spp.	Perennial Dicot	41	41				
Requienia sphaerosperma	Perennial Dicot				41		
Salsola sp.	Annual Dicot	41					
Schmidtia kalahariensis	Annual grass	7 125	2 125	1 000	500	958	1 375
Stipagrostis ciliata	Perennial grass		125	41	41		83
Stipagrostis obtusa	Perennial grass				41		
Stipagrostis uniplumis	Perennial grass			41	41	125	
Total seed density of annual grasses		**7 125**	**2 125**	**1 000**	**500**	**958**	**1 375**
Total seed density of perennial grasses			**208**	**333**	**208**	**541**	**583**
Total seed density of annual dicots		**1 916**	**750**	**541**	**541**	**500**	**458**
Total seed density of perennial dicots		**41**	**83**		**41**		
AUTUMN							
Amaranthus dinteri	Annual Dicot	750					
Bulbostylis hispidula	Annual Dicot		41				
Chamaesyce inaequilatera	Annual Dicot		41		41	41	
Dipcadi glaucum	Bulb		41				
Eragrostis lehmanniana	Perennial grass			83	41		125
Helichrysum argyrosphaerum	Annual Dicot	583	1 375	791	791	500	416
Manulea burchellii	Annual Dicot					41	
Mollugo cerviana	Annual Dicot		125		41		41
Plinthus spp.	Perennial Dicot	333	291	83			
Requienea sphaerosperma	Perennial Dicot		41				
Schmidtia kalahariensis	Annual grass	83					
Total seed density of annual grasses		**83**					
Total seed density of perennial grasses				**83**	**41**		**125**
Total seed density of annual dicots		**1 333**	**208**	**791**	**875**	**583**	**458**
Total seed density of perennial dicots		**333**	**333**	**83**			
Total seed density of bulb			**41**				

Table 5.3 (cont.) Seed densities (seeds/m²) in the seasonally germinable seed bank (direct examinations) along a grazing gradient from the watering point on the farm Alpha in the Kalahari duneveld.

WINTER		Seed density (seeds/m²) at different distances from a watering point (midpoint of section given in m from watering point)					
SPECIES	**LIFE FORM**	**15**	**60**	**150**	**330**	**630**	**1170**
Amaranthus dinteri	Annual Dicot	667					
Helichrysum argyrosphaerum	Annual Dicot	291	667	875	541	583	500
Plinthus spp.	Perennial Dicot		41				
Schmidtia kalahariensis	Annual grass	541	375	83	375	83	250
Total seed density of annual grasses		**541**	**375**	**83**	**375**	**83**	**250**
Total seed density of perennial grasses							
Total seed density of annual dicots		**1 000**	**667**	**875**	**541**	**583**	**500**
Total seed density of perennial dicots			**41**				
SPRING							
Amaranthus dinteri	Annual Dicot	1 166	41	41			
Aristida adscensionis	Annual grass						125
Chamaesyce inaequelatera	Annual Dicot				41		
Dimorphotheca polyptera	Annual Dicot				41		
Eragrostis lehmanniana	Perennial grass			125			41
Eragrostis porosa	Annual grass				41	125	41
Helichrysum argyrosphaerum	Annual Dicot	125	83	208	291	250	125
Indigofera alternans	Annual Dicot					41	
Manulea burchellii	Annual Dicot			41		41	
Mollugo cerviana	Annual Dicot		83				
Salsola sp.	Annual Dicot	41					
Schmidtia kalahariensis	Annual grass	8 708	3 166	291	625	1 333	2 250
Stipagrostis ciliata	Perennial grass			41	208		
Tribulus zeyheri	Annual Dicot			41			
Total seed density of annual grasses		**8 708**	**3 166**	**291**	**667**	**1 458**	**2 416**
Total seed density of perennial grasses				**166**	**41**		**41**
Total seed density of annual dicots		**1 333**	**208**	**333**	**375**	**333**	**125**
Total seed density of perennial dicots							

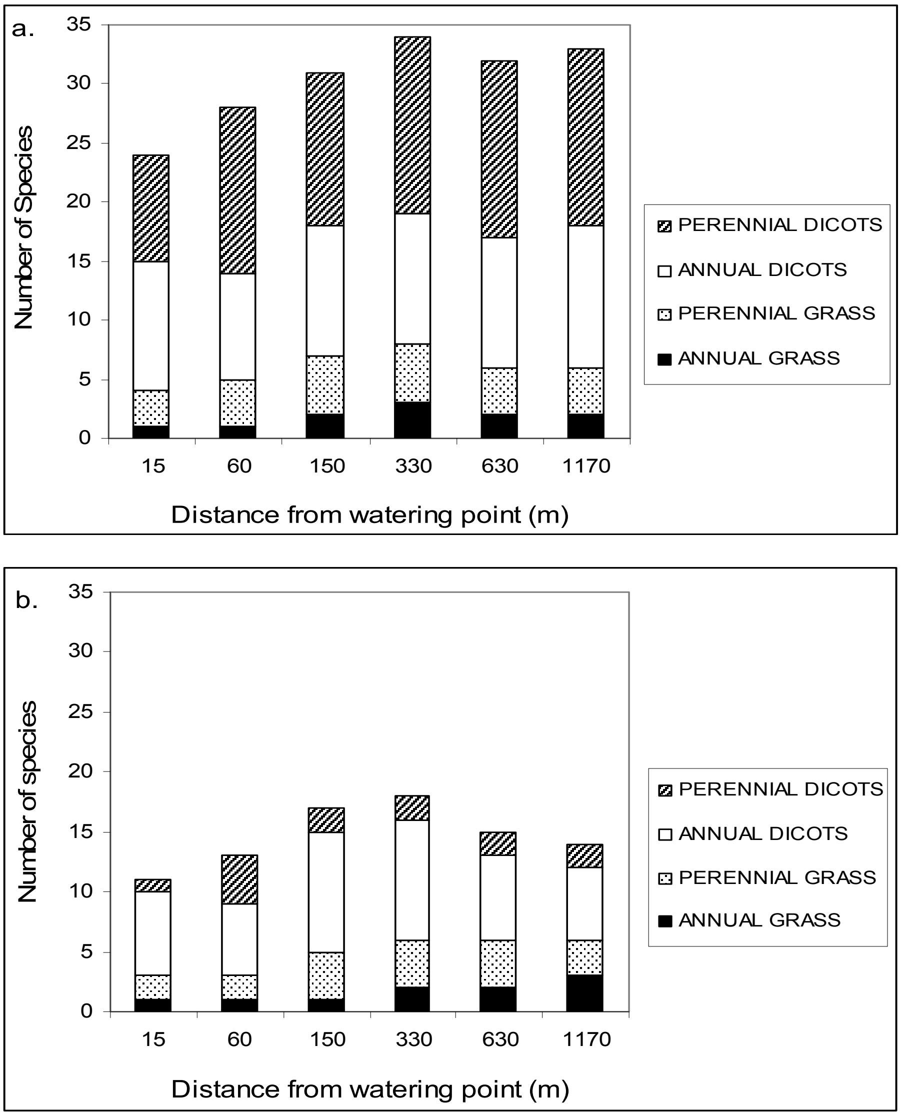


Figure 5.6 Contributions of different life forms to a. the aboveground flora and b. the belowground flora along a grazing gradient from a watering point on the farm Alpha in the Kalahari duneveld.

Table 5.4 The presence of species over the course of the year 2004, aboveground (shaded areas) and belowground (crosses) along a grazing gradient away from a watering point on the farm Alpha in the Kalahari duneveld

	Occurrence of species at mean distances (m) from the watering point							
Family and species	**15**	**60**	**150**	**330**	**630**	**1170**	**Growth form**	**A/P**
ACANTHACEAE								
Monechma incanum			▨				Dwarf shrub	P
AMARANTHACEAE								
Amaranthus dinteri	▨ x	▨ x	x	x			Herb	A
Amaranthus praetermissus	▨						Herb	A
Hermbstaedtia fleckii				x			Herb	A
Sericorema remotiflora						▨	Dwarf shrub	P
APOCYNACEAE								
Cynanchum orangeanum	▨					▨	Herb	P
ASPARAGACEAE								
Asparagus nelsii						▨	Shrub	P
ASTERACEAE								
Dicoma capensis		▨	▨	▨	▨	▨	Herb/creeper	P
Dimorphotheca polyptera		▨	x	x	▨	▨		
Helichrysum argyrosphaerum	▨ x	▨ x	x	▨ x	▨ x	▨ x	Herb/creeper	A
Helichrysum arenicolum	▨						Herb/creeper	A
Hirpicium echinus	▨	▨	▨				Dwarf shrub	P
Hirpicium gazanoides			x				Herb	A
AIZOACEAE								
Plinthus sp.	x	▨ x	▨ x		▨	▨	Dwarf shrub	P
BIGNONIACEAE								
Rhigozum trichotomum	▨	▨	▨	▨	▨	▨	Shrub	P
CUCURBITACEAE								
Cucumis africanus	▨	▨	▨	▨	▨	▨ x	Creeper	A
CONVOLVULACEAE								
Merremia verecunda				▨	▨		Creeper	A
CYPERACEAE								
Bulbostylis hispidula		x	▨ x	▨ x	▨ x	▨ x	Sedge	A
EUPHORBIACEAE								
Chamaesyce inaequilatera		x	x	x	x		Herb	A
Jatropha erythropoda				▨		▨	Herb	P
Ortanthera jasminiflora				▨			Creeper	P
FABACEAE								
Acacia haematoxylon				▨	▨		Tree	P
Acacia mellifera			▨	▨			Tree	P
Cullen obtusifolium	▨						Herb/creeper	P
Indigofera alternans	▨	▨	▨	▨	▨ x	▨	Herb/creeper	A
Melolobium microphyllum						▨	Herb	P
Parkinsonia africana	▨						Tree	P
Requienia sphaerosperma	▨	▨ x	▨ x	▨ x	▨ x	▨	Herb	P
Senna italica	▨	▨	▨	▨	▨		Creeper	P
GERANIACEAE								
Monsonia angustifolia				▨			Herb	P
GISEKIACEAE								
Gisekia africana			▨	▨	▨	▨	Herb/creeper	A

Table 5.4 (cont.) The presence of species over the course of the year 2004, aboveground (shaded areas) and belowground (crosses) along a grazing gradient away from a watering point on the farm Alpha in the Kalahari duneveld

	Occurrence of species at mean distances (m) from the watering point							
Family and species	**15**	**60**	**150**	**330**	**630**	**1170**	**Growth form**	**A/P**
LIMEACEAE								
Limeum arenicolum	▨			x			Herb/creeper	A
Limeum argute-carinatum	▨	▨	▨	▨	▨	▨	Herb/creeper	A
Limeum fenestratum						▨	Dwarf shrub	A
Limeum viscosum	▨	▨	▨	▨ x	▨	▨	Herb/creeper	A
MOLLUGINACEAE								
Mollugo cerviana	x	x	▨ x	▨ x	x	x	Herb	A
Pharnaceum sp.	x		x			x	Herb	A
PEDALIACEAE								
Harpagophytum procumbens						▨	Herb/creeper	P
Sesamum triphyllum	▨	▨	▨		▨	▨	Herb	A
PHYTOLACCACEAE								
Lophiocarpus polystachys		▨	▨			▨	Herb	A
POACEAE								
Aristida adscensionis	▨		▨	▨	▨	▨	Grass	P
Centropodia glauca			▨				Grass	P
Eragrostis lehmanniana	▨ x	▨ x	▨ x	▨ x	▨ x	▨ x	Grass	P
Eragrostis porosa				▨ x	x	x	Grass	A
Schmidtia kalahariensis	▨ x	▨ x	▨ x	▨ x	▨ x	▨ x	Grass	A
Stipagrostis ciliata	▨ x	▨ x	▨ x	▨ x	▨ x	▨ x	Grass	P
Stpagrostis obtusa		▨	▨	▨ x	▨ x	▨ x	Grass	P
Stipagrostis uniplumis	▨	▨	▨ x	▨ x	▨ x	▨	Grass	P
PORTULACACEAE								
Talinum crispatulum				▨	▨	▨	Herb	P
SCROPHULARIACEAE								
Aptosimum albomarginatum		▨	▨	▨	▨	▨	Dwarf shrub	P
Aptosimum marlothii					▨		Dwarf shrub	P
Manulea burchellii			x	x	x	x	Herb	A
Peliostomum leucorrhizum						▨	Herb	P
STERCULIACEAE								
Hermannia modesta		▨	▨	▨	▨	▨	Herb	P
Hermannia tomentosa	▨	▨ x	▨		▨		Dwarf shrub	P
VIOLACEAE								
Hybanthus densifolius				▨	▨	▨	Herb	A
ZYGOPHYLLACEAE								
Tribulus zeyheri	▨ x	▨ x	▨ x	▨	▨ x	▨ x	Herb/creeper	A

A = Annual species; P = Perennial species

5.4.3 Discussion

It is difficult to come to conclusions about rangeland degradation by looking at the seasonally germinable seed bank at one point in time only. It is important to sample the seed bank in different seasons in order to get a better picture of changes in species composition and density of the seed bank in different seasons. Specific germination requirements of all the species present in the soil are not likely to be met by a single prescribed germination treatment. Some seeds might also be in a dormant state, while other seeds do germinate, but for some reason the seedlings do not emerge (De Villiers *et al*., 1994). Thus in a study such as this, better results can be gained by using the seedling emergence together with the flotation method.

If sampling is done over several seasons, the seedling emergence method is a good way to identify perennial grass species which form transient seed banks. Seeds of many species of grassland and other relatively undisturbed habitats remain on, or very near to the surface after dispersal and germinate as soon as their requirements for moisture and suitable temperature are met. Such species frequently only form a transient seed bank, with no carry-over form one year to the next (Roberts, 1986). Several authors emphasize the importance of sexual reproduction of perennial grass species in the recovery of degraded rangelands (Mayor *et al*., 2003). However, seeds of perennial grass species are usually scarce in the soil and this would explain, at least in part, the slow recovery of disturbed perennial rangelands (Mayor *et al*., 2003).

In this study, the seeds of perennial grass species were also scarce in the soil, but their relative abundance did give an indication of a grazing gradient. For example the number of perennial grass species, as well as their relative contribution to the seed bank, increased away from the watering point. Thus by only looking at the transient portion of the seed bank gained by the seedling emergence method, certain effects of grazing pressure could be identified. Peco *et al.* (1998) predict that grasses are favoured in the absence of grazing. This effect can be seen in the present study, by the change in seed bank density and composition of the perennial grass seeds such as the *Stipagrosits* and *Eragrostis* species across the transect. The establishment and longevity of the seed banks of key species (i.e. pasture grasses), is an important aspect of rangeland ecology, especially given the possibility that the originally dominant and palatable grass species are likely to be prone to extinction (O’Connor & Pickett, 1992).

In seed bank studies done in Ethiopia along a distance gradient from water, Solomon *et al.* (2006), found that there were no significant differences in graminoid seedling/plant densities along the distance gradients from water. The species composition of the graminoids in the *seed bank* however showed variation in near, middle and far sites. This indicated that seed bank composition of the graminoids could reflect the grazing impacts better than the total seedling/plant density (Solomon *et al*., 2006). This may however not be the case if the grazing disturbance exceeds a certain threshold of degradation or if the degradation spreads uniformly outwards from the borehole under continued livestock pressure. In such occurrence, the composition of graminoids may exhibit homogenous trends along the gradient (Solomon *et al*., 2006). In semi-arid Patagonia, the abundance and diversity of the palatable perennial grass species decreased with increasing grazing pressure (Bertiller, 1996).

In this study the flotation method gave a very good insight into the permanent portion of the soil seed bank. Most hard-seeded species were not detected by the seedling emergence method, and thus no accurate conclusions could be drawn from the hard-seeded species that did germinate. The flotation results indicated a pattern in the way that hard-seeded species reacted to grazing pressure. According to Peco *et al.* (1998), forbs tend to respond positively to grazing. Also, species or life-forms which colonize disturbed habitats possess larger/more persistent seed banks than those of less disturbed habitats (Bertiller & Aloia, 1997). In this study, *Tribulus zeyheri* seeds and *Indigofera alternans* seeds were most abundant in the first two sections of the transect but also relatively abundant in the rest of the transect. Heavy grazing can promote seedling recruitment of forbs (Solomon *et al*., 2006) by reducing the suppressive effect and seed production of the grass component, thereby allowing forbs to reproduce and contribute an abundance of seeds to the soil seed bank (Solomon *et al*., 2006). In semi-arid *Festuca pallescens* grasslands in Patagonia, bare soil patches created by grazing animals were colonised by annuals or non-palatable perennials rather than by dominant perennial grasses (Bertiller, 1992).

In contrast, *Limeum* spp. seeds were most abundant in the sections of the transect under least grazing pressure, namely at 150 m, 330 m and 630 m mean distances in the transect. The sections closest to the watering point and closest to the fence, have much smaller *Limeum* spp. seed concentrations. These effects could not be detected when using the seedling emergence method. On the other hand, the seedling emergence method detected many species with Type II seed banks which could not be detected using the flotation method. *Schmidtia kalahariensis* (Type II) was most abundant in sections near to the watering point and also near to the fence. *Schmidtia kalahariensis* is a species which is favoured under sustained grazing. Such species include unpalatable species and species with 'r-selected' life-history characteristics such as short-lived tufts and high output of small, long-lived and well-dispersed seeds (O'Connor & Pickett, 1992). *Helichrysum argyrosphaerum* (Type II) seemed to be abundant in equal numbers in the seed bank throughout the transect without being affected by grazing pressure. Most of the other Type II seed bank species did not show a particular pattern of response to grazing pressure, except that the sacrifice zone had a very low species richness.

The results gained from the transient seed bank of the perennial grass species, and those gained from the hard-seeded species detected by the flotation trials could be used to detect a grazing gradient. Therefore in future seed bank studies in the Kalahari, the seed banks of perennial grasses, the seed bank of the annual grass species *Schmidtia kalahariensis*, and the seed banks of hard-seeded species such as *Limeum* spp. and *Indigofera alternans* can be used as indicators to detect grazing pressure or degree of veld degradation in the Kalahari duneveld.

5.4.4 Conclusions on seed bank types and growth forms

If there is a disturbance to the plant community, the seed bank may intervene in re-establishing the original community. This relationship between the composition of the seed bank and the vegetation is particularly important for the vegetation that appears under different management regimes (Lopez-Marino *et al*., 2000). An understanding of the population dynamics of buried viable seeds is of considerable practical significance. The determination of the composition of the seed bank in the light of the knowledge of long-term viability of the species involved, is clearly of great value in providing a basis for management and control strategies (Shaukat & Siddiqui, 2004). In this study, the types of species that occurred belowground and their seed bank types, could give an indication of the extent of degradation that has occurred in the rangeland.

Soil seed banks are important in savanna ecosystems where grasses count as a large part of the vegetation and their role is threefold. Firstly, the seed bank is a potential pool of propagules for regeneration of grasses after disturbance. Secondly, it may reduce the probability of population extinctions. Thirdly, it is likely to be the major source in establishing aboveground plant communities following environmental triggers such as rainfall.

The vegetation of arid rangelands can vary a great deal between seasons and between years, so it is often difficult to obtain accurate measures of rangeland condition (Navie *et al*., 1996). Seed banks provide important information additional to that of the standing vegetation about the condition of a rangeland. Most importantly, the seed bank provides insight into the possible renewal of the rangeland by germination from existing resources (Navie *et al*., 1996). Seed banks are less affected by present environmental conditions than is the vegetation, as they 'dampen' out the effects of seasonality and occurrences such as droughts, allowing an assessment relatively independent of recent events (Navie *et al*., 1996).

CHAPTER 6

SEASONAL VARIATION IN SOIL SEED BANK SIZE AND SPECIES COMPOSITION IN SELECTED HABITATS IN THE KALAHARI

6.1 INTRODUCTION

The temporal and spatial variation in opportunities for regeneration by seed, appear to play a vital part in the maintenance of diversity in herbaceous vegetation (Thompson & Grime, 1979). The nature and extent of hazards that individuals have to overcome during the establishment process, determine recruitment of species in the community (called ‘habitat’ in this study) (Rebello *et al*., 2001). Soil seed banks are important components of vegetation dynamics which in turn affect ecosystem resilience and resistance (Snyman, 2005).

To understand the dynamics of plant communities, specifically in arid areas, knowledge of seedling responses to different environmental conditions is of prime importance (Snyman, 2005). Germination strategies can be defined as response patterns of species (or groups of species) to sets of environmental conditions (Lavorel *et al*., 1993). Their interaction with the temporal distribution of disturbances, determines patterns of local and regional co-existence (Lavorel *et al*., 1993).

The type of environment will determine the ratio of annual to perennial plant species present as well as the type of seed bank which is formed (transient or persistent). Plant species with certain reproductive strategies will be optimally suited to certain environments. Plant communities form in response to habitat characteristics such as soil moisture/drainage (Pugnaire & Lazaro, 2000; Snyman, 2004), soil type (Skarpe, 1986; Coffin & Lauenroth, 1989; Ma *et al*., 2006), wind (Ma *et al*., 2006), soil litter (Rebello *et al*., 2001), soil temperature (Snyman, 2004), radiation (Pierce & Cowling, 1991; Gutierrez *et al*., 2000), facilitation effects by other plants (Pugnaire & Lazaro, 2000), topography/slope (Ortega *et al*., 1997; Caballero et al., 2005; Ma *et al*., 2006), nutrient content (Pierce & Cowling, 1991) and disturbance regimes. These factors will all play a role in shaping plant community composition in different habitats in an ecosystem.

In addition to this, the seed bank size and composition will fluctuate between seasons (Thompson & Grime, 1979; Hodgkinson *et al*., 1980; Henderson *et al*., 1988; Coffin & Lauenroth, 1989; Pierce & Cowling, 1991; Russi *et al*., 1992; Lavorel *et al*., 1993; Ortega *et al*., 1997; Lopez-Marino *et al*., 2000; De Villiers *et al*. 2002; Lopez, 2003; Mayor *et al*., 2003; Caballero *et al*., 2005). Recruitment of reproductive individuals of annual plants depends chiefly on the abundance of germinable seeds (Rebello *et al*., 2001).

The aim of this chapter was to compare the seed bank size and composition between five habitats, in the Kalahari duneveld, namely dune crest, dune slope, dune street, calcrete outcrop and riverbed. Additionally, the seasonal changes in seed bank size and species composition in each habitat were explored. The seedling emergence method was used to not only determine the readily germinable seed bank for each habitat, but re-examination trials were done to assess the accuracy of direct seedling emergence trials. Furthermore, the species richness of the aboveground flora was compared to that of the seed bank for five habitats and over four seasons. Similarities between the species composition of the seed bank and of the aboveground flora were also assessed in each of the habitats and seasons. Lastly the seed bank types and growth forms occurring in each habitat, over four seasons were compared.

6.2 SEED BANK SIZE AND SPECIES COMPOSITION

6.2.1 Introduction

A complete evaluation of the seed composition of soils is difficult, and the results may be biased by the evaluation technique employed (Manders, 1990) and most researchers have been able to make only general, qualitative statements concerning the seed bank (Bigwood & Inouye, 1988). One method by which a potential flora is assessed, is via identification and counting of seedlings emerged from the soil under controlled conditions (Barberi *et al*., 1998). Soil samples are spread in trays in a greenhouse and kept under those conditions known to promote the germination of as many species and individuals as possible (Ter Heerdt *et al*., 1996). The seedling emergence technique usually underestimates the number of viable seeds present, as the conditions for germination may not be optimal for all species (Manders, 1990). However, seedling emergence methods are simple and appropriate for large-scale studies (Ter Heerdt *et al*., 1996) and are widely used to assess seed densities in soil (Bossuyt *et al*., 2000).

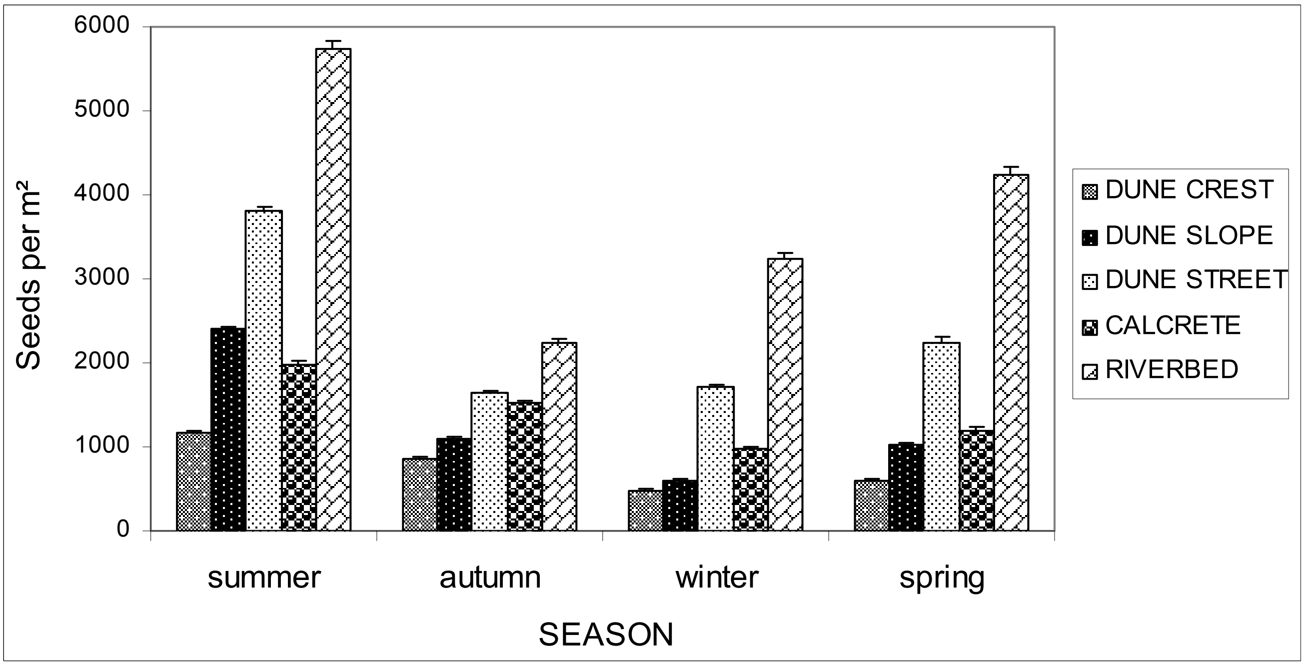


Figure 6.1 The size of the readily germinable seed bank (mean number of seeds/m² with SD) in five habitats over four seasons as obtained by the seedling emergence method directly after collection.

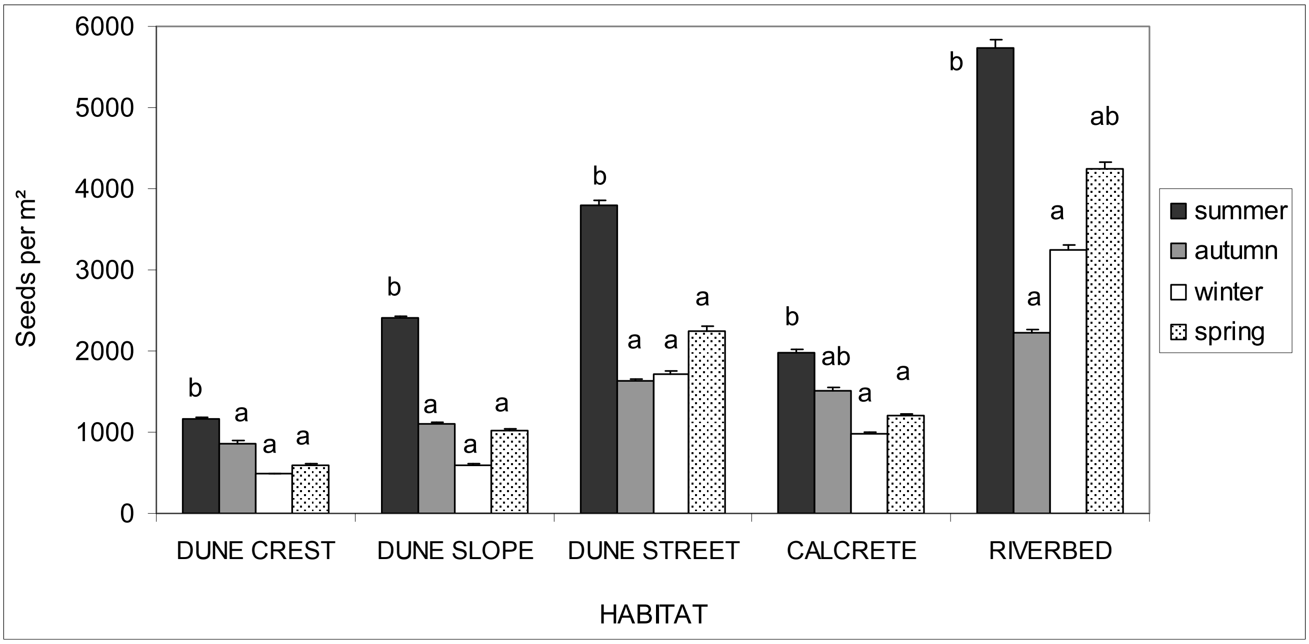


Figure 6.2 The seasonal differences in the size of the readily germinable seed bank (mean number of seeds/m² with SD) in five habitats as obtained by the seedling emergence method directly after collection. Bars with the same letter within a habitat do not differ significantly at $p < 0.05$.

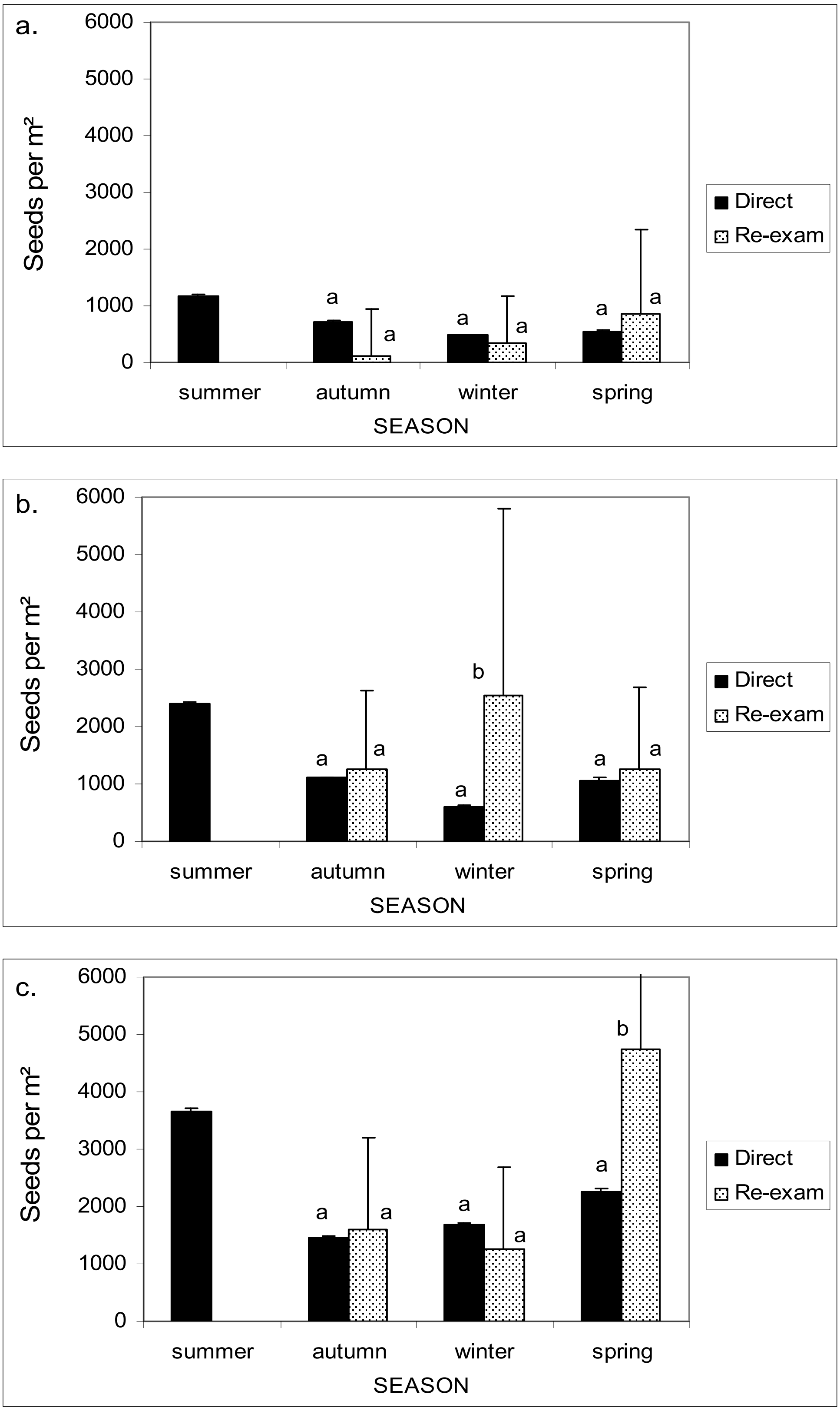
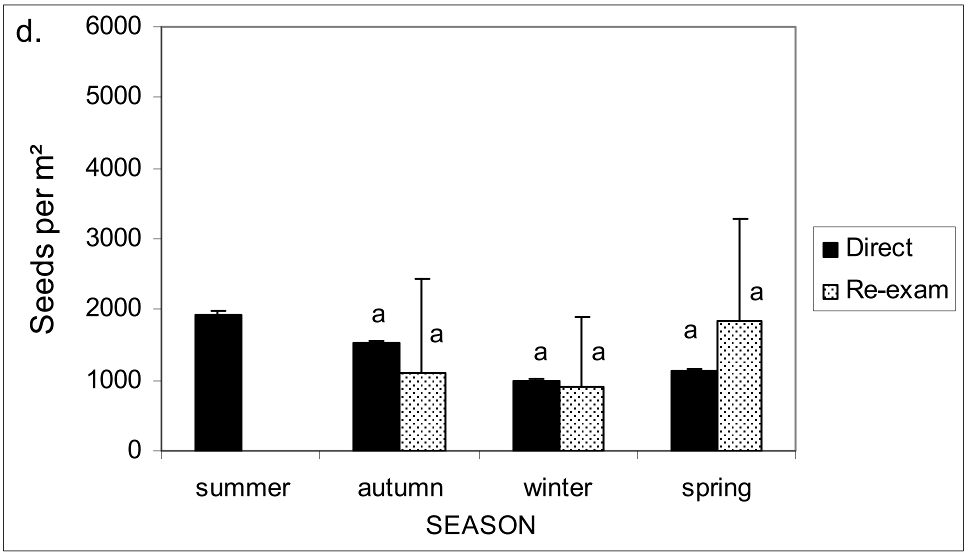


Figure 6.3 Comparison of seed bank size (mean number of seeds/m² with SD) obtained from soil samples collected in five habitats in the southwestern Kalahari when examined directly after collection (n=60) and re-examined in summer (n=20) a. Dune crest; b. dune slope; and c. dune street. Bars with the same letter do not differ significantly at $p < 0.05$.



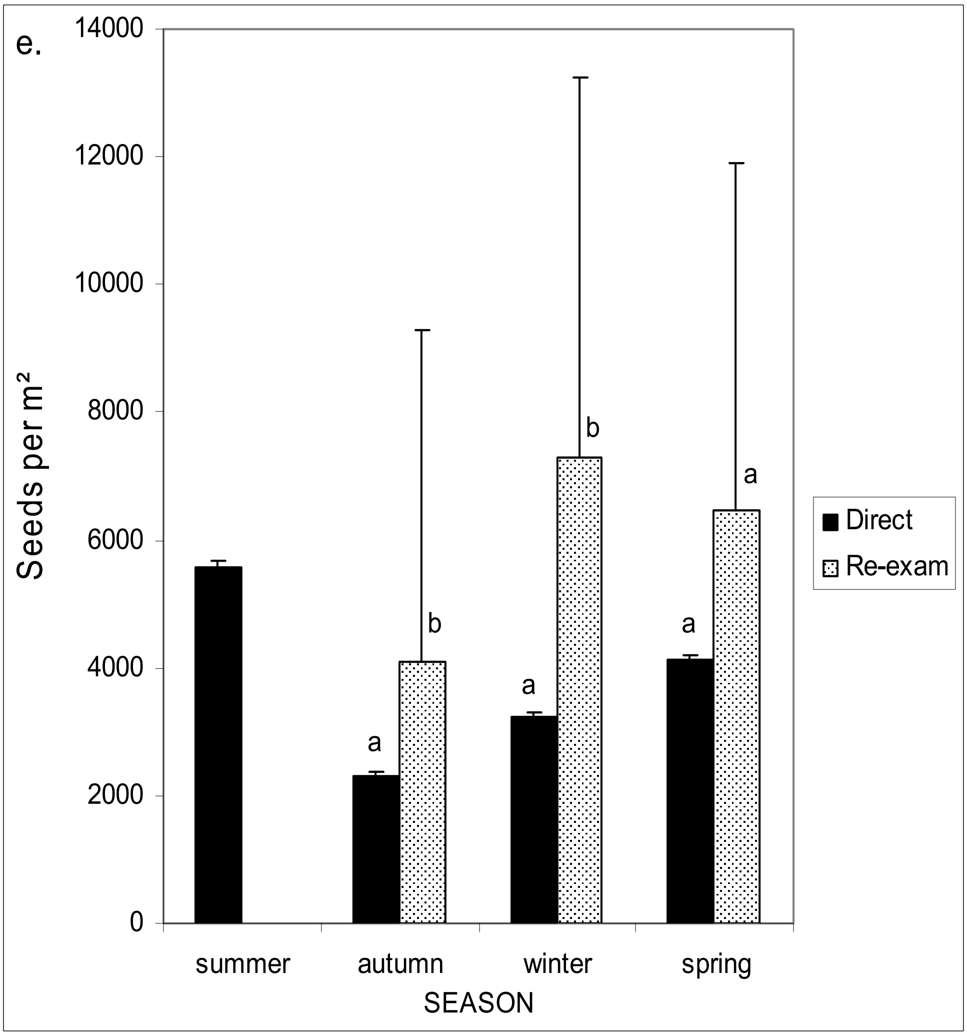


Figure 6.3 (cont.) Comparison of seed bank size (mean number of seeds/m² with SD) obtained from soil samples collected in five habitats in the southwestern Kalahari when examined directly after collection (n=60) and re-examined in summer (n=20). d. calcrete outcrop; and e. riverbed. Bars with the same letter do not differ significantly at $p < 0.05$.

6.2.2 Results

The seedling emergence method was used to compare the size of the readily germinable seed bank of each of the five habitats over four seasons. Changes in seed bank size over the entire year showed a consistent pattern, with the summer seed banks of all habitats always the largest, while the spring or autumn seed banks were always the second-largest (Figures 6.1 and 6.2). One-way ANOVA tests showed that in all habitats, season was a significant factor in determining seed bank size with $p < 0.00$ for all habitats except the the calcrete habitat where $p=0.0514$.

The riverbed consistently had the largest seed bank. In summer its seed bank was largest and estimated to contain 5 733 seeds/m², while its smallest seed bank was in autumn at 2 233 seeds/m² (Figures 6.1 and 6.2). In contrast, the dune crest habitat always had the smallest seed bank, out of all habitats, in all seasons. Its largest seed bank was in summer (1 166 seeds/m²) while its smallest seed bank was in winter (483 seeds/m²).

The dune street had the second largest seed bank over all seasons, compared to the other habitats. Its largest seed bank was in summer (3 800 seeds/m²) with a large reduction in size in autumn (1 633 seeds/m²) (Figures 6.1 and 6.2) and hardly any changes until late spring. The calcrete outcrop habitat did not display large changes in seed bank size over the course of the year. January displayed the largest seed bank (1 983 seeds/m²) but the seed bank size only slightly decreased in autumn (1 516 seeds/m²). The dune slope had its largest seed bank in summer (2 400 seeds/m²) but its seed bank size shrank four-fold towards winter (600 seeds/m²).

The seedling emergence method was also used to do a re-examination or duplicate experiment for soil samples collected during autumn, winter and spring. This was done by allowing the seed bank collected during these seasons to germinate during the optimal growing season (summer) (Figure 6.3). The re-examinations of the seed bank sizes did not show a consistent pattern of increased seed density in all habitats, except for the re-examined spring-collected samples for all habitats which showed higher seed densities in summer (with the dune street seed bank more than doubling, from 2 250 − 4 740 seeds/m²). The riverbed was the only habitat that showed a large increase in germinable seed bank size for all three seasons when re-examinations were done in summer (Figure 6.3e).

The patterns of seed germinability observed during autumn and winter were not consistent between the habitats. Re-examinations of dune crest seed banks of autumn- and winter-collected samples did not show a greater germinability when exposed to summer conditions. The autumn-collected seed bank gave an estimate of 716 seeds/m² when examined directly after collection, and only gave an estimate of 116 seeds/m² for the re-examination. The winter-collected seed bank also decreased in size for the re-examination (from 483 − 350 seeds/m²). Re-examinations done for dune slope seed banks of autumn-collected samples hardly showed an increase in germinability (from 1 100 − 1 250 seeds/m²) whereas the winter-collected samples showed a great increase (more than three-fold) in the size of the germinable seed bank (from 600 − 2 550 seeds/m²). Re-examinations of the dune street and calcrete outcrop's autumn- and winter-collected samples did not show a great difference in seed bank size compared to the direct experiments.

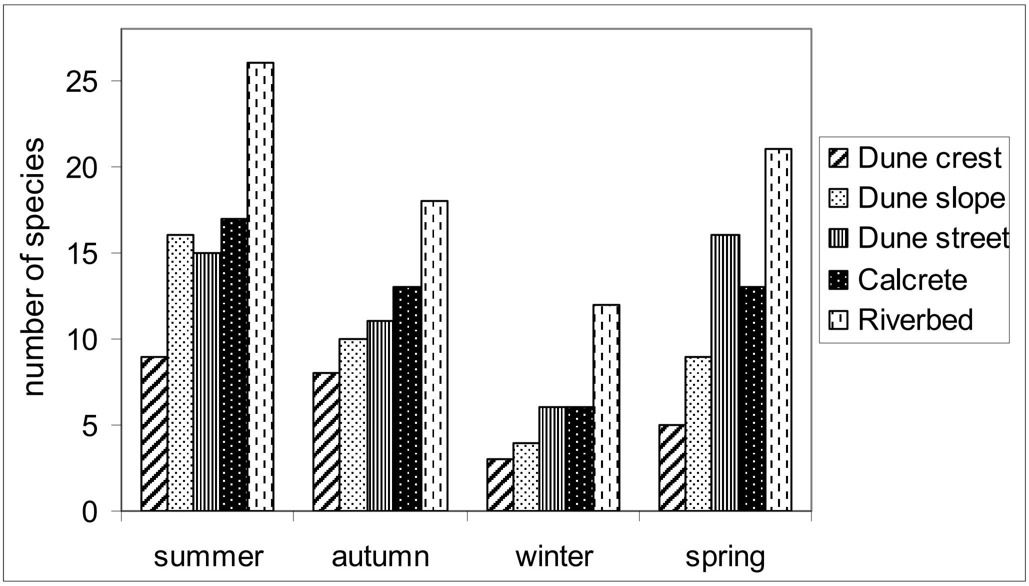


Figure 6.4 Species richness of the germinable seed bank in five habitats over four seasons as obtained by the seedling emergence method directly after collection.

Figure 6.4 shows that the riverbed habitat had the largest number of species present in the readily germinable seed bank over all four seasons. The dune crest habitat always had the lowest species richness of all habitats, over all seasons. The dune crest habitat had three species in its winter seed bank while the riverbed habitat had 12 species in its winter seed bank. The dune crest habitat had nine species in its summer seed bank while the riverbed habitat had 26 species in its summer seed bank.

In general, all habitats had the greatest number of species in summer. All habitats had the least number of germinable species during winter. The calcrete outcrop habitat had six species in its winter seed bank, the dune slope had four species and the dune street six species.

6.2.3 Discussion

No studies have to date been done on seed banks of the southwestern Kalahari. Some studies have been done on seed bank dynamics of other regions in arid southern Africa (Van Rooyen & Grobbelaar, 1982; De Villiers *et al.*, 1994; De Villiers *et al*., 2002; Snyman, 2004; Jones & Esler, 2004). A similar study to the present one has been conducted on seed banks of selected habitat types in Maputaland, South Africa (Kellerman, 2004; Kellerman & van Rooyen, 2007).

For the direct germination experiments, the largest seed bank was found in summer in all the habitats. This could be attributed to seed dormancy having been broken before the soil samples were collected. Furthermore, conditions were favourable for germination. Thus both the persistent and transient components of the seed bank could create the largest readily germinable seed bank in summer. The smaller seed bank sizes for the direct germination trials for spring-collected samples of all habitats, showed that seeds were still conditionally dormant and had not achieved their full germination potential as the seeds in summer. Also, the perennial grasses had not set seed at this stage. The re-examinations of spring-collected soil samples showed that either many seeds had been dormant in spring and/or that conditions for germination had not been favourable in spring. This could be observed for all the habitats. For the riverbed and dune slope habitats, the winter seed banks of the re-examinations were much larger than either the summer or spring re-examinations and were more than double the size of the winter seed banks estimated by direct germination. The high values for the re-examination indicated a large input of dormant seed in late autumn or early winter, but that these seeds had either already germinated by the time of the spring collection or that many seeds had been removed by predation.

The time of sampling the soil for the study of the seed bank is an important factor influencing results obtained (Lopez-Marino *et al*., 2000). Coffin and Lauenroth (1989) found that temporal variability between seed banks was more important than spatial variability between sites. Precipitation and temperature have been found to influence the timing of seed production and dispersal in shortgrass plant communities (Coffin & Lauenroth, 1989). Another possibility for the temporal differences in seed bank size is that species may be opportunistic in their germination behaviour. Seeds of many grassland species appear to germinate as soon as their soil moisture and temperature requirements are met rather than forming a large persistent seed bank. The seasonal variability in the number of stored seeds indicates the transient state in the seed bank (Coffin & Lauenroth, 1989).

All re-examinations of the riverbed seed banks were much larger than the direct trial results. This can be attributed to the type of species occurring in the riverbed and the type of environment experienced by the plants in the riverbed. The riverbed is a very unpredictable and harsh environment. The clay/silt soil can become very dry and cracked in hot weather. Only shrubs and herbs whose roots can survive the cracking clay can survive. Also the riverbed becomes periodically flooded showing that the species have to survive waterlogged conditions as well. Most species present in the riverbed were annuals. Coffin and Lauenroth (1989) looked at seed bank size of plant communities on fine-textured and coarse-textured soils in a grassland ecosystem. They found that annuals were significantly more abundant on the fine-textured (clay) site, while the cover and density of perennial shrubs and forbs were significantly greater on the coarse-textured (sandy) site. Most of the seeds produced on the fine-textured site were from annuals, most of the seeds on the coarse site were from perennial grasses (Coffin & Lauenroth, 1989). Such a difference could also be observed in the Kalahari savanna where there are differences in soil texture between the dune habitats and the riverbed habitat.

Annuals can survive as seeds in the soil for most of the year when conditions become intolerable. Annuals produce copious amounts of seed and are also opportunistic species and they rely on seeds for propagation and survival. The riverbed seed banks were always the largest relative to the other habitats throughout all seasons. Many of the species in the riverbed habitat seemed to be opportunistic as there were many germinable seeds in the seed banks collected in the riverbed during winter and spring. This would explain the large seed banks recorded from direct germination (due to the species' opportunistic nature) and the even larger seed banks recorded from the re-examinations in this habitat when conditions were truly favourable. Pierce and Cowling (1991) predict that large seed banks occur in communities subject to recurrent, large-scale disturbances. This would be due to the life spans of most of the component species being shorter than the average disturbance interval and where recruitment is confined to the immediate post disturbance period (Pierce & Cowling, 1991).

The greatest contrast to the riverbed seed bank results are those from the dune crest. The dune crest is a very exposed and windswept environment thus only a small number of seeds were found in the dune sand. Another probable reason for the small seed banks was that the dominant and diagnostic species found on the dune crest was *Aristida amabilis,* which mostly reproduces via stolons and very seldom via seed production. Most recorded seeds were probably from soil samples collected near clumps of *Aristida amabilis* where windblown seeds got trapped. Ma *et al*. (2006) measured seed bank densities of dune vegetation in three microhabitats namely, dune crest, dune plinth and inter-dune basin. They observed differences in the number of viable seeds in the soils of the three microhabitats. They found that microhabitat is a factor influencing soil seed bank size of different species. Ma *et al* (2006), attribute the differences in numbers of viable seeds of sand stabilising species (i.e. pioneer) observed in soils of different microhabitats to two factors. The first factor is the biotic factor which includes morphological, anatomical and physiological characteristics of seeds and their relationship to animals. The second is the abiotic factor which includes wind, rainfall, soil crust, soil structure and physical forces. In contrast to the present study, they found that many species had higher viable seed numbers in the dune crest (Ma *et al*., 2006). However, for the majority of species in both studies, the number of seeds in the seed banks was highest in the inter-dune basin. Ma *et al.* (2006) attribute this to the action of wind, rainfall, topography and seed morphological attributes.

The dune street had a relatively large germinable seed bank throughout the year. This indicates that there were also seeds of annuals and opportunistic species present which were germinable during winter and spring. The dune crest, dune slope and calcrete habitats showed a more conservative pattern where the germinable seed bank decreased in autumn and further decreased in winter and increased slightly in spring, with the biggest seed bank in summer. This may indicate that a higher percentage of perennial seeds were present in the germinable soil seed bank in summer. Perennials do not form very large seed banks and are generally not opportunistic species and thus their seeds would not be expected to be germinable throughout the year. In the grasslands that Jalili *et al*. (2003) studied, the effect of different types of management, and hence the severity of disturbance, was clear: there were more seeds in the soil in the scrubby grassland where the intensity of grazing was high, compared with steep grassland with only moderate grazing. Jalili *et al*. (2003) believe that the grazing of flowers and seeds caused a reduction in seed numbers in the seed rain and consequently the soil causing seed density to be significantly lower in grazed sites. However, the major contributors to the higher density of seed should be considered i.e. the types of species should also be considered to ascertain whether a certain seed bank size is naturally low or artificially low (Jalili *et al*., 2003).

Pierce and Cowling (1991), studied the seed banks of three different habitats/vegetation types (grassland, fynbos and thicket) within the coastal dune vegetation of the southeastern Cape. They pointed out that seed bank characteristics such as size and species composition were primarily a function of plant life history and seed physiology and that the selection for these traits was strongly influenced by disturbance regime. Grassland should have continuous small-scale disturbances due to grazing, hoof action and mole hills (in this case: squirrel warrens), which resulted in small open patches which provided opportunities for continual recruitment in grassland species from soil-stored seed banks. In contrast, less-disturbed plant communities should have smaller seed banks, especially those with long-lived trees and shrubs. Determination of size or composition of seed banks by germination may not give an accurate reflection of true size and composition as germination cues supplied in the field may be lacking (Pierce & Cowling, 1991).

The species richness of the seed banks in each habitat was not directly proportional to the seed bank size for each habitat (Figure 6.1 & 6.4). The differences in seed bank size between different habitats was greater than the difference in species richness between habitats. However, it was clear that the riverbed habitat had the greatest number of species in the Kalahari duneveld region, in addition to having the greatest seed bank size over all seasons. The differences in species richness between the riverbed and the other habitats was not as large as the seed bank size between the riverbed and the other habitats.

Jalili *et al*. (2003) found that the representation of species in the seed bank varied significantly with habitat. McIntyre and Lavorel (1994) found that lithology accounted for the most inter-site variability in species composition, but that topography (slope position and altitude) also affected variability in species composition. Caballero *et al*. (2005), found that in a semi-arid gypsophyte community, landform variables were selected among the best predictors, such that, seedling counts per quadrate might be interpreted as a result of physical processes regulating secondary dispersal and subsequent accumulation on the flattest bottom areas. They also suggested microslope and runoff as key factors for seed density in a gypsum community. Perennial cover also plays a role in species composition of seed banks. Some species exclusively occur on the thicker and harder crusted gypsum surfaces (Caballero *et al*., 2005). Similar trends could be seen in the Kalahari duneveld where the smallest number of species occurred on the dune crest where the windiest conditions occur. The moist dune slope with deep sand encouraged certain species assemblages and the dune street created a ‘hollow basin’ into which seeds of many species were blown. The calcrete outcrop provided many niches and hollows for seeds to collect and find protection from disturbance once germinated. The riverbed provided an ideal environment for many annual species to co-exist and proliferate. Thus species richness in each habitat was determined to a certain extent by abiotic forces working within each habitat.

The dune crest, dune slope and calcrete habitat followed the expected pattern of species richness of germinable seeds over all four seasons. Namely that the species richness of the germinable seed bank was greatest in summer (when dormancy is broken and when plants start to set seed), slightly smaller in autumn (as dormancy sets in and predation, decay occurs), smallest in winter and larger again in spring as seeds of more species become germinable again. Seasonal changes exert a certain control on seed bank species (Caballero *et al*., 2005) and seasonal changes in density can vary widely among species. However, a seed bank should be present for most species at most sampling dates and thus seed banks should keep a constant structure even under substantial variation in density (Caballero *et al*., 2005). It is usually possible to detect seasonal patterns in seed bank composition, which allows seasonal germination strategies to be described from the temporal distributions of abundances of different species (Lavorel *et al*., 1993).

The dune street habitat was the only habitat that did not display the expected pattern for species richness in the seed bank over the four seasons. It differed from the other habitats in that the species richness was as large in spring as in summer. This could indicate that some of the species present in the seed bank have seeds that prefer to germinate in spring. However, determination of size or composition of seed banks by germination may not give accurate reflection as germination cues supplied in the field may be lacking. The seedling emergence method may give special emphasis to the transient component and therefore bias results (Pierce & Cowling, 1991). Thus the species in this study that germinate under the experimental conditions may be different to those that would have germinated under *in situ* Kalahari conditions.

6.2.4 Conclusions on seed bank size and species composition

Seed bank density differed between each of the five habitats in this study. Habitat type does play a role in the type of vegetation that develops and thus also in the size of the corresponding seed bank. The vegetation of the dune crest was dominated by a perennial grass which mostly reproduces vegetatively. The corresponding seed bank density was thus very small. The vegetation of the riverbed was composed of many annual species. The annual species form persistent seed banks which are high in density. This habitat thus had the largest seed bank density of the five habitats.

The seedling emergence method was used to determine seasonal changes in seed bank size in each habitat. Seed banks were typically largest in summer and smallest in winter, in all habitats. Seedling emergence re-examination trials for spring-collected soil samples estimated that the seed banks were actually larger than what the direct seedling emergence trials predicted. Duplicate trials can thus be used to get a more accurate estimate of the number of viable seeds in each habitat in a certain season.

Species richness differed between each of the five habitats in this study. Habitat type does play a role in species richness of the plant community, as well as species richness of the corresponding seed bank. The dune crest habitat was a wind-swept habitat and consequently had very few species in its vegetation and few species in its seed bank. The riverbed habitat was also a much disturbed habitat, but the type of disturbance was severe drought with intermittent flash floods. Instead of the species richness being small (as in the case of the dune crest) the disturbance favoured many species with an annual life history. Thus species richness in the habitats differed due to disturbance type, soil type, radiation, soil depth and perennial cover.

6.3 COMPARISON OF THE ABOVEGROUND AND BELOWGROUND FLORAS

6.3.1 Introduction

Similarity between seed bank and standing vegetation has been frequently studied in different plant communities, aiming to improve the understanding of the role of seed banks in successional and regenerational processes. In grasslands the degree of similarity differs across habitats and environmental conditions, successional stages and type of disturbance (Osem *et al*., 2006). The relationship between seed bank and vegetation are particularly important in semi-arid and arid rangelands where factors constraining germination, establishment and plant survival shift from soil to canopy resources along productivity gradients. A better understanding of such processes is needed for the establishment of adequate conservation and management policies in semi-arid regions (Osem *et al*., 2006).

In grassland, ruderal and other plant communities, seeds of some species may be present for only part of the year whereas others contribute to the persistent seed bank. After disturbance, the vegetation which develops will depend to a considerable extent on which species are represented in the seed bank and on their requirements for germination (Roberts, 1986). Understanding seed bank ecology is a key to elucidating community development and its dynamics and may be useful in various practical aspects of management and conservation of natural and semi-natural ecosystems (Shaukat *et al*., 2004). The composition of the seed bank depends on the production and composition of the present and previous plant communities, as well as the longevity of the seeds of each species under local conditions (Lopez-Marino *et al*., 2000).

In this section differences between the aboveground flora and belowground flora are examined in each of the five habitats. The seasonal differences within each habitat are also examined. Data on the species richness of the aboveground vegetation was derived from the Braun Blanquet method of vegetation survey. Data of the species richness of the seed bank were collected using the seedling emergence method.

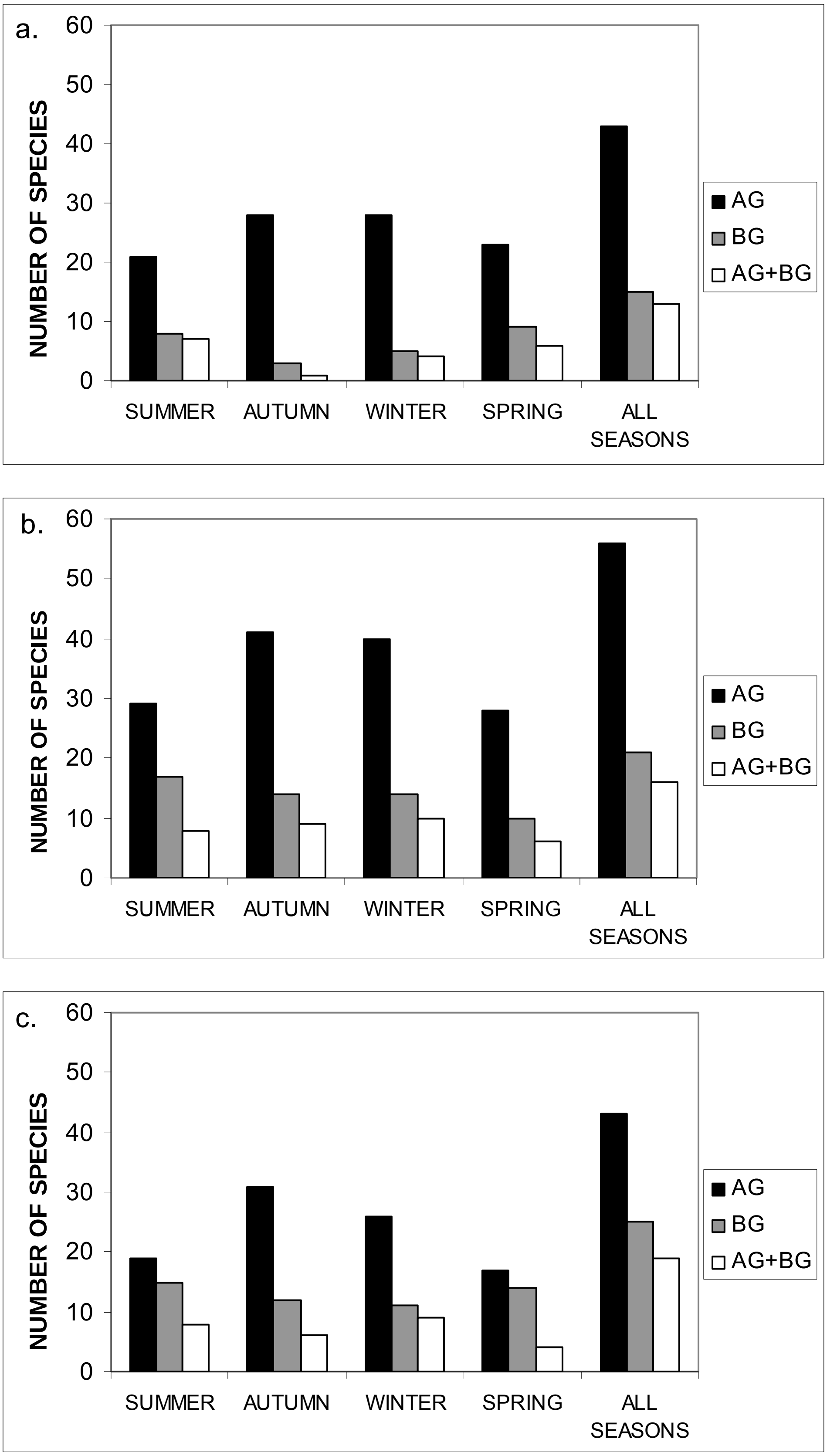
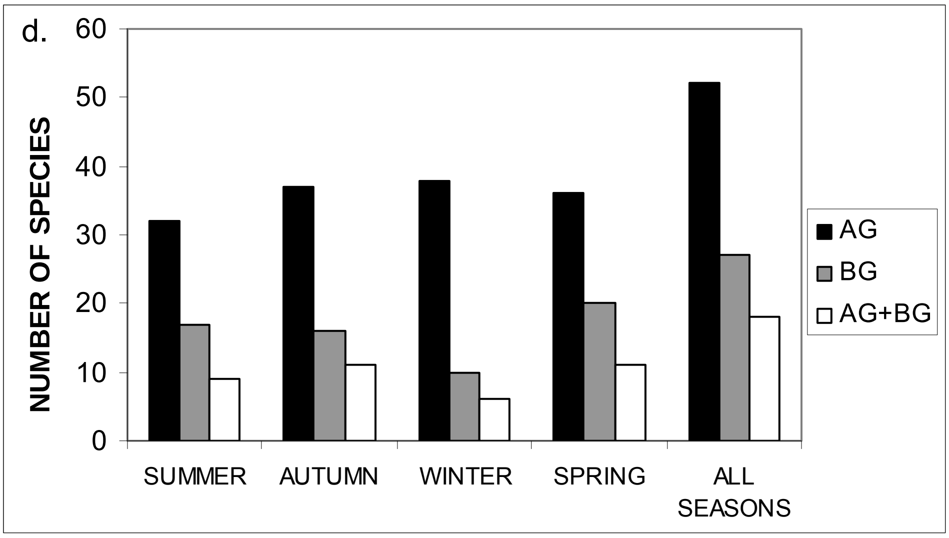


Figure 6.5 Seasonal comparisons of the aboveground (AG) and belowground (BG) floras and species common to both floras (AG+BG) in five habitats on the farm Alpha in the Kalahari duneveld. a. Dune crest; b. dune slope; and c. dune street.



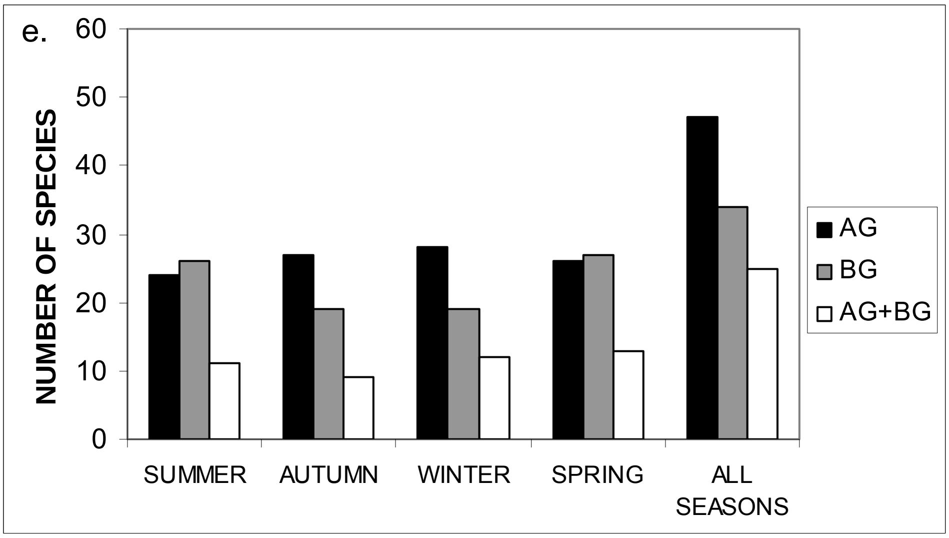


Figure 6.5 (cont.) Seasonal comparisons of the aboveground (AG) and belowground (BG) floras and species common to both floras (AG+BG) in five habitats on the farm Alpha in the Kalahari duneveld. d. calcrete outcrop; and e. riverbed.

Table 6.1 Percentage similarity between aboveground and belowground floras in the five habitats (over four seasons) on the farm Alpha in the Kalahari duneveld

	Similarity between aboveground flora and seed bank (%)				
	Summer	**Autumn**	**Winter**	**Spring**	**All seasons**
Dune crest	46	33	43	50	53
Dune slope	28	30	16	31	35
Dune street	33	4	14	26	30
Calcrete	28	22	25	21	29
Riverbed	42	19	35	24	44

6.3.2 Results

The dune crest, dune slope, dune street and calcrete outcrop habitats all had notably more species in the aboveground flora than in the belowground flora, over all seasons. Only the riverbed habitat sometimes had a larger belowground flora than aboveground flora. All habitats had a larger aboveground flora in autumn and winter than in spring and summer. The reverse trend was evident for the belowground floras of all habitats (Figure 6.5).

The dune crest habitat had a small belowground flora throughout the year. Many species which were found aboveground, were also present in the seed bank (Figure 6.5a and Table 6.1). The contrast between the number of species found aboveground and those found belowground, was large. For example the dune crest's summer aboveground flora had 21 species while the summer seed bank had eight species. The dune crest's autumn aboveground flora had 28 species while the autumn seed bank flora only had three species.

The dune slope habitat had many species aboveground throughout the year but the species count in the seed bank was relatively small in comparison, especially during spring (where there was a difference of 18 species, which was unexpected if compared to the other values). The aboveground flora contained many of the species which were present in the seed bank. However, there were six species contained in the seed bank which were never present in the aboveground flora, over the four seasons (ALL seasons).

The difference between the aboveground and belowground flora size in the dune street habitat, was not as extreme as in the dune crest and dune slope habitats. The species richness of the aboveground flora (43 species) was somewhat larger than the species richness of the seed bank (25 species), cumulatively for all four seasons (ALL seasons). However, in this habitat there was also a portion of the belowground flora (19 species) which was never encountered aboveground during the entire year. The aboveground flora of the calcrete outcrop was relatively large and relatively consistent in size throughout the four seasons. There were a notable number of species (nine species) that were present in the seed bank but which were never present aboveground over the four seasons.

Relationships between the above- and belowground floras in the riverbed habitat differed from those in other habitats. During spring and summer the seed bank flora was larger than the aboveground flora. Also, there was not such a great difference in size between the seed bank and aboveground flora during autumn and winter. The total number of species present in the riverbed aboveground flora, was not as large as expected, as this habitat has the biggest seed bank size over the four seasons. There were also a notable number of species (nine species) present in all the riverbed seed banks, which were never seen aboveground.

6.3.3 Discussion

Whether vegetational differences are the result of environmental differences or of limited seed dispersal, can be addressed through the examination of the buried seeds (Roach, 1983). The species of seed in the soil are often different from the species that form the standing vegetation (Roach, 1983). Similarity between seed bank and standing vegetation has been studied frequently in different plant communities, aiming to improve the understanding of the role of seed banks in successional and regenerational processes (Osem *et al*., 2006). In grasslands the degree of similarity differs across habitats and environmental conditions, successional stages and types of disturbance (Osem *et al*., 2006). Variation in seed bank – vegetation similarity has been found in relation to several environmental gradients including precipitation, edaphic conditions, salinity, nitrogen availability and altitude (Osem *et al*., 2006). Proposed mechanisms determining seed bank – vegetation similarity include inhibition or promotion of germination; variation in seedling emergence, establishment and survival; changes in the proportion of annual versus perennial species, species with persistent versus transient seed banks, or species differing in tolerance to abiotic stresses (Osem *et al*., 2006).

The dune crest, dune slope, dune street and calcrete habitats all displayed a similar pattern in species richness for above- and belowground floras. The number of species aboveground tended to be largest during autumn and winter when most species were still present aboveground. This pattern changed from winter to spring. The number of plants from the previous season were no longer so abundant as they had died down after the winter. Thus the spring and summer species aboveground were much fewer as the seedlings of the new set of adult plants were only beginning to germinate during the warm weather. However seed bank species richness showed a contrasting pattern. The species richness of the seed bank declined as the germinability of the seeds declined in autumn and winter as dormancy set in making less species available for germination. The species richness of the seed bank increased in spring and summer as dormancy was broken.

The dune crest habitat had the least number of species in its seed bank. This was expected because this habitat is very windswept with seeds only finding anchorage in the soil in depressions or grasses. However, the number of species found aboveground was proportionally much larger than would be expected. The grass *Stipagrostis amabilis* was the dominant grass on the crests. The other species found on the crest had few individuals which just happened to find anchorage in an opportunistic way. This may explain why a number of species found aboveground were not found belowground through most of the seasons. This habitat had a very small seed bank in autumn and winter in comparison to the other habitats.

Throughout the year, the dune slope had a certain proportion of species aboveground which were never found belowground. Perennial grass species form small transient seed banks, which could explain the large gap between the number of species aboveground compared to belowground. The difference between seed bank and aboveground species numbers were proportionally large for this habitat. Usually, low similarity occurs in grasslands dominated by perennial species (Peco *et al*., 1998; Osem *et al*., 2006). This has been explained by the minor contribution of dominant perennial meadow species to the formation of seed banks (Peco *et al*., 1998). This is because they alternate sexual reproduction with vegetative form reproduction and their seeds have a short-term persistence in the soil (Peco *et al*., 1998; Amiaud & Touzard, 2004).

The dune street was quite species poor aboveground but there was not such a great contrast between the number of species aboveground and belowground as in the previous two habitats. This could indicate a large persistent seed bank formed by annuals which flourished in the much disturbed/grazed habitat. Annuals form persistent seed banks with copious seeds. This could indicate that this habitat was not as stable as the other two dune habitats, which have a smaller and transient seed bank. The calcrete outcrop had many species aboveground but also a fairly large number of species in the seed bank. There were many species belowground that were never found aboveground throughout the year. The high species richness was probably due to the calcrete being a unique environment to which many species are endemic but where seeds from the surrounding habitats also add to the aboveground species richness. There were many niches and hollows where the seeds could collect and it was bordered by all the other habitats.

The riverbed showed a very different pattern to the other habitats. This habitat had a seed bank containing many species and the aboveground flora was less rich than the belowground flora for some seasons. The riverbed is a harsh environment where mostly only annuals can survive. Annuals are not always represented aboveground and often survive in the seed bank for a number of years. There was not really a large difference in the species richness between the seed bank and the aboveground flora. Higher similarity (between seed bank and vegetation) has been found in (plant) communities dominated by annuals (Osem *et al*., 2006). In such communities, most of the vegetation develops each year from the available seed bank and, therefore, the seed bank at the onset of the growth season should correspond to species composition and plant density in the vegetation. The riverbed habitat could be regarded as a system that is subject to a regime of frequent and unpredictable disturbances either by flooding or by drought (Henderson *et al*., 1988; Peco *et al*., 1998; Armiaud & Touzard, 2004). The common denominator of such systems is the predominance of annual species (Peco *et al*., 1998; Armiaud & Touzard, 2004). It is suggested that in such systems the seed bank is the major source of seedling recruitment after disturbances. This is a crucial role generally played by seed banks in ecosystems where disturbances do not allow plants to reproduce each year (Armiaud & Touzard, 2004).

6.3.4 Conclusion on comparisons between aboveground and belowground floras

Buried viable seeds help to define the flora of a given ecosystem (Major & Pyott, 1966). This is especially true in a desert or arid environment where certain species survive as seeds in the soil seed bank for a season or for a number of years. It is thus important to define habitats in semi-arid or arid areas not only by their aboveground flora but also by their belowground flora. Seasonal vegetation changes in the five habitats can be contrasted with seasonal changes in their corresponding seed banks in order to more fully understand the dynamics of the vegetation in the Kalahari.

In habitats where the contrast between the number of species in the aboveground vegetation and number of species in the readily germinable seed bank is large, one would expect many species to form transient seed banks and thus not be well represented in the seed bank (e.g. dune slope and dune crest habitat). These habitats also have their largest readily germinable seed banks in summer, as perennial grasses tend to germinate in this season. Some habitats did not have such a large contrast between seed bank species richness and aboveground species richness (e.g. riverbed habitat). Such a habitat has many annual species in its vegetation, which produce persistent seed banks. Thus annual species which are represented belowground may have died off aboveground, and thus increasing the species richness of the persistent seed bank. Such habitats also have a large readily germinable seed bank in spring.

Despite the differences between the habitats, all five habitats had a portion of species in their seed banks which were never seen aboveground, and species in their vegetation that were not detected in the seed bank. Some species which were represented aboveground, may have been represented belowground, but had persistent seed banks or hard-seeded seeds that did not react to the germination cues. The species that were represented in the readily germinable seed bank only, may not have found tolerable conditions to grow in once they had germinated.

6.4 SPECIES COMPOSITION, SEED BANK TYPE AND GROWTH FORMS

6.4.1 Introduction

Three broad classes of seed longevity in the soil have been acknowledged:

1) transient
2) short-term persistent and
3) long-term persistent.

These types range from transient seed banks constituted by seeds which germinate in greater numbers directly after dispersal, to persistent seed banks which remain dormant in the soil over long periods. In grassland, ruderal and other plant communities, seeds of some species may only be present for part of the year whereas others contribute to the persistent seed bank (Roberts, 1986). By classifying the seed banks of different species into types, the role of seed banks in vegetation dynamics or in the ecology of individual species can be assessed (Thompson & Grime, 1979). Although each plant species may display a characteristic seed bank strategy,dominant strategies can vary in different habitats (Bertiller & Aloia, 1997). Persistence of seeds in soil varies between species and between habitats. The extent of germination shortly after seed fall depends on whether the temperature, moisture and light requirements of the otherwise non-dormant seeds are met (Roberts, 1986).

Direct evidence for the longevity of seeds in the soil can only be gained from burial experiments. Since such work has been carried out for a few species and is very time-consuming, scientists have to rely on indirect methods for the estimation of the longevity of seeds in soil (McDonald *et al*., 1996). The direct seedling emergence method was used to gain insight into the germination behaviour and seed bank types for the species present in the readily germinable seed bank in each habitat and in each season. Furthermore a canonical correspondence analysis (CCA) (Version 4.5, Microcomputer Power, Ithaca, New York) was used to compare the species composition of the readily germinable seed bank within each habitat over four seasons. This analysis showed the temporal distribution of the readily germinable species in the seed bank for each habitat.

6.4.2 Results

In all habitats the two *Helichrysum* species (*Helichrysum argyrosphaerum* and *Helichrysum arenicolum*) showed consistent germination patterns, namely that they germinated in the seasons of autumn and winter (Figure 6.6). Another species that was common to all habitats, *Schmidtia kalahariensis*, clearly preferred the warmer months of spring and summer to germinate. But this annual grass tends to germinate mostly readily in spring. The perennial dwarf shrub, *Felicia clavipilosa*, tended to germinate most readily in the cooler autumn and winter months in the riverbed and calcrete outcrop habitats. The herb *Gisekia africana*, germinated from samples taken in the dune street and dune slope habitats. In both instances this species clearly germinated exclusively in spring. Most of the perennial grasses (and some annual grasses) preferred to germinate during summer but sometimes already germinated in spring (e.g. *Eragrostis lehmanniana, Eragarostis bicolor, Eragrostis porosa, Stipagrostis obtusa, Stipagrostis ciliata*). *Amaranthus dinteri* and *Amaranthus praetermissus,* annual pioneers germinating in a wide range of habitats, did not show a preference for germinating in a particular season. The dwarf shrub *Plinthus* species, were found in most habitats, germinating in the cooler months of the year. The herb *Limeum argute-carinatum*, was a spring germinator.

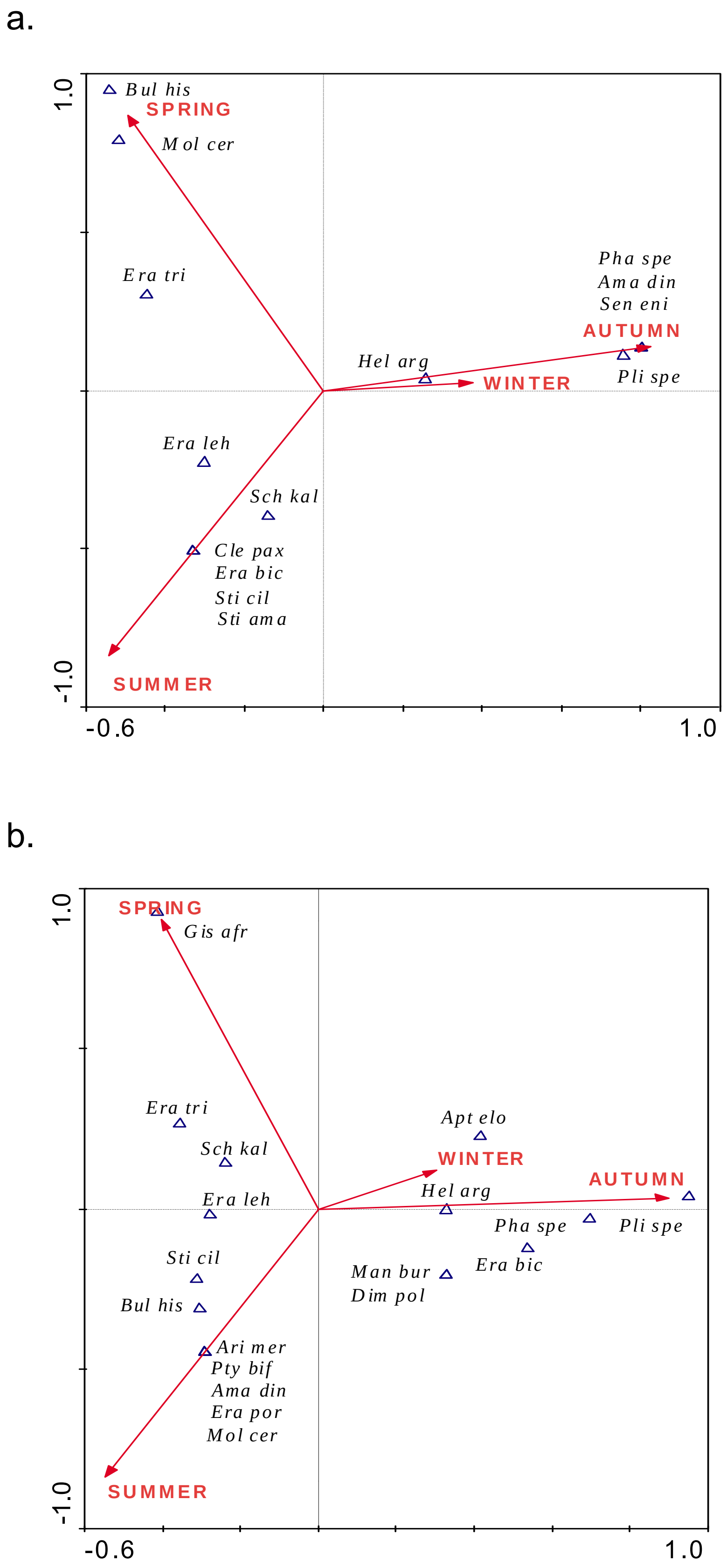


Figure 6.6 Ordinations showing the temporal distribution of the readily germinable seed bank (direct germination) in five habitats on the farm Alpha in the Kalahari duneveld a. Dune crest; b. dune slope.

c.

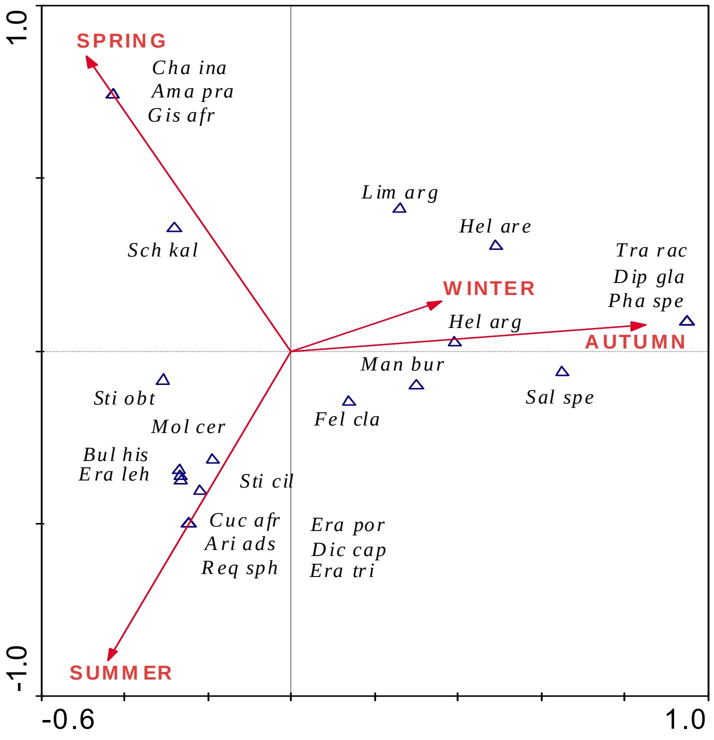


Figure 6.6 (cont.) Ordination showing the temporal distribution of the readily germinable seed bank (direct germination) in five habitats on the farm Alpha in the Kalahari duneveld c. dune street.

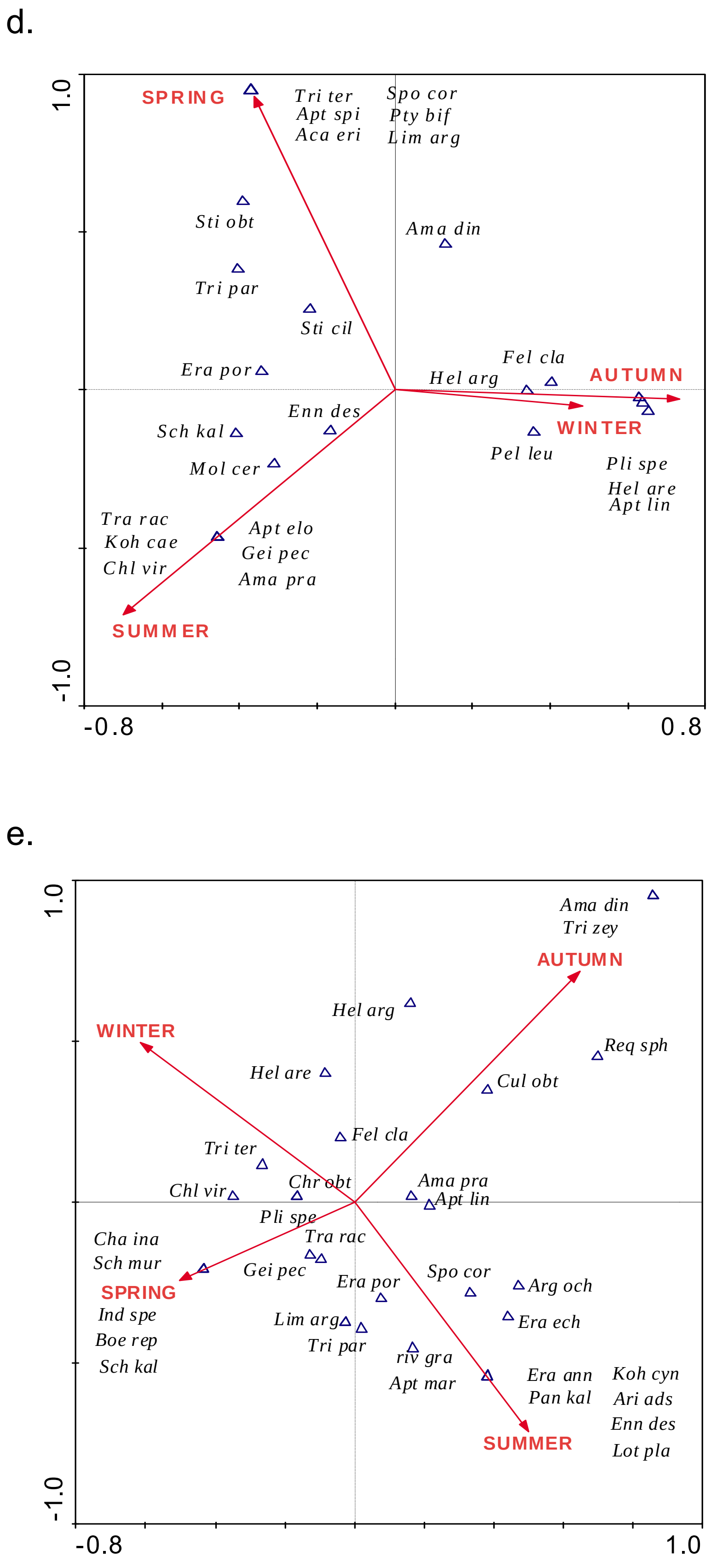


Figure 6.6 (cont.) Ordinations showing the temporal distribution of the readily germinable seed bank (direct germination) in five habitats on the farm Alpha in the Kalahari duneveld d. calcrete outcrop; and e. riverbed.

Table 6.2a Seed densities (seeds/m²) in the summer seasonally germinable seed bank (direct examination) in five different habitats on the farm Alpha in the Kalahari duneveld

		Seed densities in different habitats (seeds/m²)				
Species	**Life form**	**Crest**	**Slope**	**Street**	**Calcrete**	**Riverbed**
Amaranthus dinteri	Annual Dicot		33			
Amaranthus praetermissus	Annual Dicot				83	1 333
Aptosimum elongatum	Annual Dicot		16		16	
Aptosimum lineare	Annual Dicot					983
Aptosimum marlothii	Perennial Dicot					16
Argemone ochroleuca	Annual Dicot					216
Aristida meridionalis	Perennial grass		100			
Aristida adscensionis	Annual grass			33		16
Bulbostylis hispidula	Annual sedge		150	116		
Chloris virgata	Annual grass				16	983
Chrysocoma obtusata	Perennial Dicot					16
Cleome paxii	Annual Dicot	33				
Cucmis africana	Annual Dicot			16		
Cullen obtusifolia	Annual Dicot					116
Dicoma capensis	Annual Dicot			16		
Dimorphotheca polyptera	Annual Dicot		16			
Enneapogon desvauxii	Perennial grass				116	50
Eragrostis annulata	Annual grass					66
Eragrostis bicolor	Perennial grass	66	16			
Eragrostis echinochloidea	Annual grass					116
Eragrostis lehmanniana	Perennial grass	466	816	450		
Eragrostis porosa	Annual grass		16	316	500	250
Eragrostis trichophora	Perennial grass	66	200			
Felicia clavipilosa	Perennial Dicot			16	33	83
Geigeria pectidea	Perennial Dicot				100	100
Helichrysum arenicolum	Annual Dicot					66
Helichrysum argyrosphaerum	Annual Dicot	333	450	700	233	50
Kohautia caespitosa	Perennial Dicot				33	
Kohautia cynanchica	Annual Dicot					16
Limeum argute-carinatum	Annual Dicot					16
Lotononis densa	Annual Dicot					50
Manulea burchellii	Annual Dicot		16			
Molluga cerviana	Annual Dicot	16	66	1 083	100	
Panicum coloratum	Perennial grass					16
Peliostomum leucorrhizum	Perennial Dicot				16	
Pharnaceum sp.	Annual Dicot		33			
Plinthus spp.	Perennial Dicot				16	33
Ptycholobium biflorum	Perennial Dicot		16			
Requienia sphaerosperma	Perennial Dicot			16		16
River grass	Annual grass					466
Schmidtia kalahariensis	Annual grass	66	266	600	450	
Sporobolus coromandelianus	Annual grass					83
Stipagrostis amabilis	Perennial grass	33				
Stipagrostis ciliata	Perennial grass	16	83	133	66	
Stipagrostis obtusa	Perennial grass			33	16	
Tragus racemosus	Annual grass				16	66
Trianthema parvifolia	Annual Dicot				33	83
Total seed density of annual grasses		**66**	**283**	**950**	**983**	**2 050**
Total seed density of perennial grasses		**650**	**1 216**	**616**	**200**	**66**
Total seed density of annual dicots		**383**	**633**	**1 833**	**466**	**2 933**
Total seed density of perennial dicots			**16**	**33**	**233**	**266**
Total seed density of annual sedges			**150**	**116**		

Table 6.2b Seed densities (seeds/m^2) in the autumn seasonally germinable seed bank (direct examination) in five different habitats on the farm Alpha in the Kalahari duneveld

		Seed densities in different habitats (seeds/m^2)				
Species	**Life form**	**Crest**	**Slope**	**Street**	**Calcrete**	**Riverbed**
Amaranthus dinteri	Annual Dicot	16			16	16
Amaranthus praetermissus	Annual Dicot					900
Aptosimum elongatum	Annual Dicot		66			
Aptosimum lineare	Annual Dicot					483
Argemone ochroleuca	Annual Dicot					50
Chenopodium album	Annual Dicot				16	
Chloris virgata	Annual grass					50
Cullen obtusifolia	Annual Dicot					200
Dimorphotheca polyptera	Annual Dicot		16			
Dipcadi glaucum	Bulb			16		
Enneapogon desvauxii	Perennial grass				16	
Eragrostis bicolor	Perennial grass		33			
Eragrostis echinochloidea	Annual grass					16
Eragrosatis lehmanniana	Perennial grass	33	50			
Eragrostis porosa	Annual grass				66	33
Felicia clavipilosa	Perennial Dicot				166	50
Helichrysum arenicolum	Annual Dicot			33	250	66
Helichrysum argyrosphaerum	Annual Dicot	433	500	1 100	650	283
Limeum argute-carinatum	Annual Dicot			16		
Manulea burchellii	Annual Dicot		16	16		
Molluga cerviana	Annual Dicot			66	16	
Peliostomum leucorrhizum	Perennial Dicot				50	
Pharnaceum sp.	Annual Dicot	33	133	33		
Plinthus spp.	Perennial Dicot	50	116	50	16	
Salsola sp.	Annual Dicot	16				
Requienia sphaerosperma	Perennial Dicot					33
Schmidtia kalahariensis	Annual grass		16	33	16	
Senecio eenii	Annual Dicot	16				
Sporobolus coromandelianus	Annual grass					16
Stipagrostis ciliata	Perennial grass				16	
Tragus racemosus	Annual grass			16		16
Tribululs terrestris	Annual Dicot					16
Tribulus zeyheri	Annual Dicot					50
Total seed density of annual grasses			**16**	**50**	**83**	**133**
Total seed density of perennial grasses		**33**	**83**		**33**	
Total seed density of annual dicots		**516**	**733**	**1 266**	**950**	**2 066**
Total seed density of perennial dicots		**50**	**116**	**50**	**233**	**83**
Total seed density of annual sedges				**16**		

Table 6.2c Seed densities (seeds/m²) in the winter seasonally germinable seed bank (direct examination) in five different habitats on the farm Alpha in the Kalahari duneveld

		Seed densities in different habitats (seeds/m²)				
Species	**Life form**	**Crest**	**Slope**	**Street**	**Calcrete**	**Riverbed**
Amaranthus praetermissus	Annual Dicot					283
Aptosimum elongatum	Annual Dicot		16			
Aptosimum lineare	Annual Dicot				16	233
Chloris virgata	Annual grass					1 700
Chrysocoma obtusata	Perennial Dicot					16
Cullen obtusifolia	Annual Dicot					50
Enneapogon desvauxii	Perennial grass				50	
Eragrostis porosa	Annual grass			16		
Felicia clavipilosa	Perennial Dicot			16	66	100
Geigeria pectidea	Perennial Dicot					50
Helichrysum arenicolum	Annual Dicot				133	150
Helichrysum argyrosphaerum	Annual Dicot	216	216	600	333	216
Manulea burchellii	Annual Dicot			33		
Mollugo cerviana	Annual Dicot			33		
Pharnaceum sp.	Annual Dicot		16			
Plinthus spp.	Perennial Dicot	16				33
Schmidtia kalahariensis	Annual grass	16	33	183		
Stipagrostis ciliata	Perennial grass				16	
Tragus racemosus	Annual grass					16
Tribulus terrestris	Annual Dicot					16
Total seed density of annual grasses		**16**	**33**	**200**		**1 716**
Total seed density of perennial grasses					**66**	
Total seed density of annual dicots		**216**	**250**	**667**	**483**	**950**
Total seed density of perennial dicots		**16**		**16**	**66**	**200**

Table 6.2d Seed densities (seeds/m²) in the spring seasonally germinable seed bank (direct examination) in five different habitats on the farm Alpha in the Kalahari duneveld

		Seed densities in different habitats (seeds/m²)				
Species	**Life form**	**Crest**	**Slope**	**Street**	**Calcrete**	**Riverbed**
Acacia erioloba	Perennial Dicot				16	
Amaranthus dinteri	Annual Dicot		16		16	
Amaranthus praetermissus	Annual Dicot			16		1 116
Aptosimum elongatum	Annual Dicot		33			
Aptosimum lineare	Annual Dicot					400
Aptosimum marlothii	Perennial Dicot					16
Aptosimum spinescens	Perennial Dicot				16	
Boerhavia repens	Annual Dicot					83
Bulbostylis hipidula	Annual sedge	33	16	16		
Chamaesyce inaequilatera	Annual Dicot			16		16
Chloris virgata	Annual grass					1 616
Cullen obtusifolia	Annual Dicot					50
Enneapogon desvauxii	Perennial grass				33	
Eragrostis lehmanniana	Perennial grass	100	366	50		
Eragrostis porosa	Annual grass			16	300	200
Eragrostis trichophora	Perennial grass	83	216			
Fabaceae	Annual Dicot					50
Felicia clavipilosa	Perennial Dicot				33	33
Geigeria pectidea	Perennial Dicot					50
Gisekia africana	Annual Dicot		16	16		
Helichrysum arenicolum	Annual Dicot			16		
Helichrysum argyrosphaerum	Annual Dicot	150	133	283	150	33
Limeum argute-carinatum	Annual Dicot			16	33	16
Manulea burchellii	Annual Dicot	133				
Mollugo cerviana	Annual Dicot			150	16	
Ptycholobium biflorum	Perennial Dicot				16	
River grass	Annual grass					166
Schmidtia kalahariensis	Annual grass		200	1 416	133	16
Schoenoplectus muricinux	Perennial sedge					16
Sporobolus coromandelianus	Annual grass				16	16
Stipagrostis ciliata	Perennial grass		16	16	83	
Stipagrostis obtusa	Perennial grass			16	50	
Tragus racemosus	Annual grass					133
Trianthema parvifolia	Annual Dicot				50	66
Tribulus terrestris	Annual Dicot				16	33
Tribulus zeyheri	Annual Dicot					33
Total seed density of annual grasses			**200**	**1 433**	**450**	**2 150**
Total seed density of perennial grasses		**183**	**600**	**83**	**166**	
Total seed density of annual dicots		**283**	**200**	**516**	**283**	**1 900**
Total seed density of perennial dicots					**83**	**100**
Total seed density of annual sedges		**33**	**16**	**16**		
Total seed density of perennial sedges						**16**

The species in the Table 6.2, were tentatively classified into the following seed bank types:

Seed Bank Type I (transient)	Seed Bank Type II (short-term persistent)	Seed Bank Type III (long-term persistent)
Aristida meridionalis	*Aristida adscensionis*	*Acacia erioloba*
Eragrostis bicolor	*Argemone ochroleuca*	*Aptosimum* spp.
Eragrostis lehmanniana	*Amaranthus praetermissus*	*Cullen obtusifolia*
Eragrostis trichophora	*Bulbostylis hispidula*	*Geigeria pectidia*
Panicum coloratum	*Chamaesyce inaequilatera*	*Indigofera alternans*
Stipagrostis amabilis	*Chloris virgata*	*Limeum* spp.
Stipagrostis ciliata	*Cleome paxii*	*Lotononis densa*
	Dicoma capensis	*Requienea sphaerosperma*
	Felicia clavipilosa	*Tribulus zeyheri*
	Gisekia africana	
	Helichrysum arenicolum	
	Helichrysum argyrosphaerum	
	Hermannia tomentosa	
	Hirpicium gazanoides	
	Manulea burchellii	
	Mollugo cerviana	
	Peliostomum leucorrhizum	
	Pharnaceum sp.	
	Plinthus spp.	
	Schmidtia kalahariensis	
	Schoenoplectus muricinux	
	Sporobolus coromandelianus	
	Tragus racemosus	
	Trianthema parvifolia	

The dune crest habitat's readily germinable seed bank was dominated by *Eragrostis lehmanniana* during summer at 466 seeds/m^2 (Table 6.2). Another four perennial grass species (Type I) were also found in the seed bank in summer. However the annual dicot, *Helichrysum argyrosphaerum* (Type II) made the greatest contribution to the readily germinable seed bank over a span of four seasons. Its seed bank size in this habitat ranged from 150 seeds/m^2 to 433 seeds/m^2 during the year. Eleven species with Type II seed bank made small contributions to the readily germinable seed bank of this habitat throughout the year.

In the dune slope habitat, *Helichrysum argyrosphaerum* (Type II) again dominated the seed bank in some of the seasons. Its seed bank size ranged from 133 seeds/m^2 to 500 seeds/m^2 throughout the year. Another dominant as well as diagnostic species in the readily germinable seed bank was the perennial grass *Eragrostis lehmanniana* (Type I). Its seed bank size ranged from 366 seeds/m^2 in spring to 816 seeds/m^2 in summer. The perennial grass *Eragrostis trichophora* also formed a large portion of the dune slope habitat's readily germinable seed bank. Another four perennial grasses (Type I) also contributed to the seed bank in this habitat. Ten species with seed bank Type II and two species with seed bank Type III (e.g. *Aptosimum elongatum*) contributed to the readily germinable seed bank of this habitat over the course of four seasons.

Schmidtia kalahariensis with up to 1 416 seeds/m²; *Helichrysum argyrosphaerum* with up to 1 100 seeds/m² and *Mollugo cerviana* with up to 1 083 seeds/m² (all Type II) at some stage during the year, dominated the readily germinable seed bank in the dune street habitat. Five perennial grass species (Type I) contributed to the readily germinable seed bank of this habitat during the course of the year. Nineteen species with either Type II seed banks and two species with Type III seed banks contributed to the dune street's readily germinable seed bank during the course of the year

Helichrysum argyrosphaerum with up to 650 seeds/m² (Type II); *Eragrostis porosa* with up to 500 seeds/m² (Type II) and *Schmidtia kalahariensis* with up to 450 seeds/m² (Type II) all dominated the readily germinable seed bank of the calcrete habitat at some stage during the year. Other dominant readily germinable seed bank species were *Enneapogon desvauxii*, *Felicia clavipilosa*, *Mollugo cerviana* and *Helichrysum arenicolum* (also all Type II). In addition to this eleven species with Type II seed bank and two species with Type I seed bank were present in the readily germinable seed bank of the calcrete habitat, during the course of the year.

Amaranthus praetermissus with up to 1 333 seeds/m² (Type II); *Aptosimum lineare* with up to 983 seeds/m² (Type III) and *Chloris virgata* with up to 1 700 seeds/m² (Type II) all dominated the riverbed's readily germinable seed bank at some stage during the course of the year. In addition to this nine species with Type III seed bank and twenty-one species with Type II seed bank contributed to the readily germinable seed bank of the riverbed habitat during the course of the year.

6.4.3 Discussion

The composition of the seed bank is notoriously variable both in space and time (Figures 6.1 & 6.2). Germination strategies can hence be defined as response patterns of species to sets of environmental conditions. Seasonal germination strategies can be described from the temporal distributions of abundances of different species (Lavorel *et al*., 1993).The timing of germination of certain species may affect the way each habitat is managed in relation to grazing. For example, palatable species that germinate during times of the year when not much grazing material is available will be very vulnerable to grazing pressure and trampling. Even though *Schmidtia kalahariensis* is abundant in summer and spring, it is not palatable during these months as it contains high levels of sticky acidic exuviates which cause blistering. The species is only used by wildlife later in the year when it has dried out and is no longer indigestible. Thus palatable perennial grass species are the main nutrition available to grazers in summer. Most perennial and some annual grass species showed a preference for germinating in summer. This would allow them to grow well as rain is available during the summer months. Successful germination and establishment of seeds of many arid-land and desert plants are dependent on the pattern and duration of the available soil moisture and suitable temperature for germination and growth (Shaukat & Siddiqui, 2004). Sufficient moisture becomes available following ample rain. Seeds of many species germinate only after a threshold of rain has been received (Shaukat & Siddiqui, 2004). Many plants prefer to germinate at relatively high temperatures (eg *Eragrostis lehmanniana*) while others do so at relatively low temperatures (eg winter annuals such as *Helichrysum arenicolum*).

The soil seed bank plays an important role in the composition of different plant communities and their conservation (Lopez-Marino *et al*., 2000). The plant community in each of the five habitat types would usually be described by looking at the dominant and diagnostic species present aboveground in the vegetation. However, when information is needed on how to manage such plant communities, it is important to know how vegetation will react to disturbance, by looking at the composition of the belowground flora. The composition of the seed bank depends on the production and composition of the present and previous plant communities, as well as the longevity of the seeds of each species under local conditions (Lopez-Marino *et al*., 2000).

Seed bank composition tended to differ between the plant communities of the five habitats (Table 6.2). However some species tended to dominate most of the habitats in the belowground flora. For example the dune crest habitat was dominated mostly by *Stipagrostis amabilis* aboveground, the dune slope habitat was dominated partly by *Eragrostis lehmanniana/Aristida meridionalis* and the dune street was dominated partly by *Stipagrostis ciliata*. All of these species form transient seed banks and do not produce many seeds. However, the annual herb *Helichrysum argyrosphaerum* dominated the seed bank in most seasons in these habitats as it formed many seeds and a persistent seed bank.

This trend was followed in the seed banks of all the habitats. Even though perennial species may have dominated the aboveground flora, it was often the annual or weedy species that dominated the seed banks with their persistent seed banks. For example, the opportunistic annual grass *Schmidtia kalahariensis* was not a diagnostic species in any of the habitats, but it was found in the readily germinable seed bank of all the habitats, often in great numbers. The extent to which this species establishes, will often give an indication as to the extent of disturbance or degradation in a particular habitat.

In order to define the vegetation health in a habitat, it is important to understand the seed bank dynamics, especially the transient portion of the seed bank. For example, in the dune crest, dune street and dune slope habitats, perennial grasses are the dominant and diagnostic species in the vegetation. In order to conserve these environments, it must be ensured that enough seeds are produced so that these species (Type I) are represented in the seed bank. If the proportion of the transient seed bank becomes too small, the possibility of regeneration of the perennial grass species after disturbance is decreased. In order to describe the transient portion of the seed bank, repeated sampling during the year is needed (Guo *et al*., 1999) and autumn is a time when the transient seed bank is expected to be at its seasonal peak in summer rainfall areas (Jalili *et al*., 2003). The sampling date is highly important when establishing the similarity between the seed bank and vegetation, given the annual variation in the floristic composition of seed banks (Peco *et al*., 1998).

Persistent seed banks are usually found where environmental/disturbance regimes are unpredictable and where the probability of seedling success is low or variable (Cabin & Marshall, 2000). The riverbed habitat had a large proportion of annuals in its vegetation. It would thus be expected to respond better to disturbance/degradation as many seeds were present in the persistent portion of the seed bank. This habitat had many species with Type II (persistent) and it also has the most species with Type III seed bank (‘permanent’). This habitat was thus geared towards disturbance because of the type of seed banks which were present in the soil.

6.4.4 Conclusions on seed bank types and growth forms

Informed management requires accurate and reliable information on the characteristics of many species and of the vegetation. One of the most important of these relates to seed persistence in the soil (Jalili *et al*., 2003). The capacity to form persistent seed banks allows species to survive episodes of disturbance and destruction. An understanding of persistent seed banks is the key to many aspects of practical management for agriculture and effective conservation of diverse ecosystems. Such information is also important in the definition of conservation policy and strategies (Jalili *et al*., 2003).

There is variation among species survival rates of viable seeds in the soil. Grassland species differ both spatially and temporally in seed production, seed dispersal and germination requirements (Milberg & Hansson, 1993). The interaction between the effects of soil texture on plant community composition and the low and variable patterns of precipitation found in arid regions leads to the potential for spatial and temporal variability in processes important to the storage of germinable seeds (Coffin & Lauenroth, 1989).

Survival rates of seeds of plant species in the Kalahari duneveld, depend on the type of habitat in which the plants are growing. The dune crest, dune slope and dune street habitats were dominated by perennial grasses and thus the Type I seed bank was most important in this environment. The calcrete outcrop had many perennial forbs and annual grass species, and thus the Type II seed bank was most common in this habitat. The riverbed habitat had mostly annual species, and thus seed bank Type II was also most common. This habitat also had the most species which formed permanent (Type III) seed banks. Thus, seed bank types could be used to define a habitat and the type of management which is needed in order to conserve the vegetation it supports.

CHAPTER 7

CONCLUDING REMARKS

The Kalahari duneveld is a unique area in that its topography is determined by the presence and alignment of parallel-running desert dunes which are stabilised by vegetation. This study was the first to investigate the seed bank dynamics in the Kalahari duneveld in South Africa.

The effects of a grazing gradient on the seed bank around an artificial watering point were investigated in three different ways. The results from each method were different, but together helped to get a holistic picture of the dynamics of the seed bank along the grazing gradient. The flotation method was applied to the data from this study, only in spring. The flotation method always estimated the largest value for seed bank size but it estimated the lowest values for species richness. The flotation method detected hard-seeded species which the other methods failed to detect. This data for hard-seeded species (such as *Indigofera alternans* and *Limeum* spp.) turned out to be invaluable in locating the areas of the seed bank around the watering point most altered by grazing. The flotation method was however, only applied in one season as it is very laborious and time-consuming.

The direct seedling emergence method gave a good indication of the readily germinable seed bank in each season. It did not however, give a good indication of all the viable seeds present in the soil. The seedling emergence re-examination helped to fill in the gaps to determine if viable seeds of other species had been present in the soil, but for some or other reason did not germinate in the season of collection. However, the seedling emergence re-examination failed to detect a larger seed bank size along the grazing gradient, than the direct method, as would have been expected. The direct seedling emergence method and the re-examinations both detected a much larger seed bank species richness than the flotation method could. This again highlights the fact that the tiny seeds occurring in desert seed banks usually cannot be detected using the seed extraction method.

The annual grass *Schmidtia kalahariensis*, dominated the seed bank in all sections of the transect but was especially abundant in the areas closest to the watering point and in the area which experienced fence effects. The sheer abundance of this species in the seed bank, obscured the contribution of other species to the seed bank. Only once the *Schmidtia kalahariensis* data had been removed, could reliable conclusions be reached about the overall effect of a grazing gradient on the soil seed bank. The conclusions that can be reached from these results is that different methods of sampling the soil seed bank compliment each other and fill in data gaps which one method alone cannot fill.

The methods used to estimate soil seed bank dynamics (especially the flotation), highlighted that a fence effect was experienced at the end of the transect. Thus the expected grazing gradient unfortunately did not emerge in the results. In future studies, it may be of use to study a grazing gradient in an area that is not restricted by a fence. This may give better results of a true grazing gradient, so that more accurate inferences can be made about grazing pressure due to livestock density in Kalahari rangelands.

When investigating the seed bank dynamics of five duneveld habitats, the direct seedling emergence method as well as re-examinations were used. The samples collected in summer always gave the highest values for soil seed bank size, in all habitats. The results of the re-examinations however, from the other three seasons, did not show a consistent pattern and had a very high standard deviation. This could be due to the number of re-examination samples that were used being too small to give accurate results. Another explanation could be varying seasonal behaviour of selected species in each habitat. However, the re-examinations do give a good indication of the type of seed bank of the species present in each habitat. For example, the riverbed and dune slope habitat will not be likely to show strict germination patterns over the year as the one has many opportunistic annuals that will germinate at any opportune time, while the other has a large transient portion in the seed bank which is germinable in all seasons until it is no longer viable a year later. Those habitats with only short-term persistent seed banks are most likely to have seasonal patterns in their seed banks because of innate dormancy in the seeds which only responds to certain environmental cues.

When investigating species richness of seed banks in each of the habitats, it is valuable to do the re-examination trials as many more species can be discovered in this way when used together with the direct germination trials. This also helps when comparing the aboveground flora with the belowground flora of a habitat, as the presence of each species above- or belowground and during each season, can be monitored. This in turn helps when making decisions about management of a habitat. The tentative grouping of species into seed bank types, in this study, was used as a rough guide to understand the species composition in each habitat. More detailed studies about dormancy and germination behaviour would be needed to more accurately group each species into a seed bank type and to draw more reliable conclusions about germination behaviour.

Finally, the seed bank investigations in this study were concentrated in habitats found on one farm under one type of management. Thus, this investigation may not reflect the seed bank dynamics of other farms in the Kalahari duneveld. For example, the farm on which the study was conducted, was under grazing and browsing pressure mostly by springbok, ostriches and gemsbok. Neighbouring farms may have other livestock such as sheep, goats and cattle which could exert a different type of grazing pressure, as they may favour other plant species. Thus more reliable conclusions could be drawn by including farms under different types of management, but within the Kalahari duneveld area.

CHAPTER 8

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