

**Dispersal strategies in communal versus privately-owned
rangeland in Namaqualand, South Africa**

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

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Dispersal strategies in communal versus privately-owned rangeland in Namaqualand, South Africa

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Dispersal and disturbance are significant forces in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale. Livestock is regarded as a disturbance and is major determinant of vegetation dynamics.

The study was carried in Paulshoek, one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape. The site of the present study is a 1 km² section on the southern boundary of the Paulshoek commons and includes another observatory, which extends approximately 1 km from the Paulshoek boundary into one of the adjacent privately owned farms, Remhoogte. Livestock grazing has been identified as a major threat to the biodiversity in the Succulent Karoo Biome. The aim of this study is to compare the dispersal strategies in communal with privately-owned rangeland and further focuses on the importance of myxospermy.

Based on the concept that vegetation is the most obvious external feature on which to classify ecosystems, a phytosociological classification of the vegetation of the study area was made. The six plant communities found largely reflect differences in

land type, although the effect of different grazing intensity on communal and commercial rangeland is not excluded.

The dispersal spectra of the two rangelands and the six communities were dominated by ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores. Grazing, water, and landscape seem to be the major factors influencing the composition of different dispersal types. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands.

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems. The optimum conditions for germination differed among species, but in general most species obtained their highest germination percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons.

The various ideas that have been suggested about the ecological importance of myxospermy, and its ability to fulfill various functions led to the further investigation of the origin and chemical composition of mucilaginous seeds. Results have suggested three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the cuticle of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs. The mucilage of all these diaspores investigated contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions.

Chapter 1

Introduction

The Succulent Karoo hotspot is an extraordinary global biodiversity treasure with over 6 000 plant species of which 40% is found nowhere else on earth. It is the world's most diverse arid environment (Cowling 2003) and occupies 6.5% of South Africa's land surface (Low and Rebelo 1998, Mucina and Rutherford 2006). Climatically the Succulent Karoo separates from the other biomes on the basis of the low annual rainfall, high percentage winter rain, and high absolute and mean minimum temperatures (Desmet and Cowling 1999a).

Despite low population densities in the Succulent Karoo, there are many challenges for conservation in the region. Livestock grazing has been identified as a major threat to the biodiversity in the biome. The livestock industry is based on small stock, especially goats and sheep. The exact mix of goats and sheep in a herd is determined largely by individual farmer preference and suitability of the communal area for different breeds, while on privately owned land, a single landowner usually with one herd of animals manages one or several privately owned farms (Hoffman *et al.* 1999). The mean stocking density for Paulshoek, one of the many communal wards in Namaqualand, over the last 30 years has been approximately 6 ha per small stock unit. This is twice that recommended for the region by the South African Department of Agriculture. In the neighboring commercial rangeland* (Remhoogte) a stocking density of approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999) has been maintained.

Grazing may have a negative impact on plant populations via several mechanisms: by directly increasing mortality, by reducing the competitive ability of grazed plants relative to ungrazed, less palatable plants (Milton *et al.* 1990, Milton 1994), by reducing the reproductive output of grazed individuals or by reducing the success of seedling establishment (Todd 2006, Riginos and Hoffman 2003). The combinations of these effects lead to the loss of palatable species to the benefit of unpalatable species and the replacement of perennial species by annuals and geophytes (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). An increase in species

* The term commercial rangeland as used in this dissertation refers to farming system on privately owned rangeland.

richness as a result of grazing can be interpreted as the outcome of resources becoming available as a result of reduced competition by grazed plants.

The development of sustainable management practices for dry regions used for stock and crop production need to be underpinned by an understanding of the variety of functional adaptations, which characterize the ecosystem. Vegetation is the most obvious external feature on the basis of which ecosystems are defined and classified. Therefore to assess other biological or ecological factors prevailing in an ecosystem, information on vegetation is required.

Dispersal is an important process in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Dispersal is believed to set the template from which community patterns develop (Levine and Murell 2003) and knowledge of seeds dispersal finds applications for purposes of nature conservation and ecological restoration (Strykstra *et al.* 2002). The use of plant functional traits to describe patterns in plant communities provides us with the means to understand the mechanisms of vegetation responses to environmental change which a purely floristic approach does not accomplish. Moreover, such features lend themselves to statistical treatment in the form of spectra, which show the variety, the amplitude and the proportion of the different functions involved in the internal mechanics of the community (Dansereau and Lems 1957).

Seed germination and seedling establishment are the most remarkable and critical stages during a plant's life cycle. Germination is a risky transition, especially in arid climates, between the most drought tolerant stage (the seed) and the weakest stage (the seedling) in plant development (Guttermann 1993). Determining what controls the timing of seed germination in the field requires information on the seed, environmental conditions in the habitat, and how the two interact from the time of seed maturation to germination (Baskin and Baskin 1998). Factors such as temperature, moisture, light, oxygen, nutrients as well as combinations of all play a major part in breaking dormancy and can inhibit, delay, or promote germination. The response to these factors depends on environmental and maternal influences during

seed maturation. This response in turn determines the germination traits of a species (Guttermann 1993, Fenner 2000).

The abiotic and biotic environmental factors in arid regions influence the adaptations and survival strategies of plants growing there. Arid areas or habitats are characterized by temperature fluctuations often extending beyond the limiting temperatures for germination, by recurrence of moisture deficiency and sometimes by deficiencies of nutrients in the soil. In addition, rainfall is unpredictable, and precipitation at the beginning of the growing season will not always be followed by enough rainfall for plants to complete their life cycles (El-Sharkawi *et al.* 1989, Philippi 1993). Myxospermy is a trait often associated with arid environments. Mucilaginous diaspores produce copious amounts of mucilage once they come into contact with water. If they dry out, the diaspores adhere to the soil. The origin of the mucilage and factors influencing the germination of mucilaginous seeds are poorly known. Information on the anatomy and the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems.

Aims of this study

Firstly, the study aims to give an overview of the vegetation structure and floristic composition of the communal land Paulshoek and the neighboring commercial farm Remhoogte.

Secondly, it aims to compare dispersal spectra between the communal and commercial land in the study area. Dispersal is one of the crucial steps in a plants life cycle and it is influenced by many environmental factors. A particular type of dispersal might be promoted by the land-use practice in an area.

Thirdly, special attention is given to myxospermy, one of the mechanisms restricting long-range dispersal in plant species. The light and temperature requirements for germination of selected myxospermic plant species of Namaqualand are investigated. Finally, the study also aims to give a detailed anatomical description of mucilaginous diaspores of selected plant species in Namaqualand.

Chapter 2

An overview of the Succulent Karoo Biome

2.1 Location

The Succulent Karoo occupies 6.5% of South Africa's land surface (Low and Rebelo 1998). It extends from the western part of Namibia (26°8'S, 14°56' E) southwards along the western side of the South African escarpment to the eastern border of the Western Cape Province in the Little Karoo (34°S, 23°11'E) (Rutherford 1997, Lombard *et al.* 1999). It forms part of a Greater Cape floristic region rather than part of the Palaeotropical Kingdom, which includes the Nama Karoo Biome (Cowling *et al.* 1999). The Succulent Karoo Biome is one of eight biomes in southern Africa (Mucina *et al.* 2005) and covers approximately 111 000 km² (Mucina and Rutherford 2006).

The altitude of this biome is mostly below 800 m above sea level, but in the east it may reach 1 500 m (Low and Rebelo 1998). The region experiences a low but fairly reliable rainfall (mean 170 mm per annum) with 60% of it received during winter (May to September) (Rutherford and Westfall 1986, Desmet and Cowling 1999a, Milton *et al.* 2003). Some of the eastern areas of the Succulent Karoo Biome may also receive rain at any time of the year (Hilton-Taylor 1996). Summer temperatures are relatively high but winter temperatures are seldom below 0°C (Hoffman 1996, Hilton-Taylor 1996).

The Succulent Karoo Biome is bounded by the Desert, Thicket, Nama Karoo and Fynbos Biomes. In the west it is limited by the cold Atlantic coastline, in the south by the Fynbos Biome and in the east by the Nama Karoo and Thicket Biomes (Palmer and Hoffman, 1997). The Desert Biome forms the northern boundary (Rutherford and Westfall 1986, Milton *et al.* 2003, Mucina and Rutherford 2006).

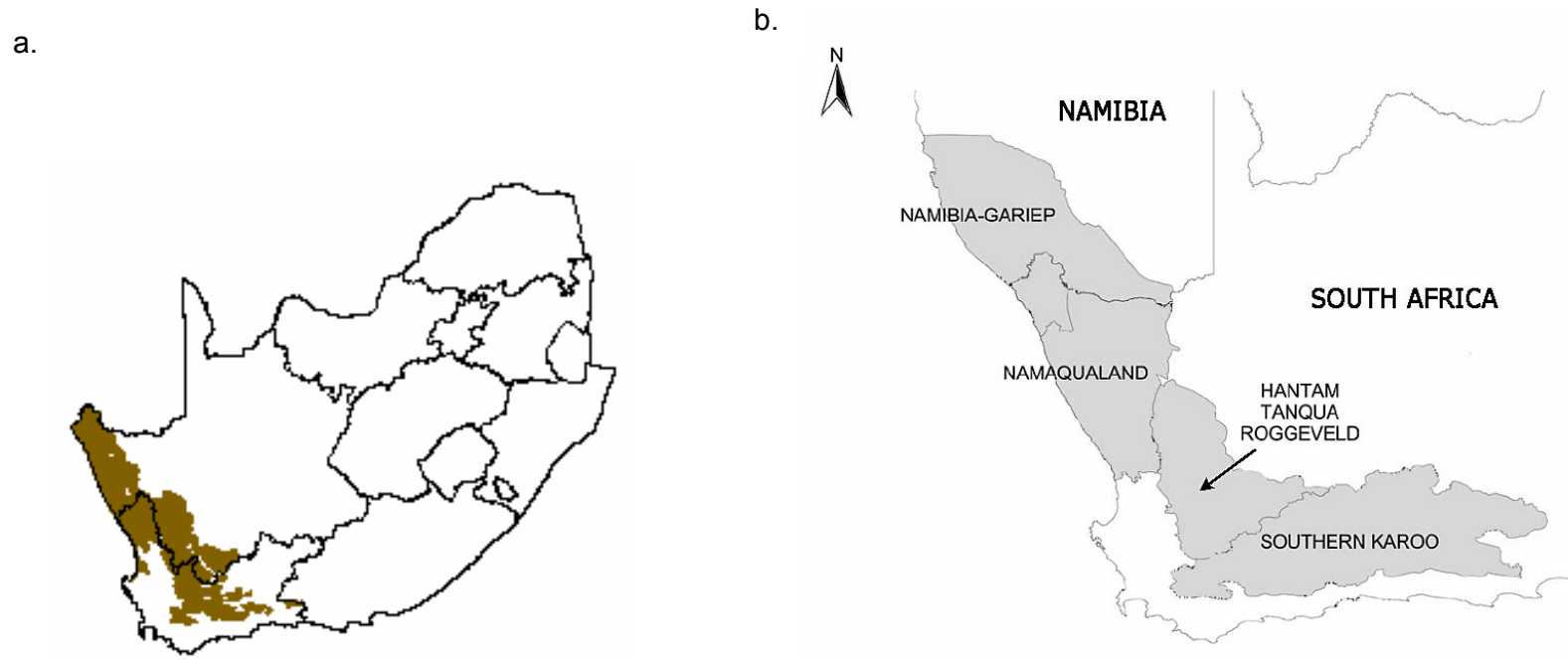


Figure 1.1 The a) location and b) SKEP planning domains of the Succulent Karoo Biome (www.SKEP.org).

Based on the topography, the total amount of rainfall received and the flora, the Succulent Karoo can be divided into 6 bioregions (Mucina and Rutherford 2006). Four of those represent traditional regions of Namaqualand (Richterveld, Namaqualand Harderveld, Namaqualand Sandveld and Knersvlakte), while the other two regions represent a series of units occupying rain shadow, low-altitude valleys and plains (Rainshadow Valley Karoo) and high-altitude semi desert plains, still characterized by prevalent winter-rainfall regime (Trans-Escarpment Succulent Karoo).

The Succulent Karoo Biome has approximately 6 356 plant species (Cowling 2003). Research in the Succulent Karoo Biome has highlighted the unique aspects of this winter rainfall desert compared to other desert with similar climates (Esler *et al.* 1999). For example, the Sonoran Desert has a flora of 2 440 species in an area which is an order of magnitude larger than the Succulent Karoo Biome, while the Sinai Desert has 1 130 species and is 1.2 times the size of the Succulent Karoo Biome (Petersen 2004). In addition to long-lived succulent plant species the Succulent Karoo has a remarkable diversity of short- to medium-lived leaf-succulent shrubs as well as a rich geophyte flora. With more than 40% of its taxa being endemic, and the high local and regional diversity; the Succulent Karoo undoubtedly has the highest level of endemism and diversity for an arid region in the world (Lombard *et al.* 1999, Esler *et al.* 1999).

2.2 Climate

Fine weather in the Succulent Karoo is associated with subtropical anticyclones whereas cold fronts are responsible for the rain during winter. Cold fronts are also associated with inversions of cold air from the south and southwest that produce characteristic cold snaps. At the biome scale, the Succulent Karoo sites separate from the other biomes on the basis of the low annual rainfall, high percentage winter rain, and high absolute and mean minimum temperatures (Desmet and Cowling 1999a).

Rainfall

The Succulent Karoo Biome experiences a broad range in rainfall from 50 to 500 mm per annum. There is a general trend for rainfall to decrease uniformly westwards (Desmet and Cowling 1999a). Most of the area, however, receives a winter rainfall of less than 150 mm per annum. The coefficient of variation of annual rainfall is relatively low and therefore; this low rainfall is relatively predictable. The meager rainfall is supplemented by fog from the Atlantic Ocean and as a result of high humidity and low temperatures, copious dewfalls occur during mid winter (www.gouritz.com, 2006).

The Succulent Karoo Biome is predominantly a winter rainfall area with most of the rainfall received from May to September. In the northeastern, eastern and southeastern parts of this biome it grades into summer rainfall. Although most of the rainfall is received in the winter months there can be great variability in monthly rainfall peaks. Even though the mean annual rainfall might be the same in some areas, within the biome, there is a great variation in the temporal distribution of rainfall (Desmet and Cowling 1999a).

Temperature

High temperatures, low relative humidity and little to no cloud cover are characteristic of this biome, which result in large annual and daily ranges of temperature. These are general characteristics of arid climates (Desmet and Cowling 1999a). However, along the west coast where there is an abundance of moisture in the air due to the predominantly onshore breeze, relative humidity is high, and temperature is regulated by the cold Benguela current (Desmet and Cowling 1999a). Mean daily minimum temperatures are highest along the west coast and increase as one moves toward the equator. In winter temperatures are mild, but occasional frosts occur on upland peaks. In summer temperatures in excess of 40°C are common. These temperatures are usually recorded when hot, turbulent air, known as “berg wind”, descends coastward from the high altitude plateau of southern Africa (Low and Rebelo 1998).

Compared to the Nama Karoo Biome, the Succulent Karoo has moderate temperatures which drop no lower than 5°C on typical winter nights and reach 15°C or more on winter days (Desmet and Cowling 1999a).

2.3 Vegetation of the Succulent Karoo

The vegetation is dominated by dwarf, succulent shrubs of which the vygies (Mesembryanthemaceae now included in the Aizoaceae) and stonecrops (Crassulaceae) are particularly prominent. Therophytes and geophytes are also common. The vegetation of the Succulent Karoo can be described as an open to sparse (15 to 50% canopy cover), low to dwarf (usually less than 1 m tall) shrubland (Hilton-Taylor 1994). During spring, especially in disturbed areas there are spectacular masses of flowering annuals (mainly Asteraceae, Brassicaceae and Scrophulariaceae) (Van Rooyen *et al.* 1992). Small trees or large shrubs (less than 3 m tall) (e.g. *Diospyros ramulosa*, *Lebeckia sericea* and *Rhus undulata*), occur on rocky outcrops and along river courses. Grasses seldom dominate in this biome (Hilton-Taylor 1994, Milton and Hoffman 1994). Acocks (1988) maintains that low grass cover is a result of overgrazing and that grasses were important prior to the European settlement.

Diversity and endemism

The Succulent Karoo contains a number of areas with concentrations of endemic species. This region is considered as one of the earth's hotspots; it is one of only two entirely arid hotspots. The flora of the Succulent Karoo Biome is unusual, both in terms of taxonomic composition and growth form mix (Desmet and Cowling 1999b). It includes 730 genera of which 67 are endemic. This is more than three times the number of endemic genera in the Arabian Sahara and North American arid lands which are an order of magnitude larger than the Succulent Karoo (Cowling and Hilton-Taylor 1999).

Not only is the total diversity high, but the Succulent Karoo also supports the richest succulent flora of the earth. Succulents make up to 29% of all plant species in the biome. The world's highest local diversity of succulents was recorded in the

mountainous desert of the Gariep area, with over 330 species in an area of just 1.3 km² (Cowling 2003). This biome has about 40% of the world's approximately 10 000 succulent species (Van Jaarsveld 1987, Smith *et al.* 1993). Succulents are associated with many of the larger families such as Aizoaceae, Asteraceae, Liliaceae, Crassulaceae, Geraniaceae, Euphorbiaceae and Asclepiadaceae.

Another remarkable group of plants in the Succulent Karoo is the geophytes. The remarkable diversity of geophytes can be seen clearly in the flora of the Goegap Nature Reserve near Springbok where they make up to 19% of the flora (Van Rooyen *et al.* 1990). In contrast, the diversity and importance of geophytes in all of the other four Mediterranean regions of the world drop off sharply as one move into winter rainfall desert regions (Rundel 1996). For example, geophytes comprise only about 1% of the floras of the winter rainfall Mojave and Sonoran Deserts in North America, and a similarly small fraction in the winter rainfall regions of the northern Sahara Desert and areas of Western Australia (Rundel 1996).

The Succulent Karoo Biome has very few affinities with other arid land floras of the world (Shmida 1985). There is a general consensus that the Succulent Karoo flora is largely derived from an ancient Cape stock (Acocks 1988, Cowling and Hilton-Taylor 1999) and shares more than half of its taxa and three quarters of the large genera with the Fynbos (Gibbs Russell 1987, Van Wyk and Smith 2001). At community scale species richness of perennial plants is unusually high in the Succulent Karoo compared with the Nama Karoo, or with other parts of the world that have a similar climate (Milton *et al.* 2003). The Succulent Karoo is closely related to the Fynbos Biome. Born *et al.* (2007) argue for the recognition of a Greater Cape Floristic region which includes all the winter rainfall areas, i.e. the Fynbos, Namaqualand region and the Hantam-Tanqua-Roggeveld region.

2.4 Vegetation and phytosociological research in the Succulent Karoo Biome

Many ecological studies have been completed in the Succulent Karoo Biome. One of the earliest attempts to describe the vegetation in a part of the Succulent Karoo was that of Adamson (1938) in the Kamiesberg. The first recognized phytosociological

study in the Succulent Karoo Biome was undertaken almost fifty years after Adamson's first description in 1938 by Le Roux (1984) who worked in the Goegap Nature Reserve. Phytosociological research continued in the Succulent Karoo Biome through the work of Lloyd (1985) in Vaalputs. This site is situated approximately 100 km southeast of Springbok. The study area is located in a transition zone between the Nama Karoo and Succulent Karoo Biome (Petersen 2004).

In 1990 Smitherman and Perry contributed to the ongoing phytosociological research in the Succulent Karoo through the completion of their study in the Karoo National Botanical Gardens. This study site is ± 2 km north of Worcester between the flats of the Breede River Valley and the Hex River Mountains. Milton *et al.* (1992) completed another descriptive vegetation study at Tierberg. The Tierberg Karoo Research Centre is situated on the southern edge of the Great Karoo and is transitional between the Succulent Karoo and the Nama Karoo. In 1996 Desmet completed a phytosociological study on the western arid coastal belt of the Succulent Karoo Biome. The study site is located between Port Nolloth and Alexander Bay and covers a narrow band, approximately 10 km wide along the coast. This study site falls within the southern zone of the Namib Desert and is one of five west coast deserts in the world lying within subtropical latitudes (Petersen 2004). De Villiers *et al.* (1999) studied the vegetation diversity at Brand-se-Baai on the Namaqualand coast, some 350 km north of Cape Town and about 80 km northwest of the nearest town, Vredendal.

The most recent phytosociological study was done by Petersen (2004). Her study area was situated at Paulshoek, one of the nine villages in the Leliefontein Communal Reserve in Namaqualand. Leliefontein is in the Kamiesberg, an escarpment at 900 to 1 500 m above sea level, about 50 km wide between the low-lying Sandveld in the west and the Bushmanland plateau in the east. A section of the Paulshoek commons is also the focus of the present study.

Petersen (2004) stratified the Paulshoek area into three altitude classes: 900 to 1 120 m above sea level corresponding broadly with the lowlands, >1 120 to 1 200 m above sea level constituting mid slopes and 1 200 to 1 400 m above sea level

comprising the upper slopes and crest. Four plant communities were identified and landscapes seemed to be the driving factor (Petersen 2004). The *Galenia africana* community was restricted to the low-lying flats and footslopes and was dominated by *Hermannia cuneifolia*, *Galenia africana*, *Hypertelis salsoloides* and *Drosanthemum floribundum*. The *Ruschia robusta* community was found on the footslopes and mid-slopes of the mountains and was dominated by *Ruschia robusta*, *Hallianthus planus*, *Crassula subaphylla* and *Eriocephalus microphyllus*. The *Pteronia glomerata* community on mid- and upper-slopes with high rock cover, was dominated by *Pteronia glomerata*, *Pteronia laterifolius*, *Eriocephalus microphyllus*, *Pelargonium karooicum*, *Asparagus capensis*, *Leipoldtia schultzei*, *Hallianthus planus*, *Ruschia robusta*, and *Rhus burchelli*. The *Diospyros austro-africana* community was restricted to the upper-slopes and crests which is the area receiving the highest annual rainfall for the entire area. It was dominated by *Diospyros austro-africana*, *Antizoma miersiana*, *Lebeckia multiflora*, *Dicerotheramnus rhinocerotis*, *Osteospermum rigidum*, *Pteronia glomerata*, *Ruschia lerouxii* and *Ruschia viridifolia*.

2.5 Conservation status of the Succulent Karoo Biome

The high species richness and unique global status of the biome require urgent conservation attention (Low and Rebelo 1998, Cowling and Hilton-Taylor 1999, Lombard *et al.* 1999). The conservation status of the biome has increased from 2% (Lombard *et al.* 1999) to 5.8% or 6 500 km² formally protected in statutory and nonstatutory reserves (Mucina and Rutherford 2006). However this area still substantially under-represents the diversity associated with the biome as it does not incorporate key ecological processes and evolutionary biodiversity drivers which include riverine and sand movement corridors, quartz patches, edaphic interfaces, climatic and upland-lowlands gradients (Mucina and Rutherford. 2006).

National parks and large reserves represent only four of the 12 bioregions (Lombard *et al.* 1999). Nationally protected areas are in the Gariep Centre (Richtersveld National Park), the Tanqua Karoo (Tankwa Karoo National Park) and the Namaqua Rocky Hills (Namaqua National Park) (Lombard *et al.* 1999). The Namaqua National park (previously Skilpad Wild Flower Reserve) now covers more than 70 000

hectares of land that was bought under the auspices of the Leslie Hill Succulent Karoo Trust. A number of provincial, local authority and private reserves occur within the Western Mountain Karoo, Bokkeveld/Olifants River/Biedou bioregion, Worcester-Robertson Karoo and Little Karoo.

Most of the region, an estimated 100 000 km², is used as communal or commercial grazing. Although this land-use can be compatible with the maintenance of biodiversity, overgrazing has severely degraded as much as two-thirds of this area (Cowling 2003). Recovery from overgrazing is not possible in a short time frame of a few decades due to the lack of dormant seeds, short dispersal distances, or the exclusion through competition by other perennials that have filled the spaces left by the demise of palatable species (Milton and Hoffman 1994). The recent expansion of the ostrich farming industry has devastated thousands of hectares in the Little Karoo, and is likely to pose a greater threat in the future. Mining and agriculture along river corridors have also had a significant impact on the region and are likely to expand in the future. Succulent species are highly prized by collectors and are threatened by illegal collection and trade (Cowling 2003). Ecotourism has good potential, as an alternative form of income generation in this biome. However, it requires that the area be properly used and managed (Lombard *et al.* 1999).

As a signatory to the Convention on Biological Diversity (United Nations Conference on Environment and Development, Rio de Janeiro, 1992), South Africa is committed to conserve its exceptionally high biodiversity. The Succulent Karoo has been identified as one of the least conserved biomes (Rutherford and Westfall 1986, Low and Rebelo 1998) and requires a large proportion of additional reserves to protect its flora.

The Succulent Karoo Ecosystem Planning Project (SKEP) has provided a 20 year vision to attempt to improve conservation management in the region. They have identified that large, conservation-worthy tracts of land are owned and used by private mining, agricultural and tour companies, as well as by communities and private farmers. There is a need to develop mechanisms to stimulate the participation of these sectors in the development of conservation areas and to

promote and facilitate innovative programs that involve local land owners in the creation of effective conservation areas within the Succulent Karoo (Cowling 2003).

2.6 Land-use practices in the Succulent Karoo Biome

A summary of historical practice and general chronology for the region is provided below, based on Hoffman *et al.* (1999). Hoffman (1997) believes it is important to reflect on these impacts in order to understand the vegetation patterns and trends of the past.

Pre-colonial period

San hunter-gathers have been in the Succulent Karoo for more than 300 000 years. Their main activity involved hunting, gathering and in some cases fishing. Although the Succulent Karoo appears to be a dry and harsh environment today with no underground water being available, in the past it was not a stumbling block to human habitation. People knew where to find water, even if they had to dig in dry riverbeds or for underground water-bearing plants to get it. Only since the end of the nineteenth century have underground aquifers been tapped by wind-driven pumps (Smith 1999). This area is dry and any rainfall event creates a micro-environment for animals. Khoikhoi were pastoralists and engaged in transhumance movement in order to exploit the seasonal differences in the availability of grazing and water resources (Hoffman *et al.* 1999).

Early colonial period

European settlement in the Succulent Karoo began around the middle of the eighteenth century (Van der Merwe 1988), and by the end of the eighteenth century there was a rapid expansion and most of the Cape Colony was occupied by colonial farmers. European colonization and settlement disrupted indigenous social structures and in this process the Khoikhoi pastoralists were forced to slavery or serfdom. By the end of the nineteenth century, private property and commercial

livestock production slowly became dominant and the pastoralist economy of the Khoikhoi became confined to the mission stations (Hoffman *et al.* 1999).

Twentieth century

The confinement to the mission stations and reserves severely constrained the Khoikhoi's ability to move with their herds or to engage in transhumance. To secure an income they started to move to the copper and diamond mines which were opened in the region from the mid-nineteenth century. For many residents, local agricultural production gradually assumed the character of supplementing and remittances (Hoffman *et al.* 1999).

2.7 Current land-use practices

There are two main agricultural production systems in the Succulent Karoo with widely differing histories, forms of land tenure, institutional arrangements, land-use practices and production objectives. The communal property regime allows residents of communal land to obtain rights to the use of natural resources if they are "registered occupiers". In contrast to the privately owned land or commercial land, communal areas have more than one farmer with various herds of different sizes. Each farmer within the communal system has his own management strategy, which he undertakes within a confined area of the commons (Hoffman *et al.* 1999).

The livestock industry on communal land is based in small stock, especially goats and sheep. The exact mix of goats and sheep in a herd is determined largely by individual farmer's preference and suitability of the communal area for different breeds. In the last 26 years stock numbers in Paulshoek have averaged nearly twice the recommended stocking density. Livestock production objectives within the communal farming systems in the Succulent Karoo are numerous, as farmers not only keep animals for consumption and selling, but also as an investment (Hoffman *et al.* 1999).

On privately owned land, a single landowner, with one herd of animals, manages one or several privately owned farms. Here the major objective is maximization of total cash income. Since the late 1960s, when extended droughts together with state intervention schemes such as the Stock Reduction schemes, reduced animal numbers (Hoffman *et al.* 1999) farmers of privately owned land have been stocking at densities recommended by the Department of Agriculture.

Several studies that have compared different biological and physical components in communal (Paulshoek) and the adjacent commercial land have highlighted a decrease of species richness on communal land. Todd and Hoffman (1999), Riginos and Hoffman (2003) and Petersen (2004) have suggested that heavy grazing on the communal land has resulted in a reduction in total vegetation cover and altered the dominance of perennials in favour of annuals and geophytes. However, they did not find any significant difference in the mean number of species per relevé.

Chapter 3

A comparison of the vegetation in communal versus commercial land in Leliefontein, Namaqualand, South Africa

3.1 Introduction

Heavy grazing is considered to be among the main threats to floristic diversity of arid and semi-arid regions world wide (Riginos and Hoffman 2003). However, some studies have shown that grazing does and some that it does not affect plant diversity; these contrasting patterns of response have frequently been attributed to differences in grazing intensity (Osem *et al.* 2002).

Grazing can have a negative impact on plant populations through several mechanisms: by directly increasing mortality, by reducing the competitive ability of grazed plants relative to ungrazed, less palatable plants (Milton *et al.* 1990, Milton 1994), by reducing the reproductive productivity of grazed individuals and the success of seedling establishment (Riginos and Hoffman 2003, Todd 2006). The grouping of these effects leads to the loss of palatable species to the advantage of unpalatable species and the substitution of perennial species by annuals and geophytes (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). A boost in species richness as a result of grazing can be interpreted as the outcome of resources becoming available as a consequence of reduced competition by grazed plants.

The improvement of sustainable management practices for dry regions used for stock and crop production needs to be underpinned by an understanding of the diversity of functional adaptations, which characterize the ecosystem. Vegetation is the most conspicuous external feature on the basis of which ecosystems are defined and classified. Therefore to assess other biological or ecological factors prevailing in an ecosystem, information on vegetation is required.

Since the beginning of the twentieth century, different methods of floristic analysis have been developed. These approaches developed into four major schools; the Zürich-Montpellier school, Uppsala School, the Raunkaier School and the Hybrid

Schools (Kent and Coker 1992). These schools use a subjective classification because the site of the vegetation sampling, the relevé is not chosen randomly, but is carefully selected as a representative area of a particular vegetation type (Kent and Coker 1992). Although the various schools did initially have differences in their approach; most methodology has now converged on the technique of the Zürich-Montpellier school. All these schools of thought are based on the community unit concept, which suggests that vegetation consists of plant communities. The plant community can be defined as the collection of plant species growing together in a particular location that show a definite association or affinity with each other.

The BIOTA* Africa network, uses a joint interdisciplinary and integrative approach to analyse changes in biodiversity and to gain knowledge for decision makers for feasible and sustainable land-use management (www.biota.africa.org). This study forms part of the BIOTA “Subproject S06” of phase II which aims to analyse biodiversity changes caused by human land-use and climate change. For this purpose long-term monitoring vegetation data are collected at selected sites in the Succulent Karoo to compare the effects of land-use practices.

3.2 Study area

3.2.1 Location

The study site is located near Paulshoek (30°20'S, 18°15'E), one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape (Figure 3.1). Paulshoek is a remote village about 50 km east of Garies and is situated in the eastern foothills of the Kamiesberg Mountain Range. The communal land of Paulshoek covers approximately 20 000 ha (Riginos and Hoffman 2003) and lies at an altitude from 980 to 1 400 m above sea level (Todd and Hoffman 1999). The Paulshoek commons is fenced on three sides by commercial farms. The site of the present study is a 1 km² section (called an observatory) on the southern boundary of the Paulshoek commons. The study site includes another observatory (1 km² section), which extends approximately 1 km from the Paulshoek boundary into one of the adjacent privately owned farms, Remhoogte (southeast from Paulshoek village).

*BIOTA = Biodiversity Monitoring Transect Analysis in Africa

a)



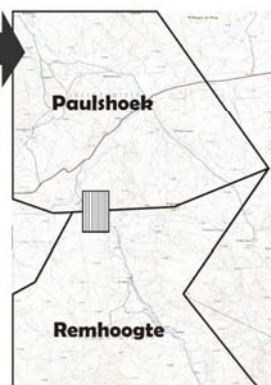
Figure 3.1 a) The Succulent Karoo Biome (shaded area) with location of study area (*).

b) The location of the study area (shaded part in Fig 3.1b).

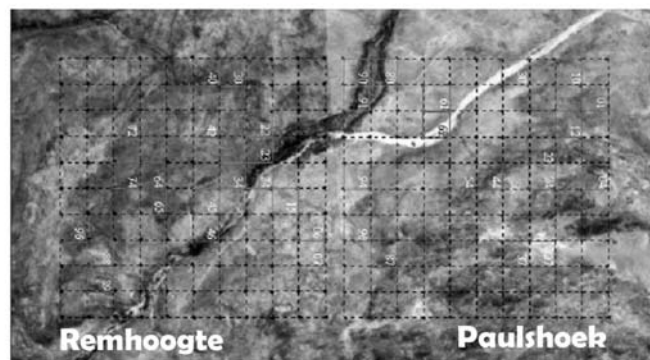
c) An aerial photograph of the two observatories on Paulshoek and Remhoogte.

d) Vegetation on the two observatories

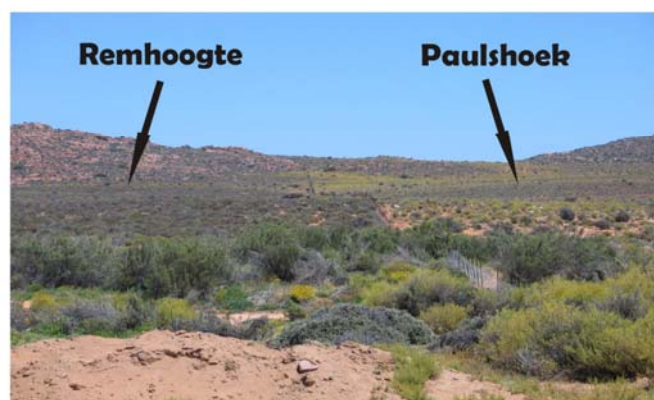
b)



c)



d)



The mean stocking density for Paulshoek over the last 30 years has been approximately 6 ha per small stock unit; which is twice that recommended for the region by the South African Department of Agriculture. Local commercial farmers maintain stocking densities of approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999). The grazing regime on the communal land is characterized by heavy and continuous grazing, whereas the neighboring commercial rangeland is moderately and rotationally grazed (Todd and Hoffman 1999, Petersen 2004).

3.2.2 Topography

The Remhoogte observatory is located predominantly in Land Type Ib132, whereas the western part of the Paulshoek observatory is classified as Land Type Ib132, but the eastern part is classified as Land Type Ib274 (Fitzpatrick *et al.* 1987). Both Land Types are characterized by terrain units 1, 3, 4 and 5. The steep mountain slopes cover around 20% of the study area and are characterized by big gneiss boulders and domes. The midslope is convex with 70% rock cover and occupies 60% of the area. The footslope and the valley are alternate in some area and have a very low rock cover (<20%). The slope shape varies from concave to straight (Fitzpatrick *et al.* 1987).

3.2.3 Geology

The geology of the study site forms part of the Namaqualand Metamorphic Province. It is part of the assemblage represented by medium to high grade infrastructural gneisses and granitoids associated with metamorphosed supracrustal rocks (Saggerson and Turner 1995). The Little Namaqualand Suite comprises a silicious series of augen gneisses (Blignaut 1977). The augen gneisses weather to a pink colour, on fresh surfaces. The principal component of augen gneiss being aggregates of quartz, plagioclase, alkali feldspars and opaque minerals (Jack 1980). Rocks are cross-bedded sandstones with a granular appearance where the feldspar has been altered and weathered out. Superficial deposits of fine-grained quartz conglomerates, shales and sandstones overlie the valley bottoms (Jack 1980).

3.2.4 Soils

The large gneiss domes, characteristic of the Succulent Karoo Biome, break down into gravel and coarse sand, which dominate the Paulshoek area. Burke (2002) suggested that soils derived from granite are generally low in clay and silt. The soils are thus coarse, with a particle size of greater than 0.1 mm, allowing rapid infiltration but with low water holding capacity (Milton and Dean 1996). The soil of Paulshoek is generally infertile. The nitrogen content is around 350 µg/g, total phosphorus of 154 µg/g, soil organic matter is 1.55% and pH ranged from 6.5 to 7.9 (Allsopp 1999). Petersen (2004) reported little evidence of soil erosion on Paulshoek except for shallow run-off gullies along some of the major footpaths and tracks. The soil in this area generally appears stable in relation to wind or water erosion despite the large bare and exposed areas. The soil becomes more vulnerable to erosion when disturbed by ploughing or footpaths. There has been no formal measurement of the extent of soil loss in the area.

3.2.5 Climate

Climate data were collected at the BIOTA weather station at the study site situated between the two 1 km² observatories. The data were collected for the period of April 2001 to February 2006. The monthly mean of various climatic parameters are represented in Table 3.1.

Table 3.1 Climate data recorded by BIOTA South from April 2001 to February 2006 at Paulshoek/Remhoogte (Observatories 24 and 25)*. Data include mean monthly values for air temperature (°C), relative air humidity (%), soil temperature (°C) at 10cm soil depth, wind speed (m/s), Rainfall (mm) and wind direction (0° = N; 90° = E; 180° = S; 270° = W)

Months	Mean monthly air temperature (°C)	Mean monthly minimum air temperature (°C)	Mean monthly maximum air temperature (°C)	Air relative humidity (%)	Soil temperature (°C)	Wind speed (m/s)	Rain (mm)	Wind direction
Jan	21.5	12.0	30.9	52.0	31.2	2.65	18.9	S
Feb	23.0	14.0	33.2	49.2	31.8	2.53	6.6	SW
March	20.1	12.2	30.08	55.8	28.2	2.40	9.6	NW-SW
April	17.5	10.25	26.31	60.2	22.8	2.35	28.0	N
May	13.8	12.2	22.9	62.8	16.3	2.18	7.6	NW
June	10.1	3.5	18.0	68.8	12.7	2.10	11.1	NW
July	10.0	3.3	18.3	62.5	11.3	2.10	19.7	N
Aug	10.2	3.4	19.2	69.3	14.2	2.50	14.1	NW
Sept	14.0	6.3	23.0	57.6	18.3	2.32	7.7	NW
Oct	16.5	7.0	26.3	53.4	22.7	2.40	21.8	N
Nov	18.8	10.2	28.4	51.4	27.7	2.60	17.4	S
Dec	20.3	10.3	30.2	51.0	31.5	2.72	6.8	S
Year	16.3						169.3	

* Data supplied by Ute Schmiedel, Institute of General Botany, University of Hamburg; Klaus Berger, Institute of Soil Science, University of Hamburg.

Rainfall

Rainfall spanning more than 100 years shows that the region is subject to periodic episodes of high rainfall which can be more than 100% above the mean, also to episodic droughts (Desmet and Cowling 1999a). Long-term records show that the majority of rain is received during the winter months (May to September) and occurs as a result of circumpolar frontal westerlies. The mean annual rainfall at

Kamieskroon is 230 mm (Mucina and Rutherford 2006) which is higher than the mean annual rainfall of 169.3 (Table 3.1) recorded by BIOTA in Paulshoek. Because Paulshoek lies on the ecotone between the summer and winter rainfall regions, it occasionally enjoys summer rainfall from thundershowers from the east. Climatic models produced by the Institute for Soil, Climate and Water suggest that the region to the northwest of Paulshoek has significantly higher rainfall (250 mm/per annum) (National Botanic Institute Claremont, South Africa) (www.maposda.net/global'report/pdf/1.satasko.pdf, 2005).

Paulshoek has a high degree of local rainfall variability despite the fact that the Succulent Karoo Biome generally has a low coefficient of variation (Hoffman and Cowling 1987, Desmet and Cowling 1999a). Winter rains are mainly received from the rain bearing winds from the northwest, especially from May to September when large frontal systems sweep past the sub-continent bringing rain to a large part of the region. During autumn and spring monthly rainfall is at its most unpredictable in Paulshoek, and large downpours can result from a single event which is usually associated with southwesterly winds and cut-off lows (Desmet and Cowling 1999a).

Fog can be an important alternative source of moisture for plants along the west coast. Although generally no direct precipitation of water occurs on the soil surface, interception by vegetation may lead to a significant amount of water entering the soil below the plant (Desmet and Cowling 1999a). The occurrence of fog in Paulshoek is relatively insignificant and is generally confined to the high-lying western part of the Kamiesberg and the low-lying valleys to the south of the village (Petersen 2004).

Temperature

Winter months in Paulshoek are surprisingly cold probably because of relatively high altitudes. The mean annual temperature is 16.3°C (Table 3.1). The mean monthly maximum temperature reaches 33.2°C in the summer (February) while the mean minimum temperature falls to 3.3°C in the winter months (July). There is a dramatic fluctuation of daily temperature between September and October (from 8.9 to 36.6°C from BIOTA data) which can be disastrous for livestock owners. These critical extremes in the climate affect livestock and crop production in this area and have

had a significant influence on the way in which people manage their natural resources (Petersen 2004).

3.2.6 Vegetation

The study area is situated within the Succulent Karoo Biome (Rutherford and Westfall 1986). Petersen (2004) described the vegetation of Paulshoek as dominated by two major vegetation types, which are closely associated with the geomorphological features of the area. In the south- to east-facing upper slopes, the large granite domes support tall shrubland dominated by a mixture of non-succulent genera such as *Eriocephalus*, *Euclea*, *Hermannia*, *Lebeckia*, *Pteronia*, *Rhus*, and succulent genera such as *Euphorbia*, *Ruschia*, *Tylecodon*. This vegetation agree with what was described as Mountain Renosterbosveld (VT 43) by Acocks (1953, 1988), and Northwestern Mountain Renosterveld (LR 59) by Low and Rebelo (1998). Mucina *et al.* (2005) describe it as Namaqualand Granite Renosterveld (FRg1). The second major type is found on flat or gently sloping rock sheets and is dominated by dwarf evergreen shrubs such as *Pentzia incana* and the poisonous kraalbos *Galenia africana* or prostrate succulents. It also covers the wide plains and broad valleys with dry water courses This dwarf shrubland contains many succulents such as *Ruschia robusta*, plants with ericoid leaves (e.g. Asteraceae), geophytes and ephemeral herbs and forms part of Acocks's (1953) Namaqualand Broken Veld (VT33), or Upland Succulent Karoo (LR 56) by Low and Rebelo (1998). Mucina *et al.* (2005) recognised three vegetation types in this area: a) the plains and broad valleys with dry water courses is described as Namaqualand Blomveld (SKn3) b) the flat, gently sloping rock sheet is described as Namaqualand Klipkoppe Shrubland (SKn 1) and c) steep slopes of the large granite domes described as Kamiesberg Mountains Shrubland(Skn6)

The area covered by observatories falls entirely within Acocks (1953) classified as Namaqualand Broken Veld and Low and Rebelo (1998) as Upland Succulent Karoo. According to the more detailed classification of Mucina and Rutherford (2006) the Namaqualand Blomveld covers the western part of the observatories, with the Namaqualand Klipkoppe Shrubland in the eastern part. A small section in the

northeastern corner of the Paulshoek observatory falls in the Kamiesberg Mountain Shrubland.

3.3 Methods

An observatory can be defined as a permanent study area of 1 km² which was chosen by the BIOTA task team based on certain ecological and biological characteristics. An observatory is further subdivided into plots and subplots of different sizes and are monitored each year. Vegetation surveys were done by the task team of BIOTA in 2002, 2003, 2004. The layout of each 1 km² observatory is presented in Figure 3.2. The individual hectares in each observatory were ranked according to habitat type and the 20 highest ranking hectares were selected for the vegetation survey. Ranking was done so that a minimum of three plots were selected per habitat type in each observatory. The layout of Whittaker plots in each hectare is also illustrated in Figure 3.2. A species inventory and counting of individuals was made by the the task team in the Whittaker plots. This was repeated annually during the three years. The data used in this study were those of 10m x 10 m plots. Soil data was also provided by a member A. Petersen*.

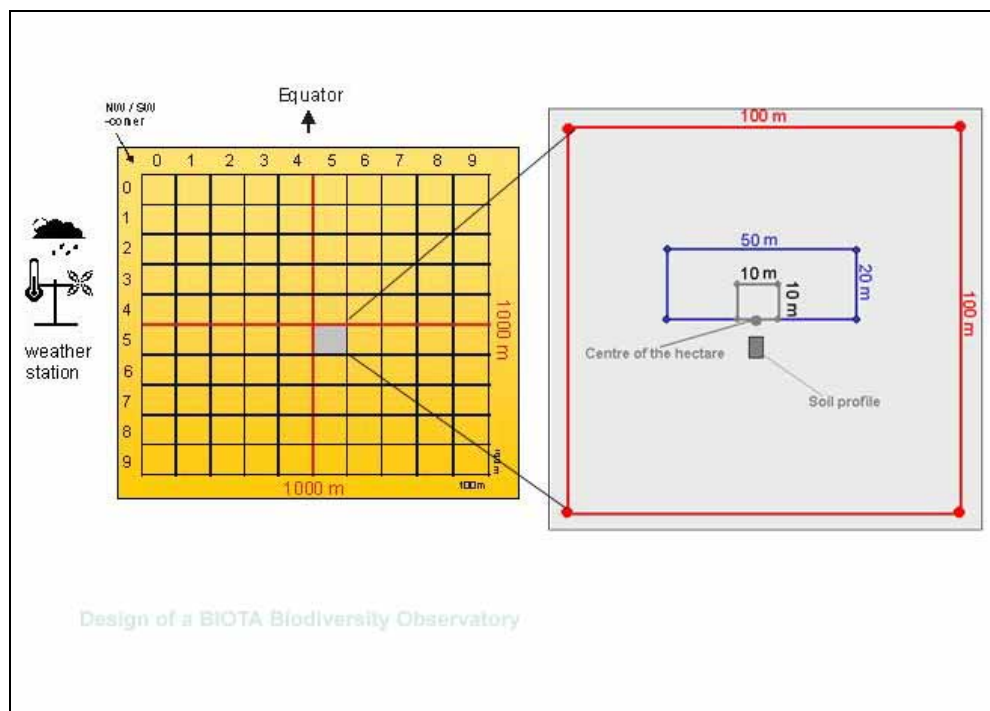


Figure 3.2 The design of the Whittaker plots in the BIOTA biodiversity observatory.

Data analysis

The values used in this study represent the mean number of individuals per species per plot across the three years. Because of the large number of individuals encountered for some species the number of individuals per species was converted to an eight-point scale as set out in Table 3.2.

Table 3.2 Eight-point scale used for the phytosociological classification

Number of individuals per species	Corresponding scaled value
0 -1	1
>1-5	2
>5-10	3
>10-25	4
>25-50	5
>50-100	6
>100-500	7
>500-1500	8

The first classification of the vegetation, based on the total data set, was obtained by the application of the TWINSpan classification algorithm (Hill 1979). Twinspan divides the data set into distinct groups on the basis of differences in floristic composition between samples or groups of samples. Further refinement of the classification was achieved by Braun-Blanquet (Zürich-Montpellier) procedures i.e the successive rearrangement of rows (species) and columns (relevés) in the matrix until a clear pattern of mutually discriminant nodes of species – relevé groups was obtained (Werger 1974, Mueller-Dombois and Ellenberg 1974, Bredenkamp and Bezuidenhout 1995). A phytosociological table including six communities was constructed

A hierarchical clustering analysis based on the incremental sum of square and chord distance in the Syn-Tax 2000 (Podani 2001) was carried out to compare with the results of the original classical table sorting. A principal coordinate analysis (PCoA) based on chord distance in Syn-Tax 2000 was used as the ordination technique to show the relationships between the relevés in multidimensional space. With the aid of an aerial photograph obtained from M. Keil* the final communities obtained were mapped. With the exception of one subcommunity, mapping could not be done at subcommunity level.

3.4 Results

The vegetation of the two observatories as other parts of Namaqualand was species rich and a total of 322 species were recorded in the 40 plots sampled. Paulshoek had a total number of 249 species with a mean of 42 species per plot. Remhoogte had a total number of 207 species with a mean number of 44 species per plot. The vegetation of Paulshoek and Remhoogte can broadly be classified as *Galenia africana*-*Lycium cinereum* shrubland. Plant species with high constancy in all communities were: the shrubs *Galenia africana*, *Lycium cinereum*, the annual herbs *Ursinia nana* and *Leysera tenella* (species group X, Table 3.3). Other plant species that were relatively common were the grass *Schismus barbatus* and the shrub *Ruschia viridifolia* (species group X, Table 3.3). The vegetation was divided into six major communities or associations of which three were further subdivided into subcommunities (Table 3.3 Figure 3.3).

The six communities were classified as follows:

- 1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water course community
 - 1.1 *Carpobrotus edulis*-*Erodium cicutarium* water course subcommunity
 - 1.2 *Oncosiphon suffruticosum*- *Lepidium desertorum* water course subcommunity
- 2 *Crassula vaillantii*-*Galenia africana* sandy valley community
- 3 *Chaetobromus dregeanus*-*Galenia africana* plains community
- 4 *Oxalis foveolata*-*Moraea serpentina* old field community
- 5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community
 - 5.1 *Anthospermum dregei*-*Polymita albiflora* rocky slope subcommunity
 - 5.2 *Pteronia ciliata*-*Eriocephalus microphyllus* rocky slope subcommunity
 - 5.3 *Cheiridopsis denticulata*-*Leipoldtia schultzei* rocky slope subcommunity
 - 5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity
- 6 *Antimima miersiana*-*Chrysocoma ciliata* rocky hills community
 - 6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hills subcommunity
 - 6.2 *Osteospermum rigidum* -*Chrysocoma ciliata* rocky hills subcommunity

The cluster analysis (Figure 3.4) and the ordination (Figure 3.5) showed similar trends on the relationships of plant communities. The position of the communities could be related to the land-use, but mostly to the position on the landscape. Community 1 that occurred in the water course and community 2 occurring in the sandy valley community were closely related. These two communities were very distinct from the other communities and were the most disturbed areas (Figure 3.4). Community 3 and 4 both occurred on the plains but differed in the previous land-use as community 4 was formerly used for agricultural purposes. Community 5 and 6 occurred in the rocky areas and were less disturbed, with community 5 restricted to the privately-owned rangeland and community 6 occurring predominantly on communal rangeland.

Table 3.3 Phytosociological table of the plant communities of Paulshoek (P) and Remhoogte (R)

Community number	1						2				3						4			5.1			5.2			5				5.3			5.4			6.1		6						
Subcommunity number	1.1			1.2																																								
Paulshoek/Remhoogte	P	R	P	P	P	R	P	P	R	P	P	P	P	P	R	R	P	P	R	R	R	R	R	R	R	R	R	R	R	R	R	R	P	P	P	P	P	R						
Releve number	9	4	6	9	8	2	2	2	2	3	9	1	9	2	8	1	1	6	5	9	7	4	2	7	8	6	6	4	3	4	0	3	0	8	0	0	4	3	1	8				
	0	6	2	1	0	3	7	4	2	0	4	0	6	3	1	5	1	1	4	6	4	2	4	2	7	5	4	5	0	0	6	4	7	7	1	4	4	7	2	8				
Species group A																																												
Carpobrotus edulis	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Dicrothamnus rhinocerotis	4	.	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Cotula coronopifolia	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Albua sp. 3	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Arctotheca calendula	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Ballota africana	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Ehrharta calycina	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Berkheya onobromoides	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Species 4	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Juncus sp. 2	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Polygonum kitaibelianum	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Bromus japonicus	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Juncus sp. 1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Species 5	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Species Group B																																												
Atriplex semibaccata	.	2	2	6	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Lepidium desertorum	.	2	.	6	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Sonchus oleraceus	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Psilocaulon leptarthron	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Amsinckia calycina	.	7	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Species Group C																																												
Crassula vaillantii	.	.	.	.	2	3	7	7	2	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Arctotis acaulis	.	.	1	.	.	.	1	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Conicosia elongata	.	.	.	.	.	.	1	1	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.																

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										5.2	5.3	5.4							
Species Group K																			
<i>Pteronia ciliata</i>	2									4 2 4 . 2 1			1	1					
<i>Othonna protecta</i>					1					1 . 2 .			1						
<i>Pteronia glomerata</i>										1 4 1									
<i>Gnidia scabra</i>										1 . 2 .									
<i>Hermania cuneifolia</i> var. <i>glabrescens</i>										1 1 .							2		
<i>Crassula atropurpurea</i>				2						2 . . 2								1	
Species Group L																			
<i>Sarcocaulon salmoniflorum</i>			3					1					2 2						
<i>Laryleachia cactiformis</i>													1 . 1						
<i>Geophyte</i> sp. 11													1 . 1						
<i>Geophyte</i> sp. 12													3						
<i>Lotononis</i> sp.													2						
<i>Pharnaceum dichotomum</i>					1								3						
<i>Senecio muricatus</i>					1								3						
<i>Antimima</i> sp. 4													1						
<i>Dimorphotheca sinuata</i>													2						
<i>Tulbaghia dregeana</i>	1												2			2			
<i>Ornithogalum</i> sp. 4													2						
<i>Adromischus filicaulis</i> ssp. <i>filicaulis</i>													3						
<i>Lessertia capitata</i>					1								2						
Species Group M																			
<i>Cheiridopsis denticulata</i>	2						3 5			5 . . 5 . 3 4 . 4 1 .									
<i>Antimima clavipes</i>				2						3 . 2 3 . 1 3 . . .									
<i>Aridaria noctiflora</i> ssp. <i>noctiflora</i>						1	1			1 . 2 1 2									
<i>Amellus microglossus</i>										4 3									
<i>Phyllobolus trichotomus</i>					2					1 1									
Poaceae										4 1									
<i>Androcymbium</i> sp. 2										1 1									
<i>Brunsvigia bosmaniae</i>					1					1 . 1									
<i>Albuca viscosa</i>										1 2								4	
Species Group N																			
<i>Leipoldtia schultzei</i>	2			4			5			4 2 3 . 6 1 2 7 6 . 6 4 7									
<i>Crassula columnaris</i> ssp. <i>prolifera</i>	4				2 1					1 1 2 . 1 2 . . 3 2 . 1 . 3									
<i>Cephalophyllum rigidum</i>										2 . 2 1 2 . . 2 . . 2									
<i>Triptaris hyoseroides</i>										2 2 . 3 . 1									
<i>Lotononis oligocephala</i>	1									2 1 . 3 . 1									

Felicia merxmuelleri
Pharnaceum sp.
Cotula barbata
Bulbine sp.1

Cheiridopsis namaquensis

<i>Crassula muscosa</i> var. <i>obtusifolia</i>	.	.	1	.	.	.	.	.	.	3	.	1	.	.	.	2	1	2	2	3	.	3	.	.	4	2	.	2	4	4	.	.	.	.	.	.
<i>Crassula subaphylla</i> var. <i>subaphylla</i>	.	1	.	.	.	.	.	.	.	1	.	1	.	2	.	2	2	.	1	.	1	.	4	.	2	2	.	2	2	.	2	.	.	.	.	.
<i>Anacampseros filamentosa</i> ssp. <i>namaquensis</i>	.	.	.	.	.	.	.	.	.	.	2	1	2	.	1	.	1	1	2	7	.	2	1	.	.	.	2	.	.	.	.	.	.	.	.	.
<i>Cheiridopsis imitans</i>	.	.	.	.	.	.	.	.	.	.	.	4	5	.	2	3	.	4	.	.	.	.	.	.	.	.	.	1	.	5	.	.	.	.	.	.
<i>Manulea cheiranthus</i>	.	.	1	.	.	.	.	.	.	.	.	.	3	.	1	.	.	3	.	2	.	3	.	.	.	2	.	.	.	.	3	.	2	.	.	.
<i>Selago divaricata</i>	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	.	2	.	1	.	.	.	.	.
<i>Hermannia amoena</i>	.	.	.	.	.	.	1	.	.	.	2	.	1	.	.	.	.	.	.	.	.	2	.	1	.	.	.	1	.	.	.	.	.	.	.	.
<i>Bulbine</i> sp. 2	.	.	.	.	.	.	.	.	.	2	.	2	.	1	.	.	.	1	2	1	.	1	.	.	.	.	.	.	1	.	.	.	.	1	.	.
<i>Ornithoglossum viride</i>	.	.	.	.	.	1	.	.	.	.	.	.	2	1	.	2	.	1	.	.	1	.	1	2	.	2	.	.	.	.	1	.	.	.	.	
<i>Tylecodon reticulatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	2	1	.	.	1	.	.	.	.	1	.

Ruscia robusta

<i>Eriospermum</i> sp.	.	.	.	.	2	.	1	.	1	1	.	1	.	1	2	2	.	.	.	.	2	1	.	.	.	.	3	1	1	.	1	.	.	.	.
<i>Ruschia aggregata</i>	.	.	.	.	.	.	.	.	3	.	.	.	.	.	2	2	.	.	.	.	1	.	.	.	.	.	.	1	3	.	4	.	.	.	.
<i>Oncosiphon grandiflorum</i>	.	.	4	4	.	5	.	.	.	.	.	.	.	.	.	3	.	.	.	.	4	.	4	3	2	.	.	.	.	.	.	.	.	.	
<i>Manochlamys albicans</i>	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	
<i>Aptosimum indivisum</i>	.	1	1	.	2	.	.	1	.	2	1	3	.	.	.	1	.	6	1	.	.	1	.	.	.	.	.	.	1	.	1	.	.	.	
<i>Drosanthemum globosum</i>	.	1	.	.	.	1	.	.	2	.	.	.	.	.	.	1	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	
Geophyte sp. 9	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	
<i>Osteospermum pinnatum</i>	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	
<i>Stipagrostis dregeana</i>	.	.	5	.	.	3	.	.	.	.	.	.	.	.	.	2	.	2	.	1	.	.	1	2	.	2	3	.	.	.	.	.	.	.	

Oxalis foveolata

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	6.1																																6.2						
Species Group R																																							
Moraea serpentina	.	.	3	.	.	3	.	.	4	5	3	5	3	5	.	6	5	6	.	4	4	4	3	3	.	5	5	.	3	4	5	2	4	.	.	.	.	.	
Helichrysum cf leontonyx	.	.	4	2	.	.	7	6	7	3	4	.	5	2	4	.	7	3	.	2	4	.	2	.	3	.	2	2	.	.	.	2	.	.	.	.	.	.	
Lotononis falcata	.	.	2	.	2	.	3	3	2	2	2	.	2	.	.	1	.	1	2	.	2	.	.	.	.	.	2	2	.	.	2	1	.	2	.	.	.	.	
Albuca cooperi	.	.	.	.	2	.	2	1	2	4	3	3	2	3	2	3	.	2	.	.	.	3	4	.	.	3	2	2	3	2	2	2	4	.	.	.	.	.	
Rhynchosidium pumilum	.	7	.	.	3	.	.	.	1	6	3	1	.	.	.	.	5	.	3	3	4	.	.	.	.	4	.	3	.	.	5	.	3	.	.	.	.		
Hypertelis salsoloides	.	1	1	.	.	5	1	.	2	.	3	2	1	.	1	.	2	1	.	.	2	.	.	.	.	1	.	.	1	1	.	2	.	.	.	.	.		
Moraea fugax	.	.	.	.	2	.	.	.	.	2	2	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.		
Galenia sarcophylla	.	.	2	.	.	3	.	.	.	3	.	1	1	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.		
Species Group S																																							
Osteospermum rigidum var. rigidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	.	
Rhus undulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.		
Microlooma sagittatum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.		
Hyobanche sanguinea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	8	.	1	.	.		
Senecio rowleyanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	.		
Species Group T																																							
Antizoma miersiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	2	1	
Arctotis laevis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	4	1	3	.		
Crassula hemisphaerica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	.	.	3	.	.	.		
Crassula sp. 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2	.	3	.	3	.	.	.		
Wahlenbergia androsacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	4	.	.	.		
Asteraceae sp.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.			
Species Group U																																							
Polymita albiflora	.	.	.	.	3	.	1	.	.	.	.	1	4	.	.	.	.	.	5	5	5	.	3	6	2	5	4	4	6	4	6	1	2	2	1	1	5	1	4
Cotula leptalea	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	4	.	4	.	3	.	.	3	.	7	.	.	.	.	.	2	.	3	5	.	
Bulbine praemorsa	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	1	.	1	2	3	.	1	2	2	.	.	
Wiborgia monoptera	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	.	.	.	.	.	.	.	2	2	2	1	.	.	.	.	.	
Zygophyllum sessilifolium	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	2	.	.	.	.	.	.	.	2	.	.	.	2	2	.	.	.	
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	3	.	1	.	2	.	1	1	.	.	.		
Acanthopsis carduiifolia	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	3	.	.	.	2	.	3	.	2	.	2	.	.	.	.	.		
Lebeckia multiflora	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	5	2	.	.	3	4	.	4	.	.	.	.	.	.	2	.	2	.	.		
Lampranthus godmaniae	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	.	.	.	1	.	1	.	.		
Felicia filifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.		
Lachenelia carnososa	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	2	.	.		



Species Group V

<i>Eriocephalus microphyllus</i> var. <i>pubescens</i>	.	.	.	.	.	.	.	.	.	3	2	4	4	4	2	3	5	2	3	.	.	2	5	4	5	2	4	5	6	4	5	5	6	5	3	.	4	2	4	2
<i>Heliophila variabilis</i>	.	4	.	.	.	3	.	.	.	3	1	3	3	2	4	2	2	2	4	4	5	4	3	4	3	2	4	4	4	5	4	5	3	4	1	.	.	2	5	
<i>Pelargonium carnosum</i>	.	.	.	.	.	.	.	.	.	.	2	.	1	.	2	1	.	1	1	.	.	4	.	1	2	1	.	1	1	4	2	.	2	2	.	1	.	2		
<i>Hermannia cuneifolia</i> var. <i>cuneifolia</i>	.	.	.	.	.	.	.	.	.	1	2	.	.	1	2	.	.	2	.	2	.	2	2	.	3	2	2	1	2	3	.	2	2	.	1	2	3			
<i>Hirpicium alienatum</i>	.	.	.	.	.	.	.	.	.	2	.	.	2	.	3	.	1	2	4	4	4	1	5	3	.	3	4	4	2	3	.	2	3	1	1	.	2	2	.	
<i>Chlorophytum undulatum</i>	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	.	2	3	3	3	.	3	2	.	2	2	3	.	1	2	2	.	.	3	1	.				
<i>Pteronia incana</i>	.	.	.	.	.	.	.	.	.	.	1	2	.	1	.	1	.	1	.	.	1	.	1	.	1	.	1	.	4	.	1	2	2	5	2	2				
<i>Cyphia longiflora</i>	.	.	.	.	.	.	.	.	.	1	2	.	2	.	.	.	.	2	1	.	1	2	.	1	2	.	1	.	1	.	1	.	1	.	1	.				
<i>Phyllobolus</i> sp. 1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	2	2	.	1	.	.	.	.	.	.	.	2	1	.	.	1	.	1	.			
<i>Eriocephalus africanus</i>	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	.	.	2	.	.	2	.	.	.	.	.	.	.	1	.	3	.	3	4	.	2	.			
<i>Crassula muscosa</i> var. <i>muscosa</i>	.	.	1	.	.	.	.	.	.	.	.	.	2	.	1	1	.	.	1	.	.	.	.	.	.	.	3	.	1	.	1	.	.	1	1	.				
<i>Crassula sericea</i> var. <i>sericea</i>	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	4	2	.	2	.	2				
<i>Tripteris sinuata</i> var. <i>sinuata</i>	.	.	.	.	4	.	.	.	.	.	.	.	2	.	3	2	.	4	.	1	1	.	.	3	.	2	2	.	2	2	2	.	1	.	2	1	4			
<i>Zygophyllum retrofractum</i>	.	.	.	.	5	.	.	.	.	.	.	.	.	.	6	3	.	4	2	.	.	.	5	.	5	.	.	.	.	1	.	2	.	.	1	.				
<i>Pentaschistis airoides</i> ssp. <i>airoides</i>	.	.	.	.	.	.	.	.	.	3	2	.	1	.	.	.	.	3	.	4	.	.	.	3	.	.	.	3	.	.	3	.	3	.	3	.				
<i>Euphorbia mauritanica</i>	.	.	.	.	.	.	.	.	.	4	.	3	.	4	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	3	.	3	.	4	.				
<i>Asparagus capensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1	1	.	2	1	.	.	.	.	.	.	.	.	1	.	1	.					
<i>Bulbine frutescens</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.				
<i>Fockea comaru</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.				
<i>Lampranthus</i> sp. 1	.	.	1	.	.	.	.	.	.	4	1	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	4	.	.	.	.	.				
<i>Adromischus filicaulis</i> spp. <i>filicaulis</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	2	1	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	1	.	1	.	.	.				

Species Group W

<i>Chrysocoma ciliata</i>	.	.	.	.	.	1	1	.	4	5	5	5	4	5	1	.	3	5	.	1	2	2	.	.	1	2	4	1	4	4	2	5	3	1	3	4	3	3
<i>Ehrharta barbinodis</i>	.	.	.	.	.	.	2	.	2	3	.	3	3	2	.	.	.	4	3	3	.	4	3	.	2	.	.	4	2	4	2	4	4	3	2	3	3	3
<i>Euphorbia decussata</i>	.	.	.	.	.	1	3	.	.	.	.	2	3	.	.	.	1	.	2	4	2	4	.	3	.	.	2	1	2	1	3	2	.	.	2	2	2	1
<i>Zaluzianskya benthamiana</i>	.	.	.	.	.	.	.	4	4	3	2	2	.	.	2	.	.	2	.	.	1	.	3	.	3	4	.	2	.	.	.	3	.	2	3	.	1	2
<i>Aizoon canariense</i>	.	.	.	.	.	2	.	.	3	5	3	4	2	3	2	.	4	5	.	.	.	.	.	.	.	.	2	.	.	2	.	3	.	.	.	4	2	
<i>Babiana attenuata</i>	.	.	.	.	.	1	.	.	.	1	.	2	.	2	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	1	2	.	.	.	.	.	
<i>Sceletium exalatum</i>	.	.	.	.	.	.	2	.	2	2	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.
<i>Galenia meziana</i>	.	.	.	.	.	4	1	.	1	3	3	4	.	1	2	.	2	2	.	1	.	.	.	.	1	.	.	.	.	1	2	.	1	.	.	.	.	
<i>Oxalis obtusa</i>	.	.	.	.	.	.	3	.	5	.	3	2	3	.	2	.	2	.	.	1	.	3	.	.	.	1	.	.	3	2	4	2	.	2	.	.	.	
<i>Dorotheanthus</i> sp.	.	.	.	.	.	2	.	2	.	.	3	2	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	3	.	

Species Group X

<i>Galenia africana</i>	.	2	2	2	4	1	6	6	4	4	5	4	4	3	6	3	2	5	6	.	.	1	.	1	4	2	1	1	3	2	2	3	3	.	2	3	2	.	
<i>Lycium cinereum</i>	.	2	.	2	4	3	.	1	2	1	2	.	2	1	2	2	3	2	1	.	.	1	3	.	2	1	1	1	.	1	.	2	2	1	.	2	.	1	.
<i>Ursinia nana</i> ssp. <i>nana</i>	.	7	.	.	2	.	3	2	3	5	5	.	4	.	7	.	2	2	4	3	.	5	.	3	4	.	4	3	.	3	3	3	.	4	3	.	1	.	
<i>Trichogyne lerouxiae</i>	.	3	.	.	5	3	4	5	.	8	5	.	.	.	3	2	.	5	.	3	5	.	.	.	3	1	2	.	4	.	3	.	3	3	.	.	.	.	
<i>Ruschia viridifolia</i>	.	5	.	.	.	.	1	.	.	.	.	.	4	1	.	.	1	.	.	.	.	.	4	.	.	.	3	1	.	2	5	3	5	3	5	.	.	.	

<i>Tetragonia fruticosa</i>	.	2	.	.	.	2	.	.	.	.	2	.	.	2	.	.	.	.	.	.	1	2	.	.	.	1	.	2	.	2	.	2	1	2	2	2	3	1	1	
<i>Leysera tenella</i>	.	8	3	7	7	4	5	5	7	4	4	3	4	.	5	2	4	5	6	.	4	2	.	.	.	3	.	.	3	3	.	.	3	.	1	.	.	4	3	
<i>Schismus barbatus</i>	6	.	1	.	2	.	4	3	3	3	3	6	5	.	.	.	.	2	4	.	.	.	.	.	.	5	.	6	1	.	.	7	.	3	.	4	2	.	.	
<i>Atriplex lindleyi</i> ssp. <i>inflata</i>	.	.	.	1	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Adromischus</i> sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
<i>Adromischus marianiae</i> var. <i>immaculatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	
<i>Albuca</i> sp. 1	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Albuca longipes</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Albuca</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	
<i>Aloe krapohlana</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	
<i>Anacampseros karamontana</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Anacampseros filamentosa</i> ssp. <i>namaquensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
<i>Androcymbium</i> sp. 1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Anisodonteia triloba</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 3	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Aptosimum spinescens</i>	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
<i>Gomphocarpus fruticosus</i>	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Asparagus</i> sp.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Avonia papyracea</i> ssp. <i>namaensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Avonia quinaria</i> sp. <i>quinaria</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Bulbine</i> sp. 1	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cephalophyllum</i> sp. 1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cheilanthes capensis</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chenopodium album</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chenopodiaceae</i>	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chrysocoma</i> sp. 1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Conophytum calculus</i> ssp. <i>vanzylia</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cotyledon papillaris</i>	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula cotyledonis</i>	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula pyramidalis</i>	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula</i> sp.1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula umbella</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Diascia rudolphii</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Dimorphotheca polyptera</i>	.	.	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

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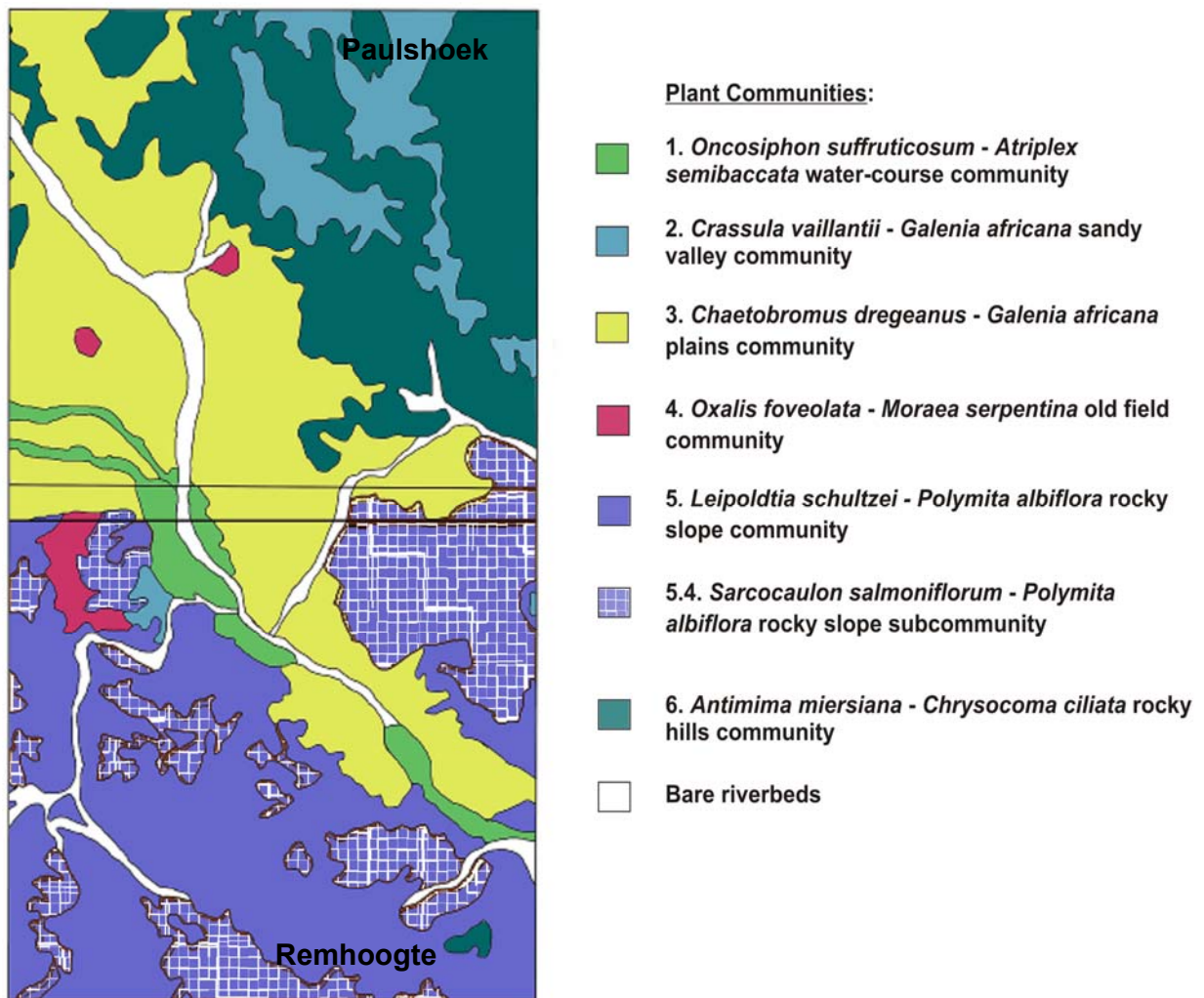


Figure 3.3 Vegetation map of observatories on Paulshoek and Remhoogte in the study area.

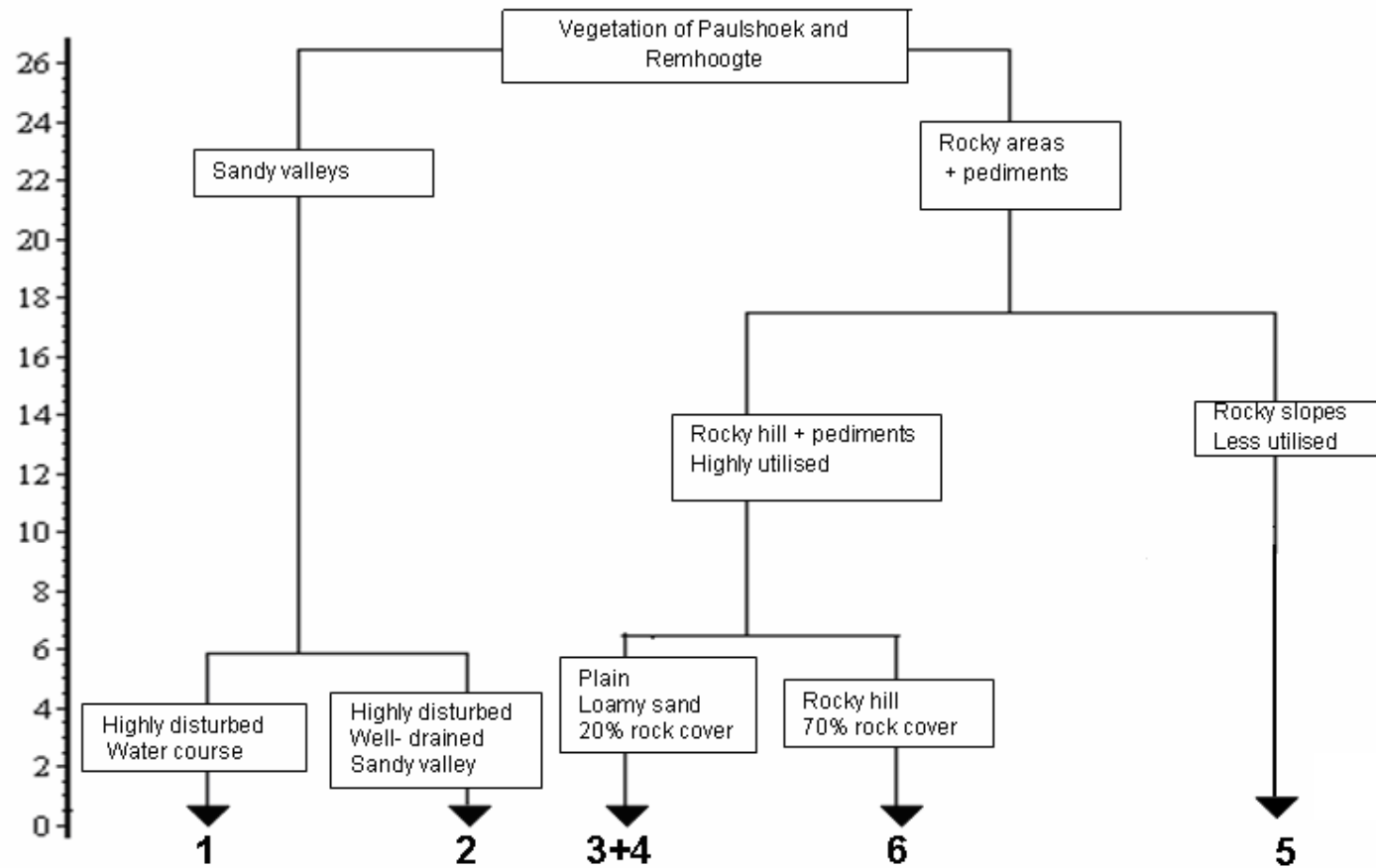


Figure 3.4 The hierarchical cluster analysis with incremental sum of squares using chord distance of the 40 relevés shows the six main plant communities of Paulshoek and Remhoogte. Numbers of plant communities correspond with numbers and descriptions of communities in the text.

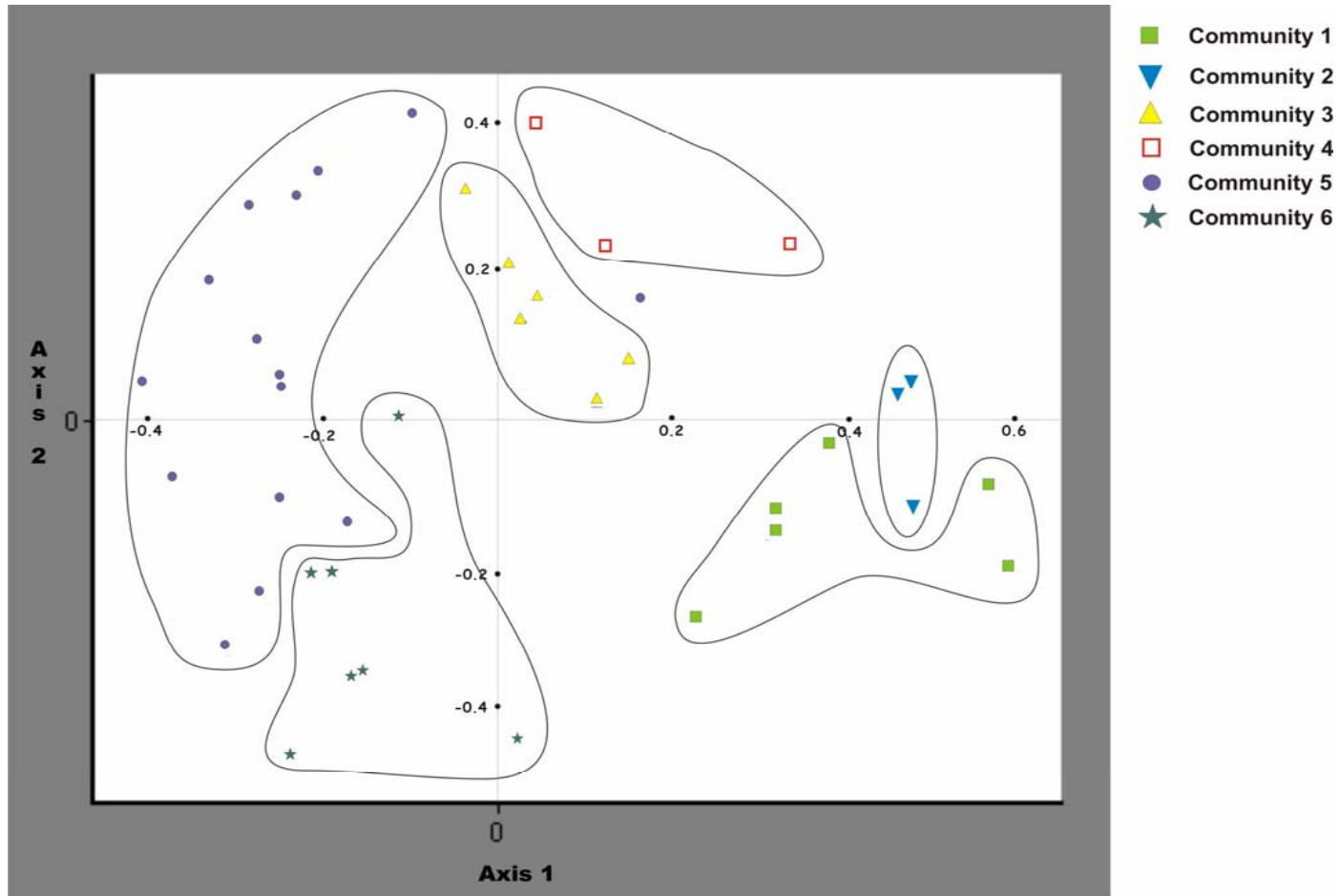


Figure 3.5 The relative positions of plant communities along the first and second axes of an ordination of floristic data by means of a principal coordinate analysis (PCoA).

Description of plant communities

1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water course community

This community is mainly restricted to the riverbed and its banks. It is a highly disturbed area with fine sandy loam soils and a rock cover of 10%. The soil pH_{H2O} ranges from 7.1 to 8.1 and the electric conductivity from 76 to 6380 µS/cm. This community has a mean of 31 species per 100 m² relevé and is linked to community 2 by species group D (Table 3.3, Figure 3.4 and 3.5). It is characterized by species group B (Table 3.3). The annual herb *Atriplex semibaccata* (species group B) and *Oncosiphon suffruticosum* (Species group D, Table 3.3) are the characteristic species of this community. Other prominent species include the annual succulent *Mesembryanthemum guerichianum* (Species group H, Table 3.3), *Leysera tenella* (species group X, Table 3.3), the shrub *Galenia africana* (species group X, Table 3.3) *Lepidium desertorum* (Species group B, Table 3.3) and *Erodium cicutarium* (Species group D, Table 3.3). This community is subdivided into two subcommunities.

1.1 *Carpobrotus edulis*-*Erodium cicutarium* water course subcommunity

This plant subcommunity is found very close to the river stream. It is generally the most disturbed habitat in most parts of Namaqualand. This subcommunity has a mean of 47 species per plot. It is characterized by species group A (species group A, Table 3.3). The perennial succulent creeper *Carpobrotus edulis* is the dominant diagnostic species with the shrub *Dicrothamnus rhinocerotis* and the perennial grass *Ehrharta calycina* found almost exclusively in this community. The dominant annual species in this subcommunity are *Leysera tenella* (species group X, Table 3.3), *Erodium cicutarium*, *Oncosiphon suffruticosum* (species group D, Table 3.3) and *Arctotheca calendula* (species group A, Table 3.3). A common shrub is *Ballota africana* (species group A, Table 3.3).

1.2 *Oncosiphon suffruticosum*- *Lepidium desertorum* water course subcommunity

This subcommunity is also found in the water stream but also includes patches some distance from the stream. In general, these are highly disturbed patches dominated by annual species. This subcommunity has a mean of 30 species per plot. It is characterized by species group B and the absence of species group A. The

dominant characteristic species are the annual herbs *Oncosiphon suffruticosum* (species group D, Table 3.3), *Atriplex semibaccata* and *Lepidium desertorum* (species group B, Table 3.3). Other conspicuous species include the succulent *Mesembryanthemum guerichianum* (species group H, Table 3.3), the annual herb *Oncosiphon grandiflorum* (Species group P, Table 3.3) and the semi-parasite *Septulina glauca* (species group D, Table 3.3).

2 *Crassula vaillantii*--*Galenia africa* sandy valley community

This community is encountered in high-lying well-drained sandy valleys which are heavily grazed by livestock. It is almost restricted to Paulshoek but occurs as a small patch in the vicinity of the water stream in Remhoogte. The soil pH_{H₂O} ranges from 6.3 to 7.7 and electrical conductivity from 15 to 32 µS/cm. It has a mean of 32 species per plot.

This plant community is differentiated by the diagnostic species of species group C such as the succulent herbs *Crassula vaillantii* and *Conicosia elongata*, and the herb *Arctotis acaulis*. The dominant species are the annuals *Lotononis falcata*, *Helichysum sp. cf. leontonyx* (species group R, Table 3.3), *Ursinia nana* subsp. *nana*, *Leysera tenella* and the grass *Schismus barbatus* (species group X, Table 3.3) and the unpalatable shrub *Galenia africana* (species group X, Table 3.3).

3 *Chaetobromus dregeanus*-*Galenia africana* plains community

This community is located on the sandy plains and footslopes. It is a well-drained area with a slight to moderate slope and a rock cover of more or less 20%. The soil pH_{H₂O} ranges from 5.7 to 7.7, and the electrical conductivity from 9.6 to 153 µS/cm. A high degree of trampling and erosion are characteristic of this area. This community covers a large area of Paulshoek and extends into Remhoogte on the plains along the water course. A mean of 55 species were recorded per plot. It is related to community 2 by the shared presence of species group F and to community 4 by the shared presence of species group G.

This plant community is characterized by species group E (Table 3.3). The dominant diagnostic species is the perennial grass *Chaetobromus dregeanus*. Prominent species in this community are the geophytes *Moraea serpentina* and *Albuca cooperi*

(species group R, Table 3.3); the annuals *Aizoon canariense* (species group W, Table 3.3), *Gazania lichtensteinii* (species group Q, Table 3.3), *Leysera tenella* (species group X, Table 3.3) and *Heliophila variabilis* (species group V, Table 3.3); the perennial shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3). The shrub *Pentzia incana* (species group Q, Table 3.3), herb *Galenia meziana* (species group W, Table 3.3) and the succulent *Mesembryanthemum guerichianum* (species group H, Table 3.3) are species with high constancy. The annual *Lessertia diffusa* and the geophyte *Ornithogalum secundum* are exclusive to this group.

4 *Oxalis foveolata*-*Moraea serpentina* old fields community

This community is found on abandoned fields on the sandy slopes on both Remhoogte and Paulshoek. The soil pH_{H2O} ranges from 6.3 to 6.8 and the electrical conductivity ranges from 30 to 114 µS/cm. There is not a specific species group distinguishing this community, which consists of relevés 11, 61 and 54. Its floristic composition shows a close affinity to community 3 by the shared species groups G and H. The dominant species in this community are the shrubs *Pentzia incana* (species group Q, Table 3.3), *Galenia Africana* (species group X, Table 3.3) and *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), the annuals *Oxalis foveolata*, *Gazania lichtensteinii* (species group Q, Table 3.3), *Leysera tenella*, and *Ursinia nana* subsp. *nana* (species group X, Table 3.3). It has a mean of 39 species per plot.

5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community

This community covers most part of Remhoogte, on rocky hills and mid-slopes. The pH_{H2O} ranges from 4.9 to 8.7 and the electrical conductivity ranges from 21 to 982 µS/cm. It is characterized by species group N. It has a mean of 67 species per plot, the highest species richness of all communities. This area is less disturbed and the difference between variants can be related to the rock size and possibly the rock cover percentage. It can be subdivided in four weakly defined subcommunities of which one (Subcommunity 5.4) was mapped separately. The dominant species are the annual *Heliophila variabilis* and dwarf shrub *Hirpicium alienatum* (species group V Table 3.3) and the succulent shrubs *Euphorbia decussata* (species group W,

Table 3.3), *Polymita albiflora* (species group U, Table 3.3) and *Leipoldtia schultzei* (species group N, Table 3.3).

5.1 *Anthospermum dregei* subsp *dregei*-*Polymita albiflora* rocky slope subcommunity

This subcommunity is characterised by the diagnostic group I (Table 3.3). The dominant species are the shrub *Pteronia ciliata* (species group K, Table 3.3), *Hirpicium alienatum* (species group V, Table, 3.3), the succulent shrub *Polymita albiflora* (species group U, Table 3.3), the annual *Phyllobolus* sp. (species group V, Table, 3.3), the geophyte *Chlorophytum undulatum* (species group V, Table, 3.3) and the grass *Ehrhata barbinodis* (species group W, Table 3.3).

5.2 *Pteronia ciliata*- *Polymita albiflora* rocky slope subcommunity

This subcommunity is found in the area with high rock cover (80%) and poorly drained soils. It does not have a diagnostic species group. It is characterized by the absence of species groups I, J and L. It consists of relevés 34, 72, 87 of species group K. It is intermediate between subcommunities 1 and 3. The dominant species are the perennial succulent *Cheiridopsis namaquensis* (species group O, Table 3.3), the shrub *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3) the succulent *Cephalophyllum rigidum* (species group N, Table 3.3), annuals *Gazania lichtensteinii* (species group Q, Table 3.3) and *Heliophila variabilis* (species group V, Table 3.3) and the geophyte *Oxalis* sp. (species group Q, Table 3.3).

5.3 *Cheiridopsis denticulata*- *Polymita albiflora* rocky slope subcommunity

This subcommunity is also found on the rocky slopes of Remhoogte and has a mean of 27 species per plot.

This subcommunity does not have a distinctive species group. It is composed of the five relevés 65, 64, 45, 30 and 40. It is characterized by the absence of species group I, K and L (Table 3.3). In addition to common species other dominant species include the perennials *Hermannia cuneifolia* var. *cuneifolia* (species group V, Table 3.3), and the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Hirpicium alienatum*, *Eriocephalus microphyllus* var. *pubescens* (species group V, Table, 3.3), the succulent shrubs *Polymita albiflora* (species group U, Table 3.3), *Leipoldtia*

schultzei (species group N, Table 3.3), the geophyte *Chlorophytum undulatum* (species group V, Table, 3.3). These species are not particularly good choices of high constancy. They were not encountered in all the relevés, whereas there are many species that were.

5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity

This subcommunity is found on plains and is characterized by species group L. It is strongly related to the previous subcommunity but has some exclusive species. The dominant species are the perennials *Leipoldtia schultzei* (species group N, Table 3.3), *Wiborgia monoptera* (species group U, Table 3.3), *Polymita albiflora* (species group U, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table, 3.3), *Chrysocoma ciliata* (species group W, Table 3.3), the succulent shrubs *Euphorbia decussata* (species group W, Table 3.3), the grass *Ehrharta barbinodis* (species group W, Table 3.3) and the annual *Heliophila variabilis* (species group V, Table 3.3).

6 *Actotis laevis*-*Tetragonia fruticosa* rocky hills community

This community is restricted to the uplands with boulders and highly rocky areas of Paulshoek. The soil pH_{H₂O} ranges from 5.3 to 7.8 and the electrical conductivity from 77 to 285 µS/cm. It has a mean of 41 species per plot. This community is characterized by the presence of species group T and to a lesser extent species group S. The dominant species of this community include the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Arctotis laevis* (species group T, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), *Pteronia incana* (species group V, Table 3.3), *Ruschia viridifolia* (species group X, Table 3.3), *Polymita albiflora* (species group U, Table 3.3), the grass *Ehrharta barbinodis* (species group W, Table 3.3). It can be subdivided into two subcommunities.

6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hill subcommunity

This subcommunity does not have a specific species group. It is characterized by the absence of species group S and differs from subcommunity 6.2 by the presence of species group R. The dominant species of this variant are the geophytes *Albuca cooperi* (species group R, Table 3.3) and *Chlorophytum undulatum* and the perennial shrub *Hirpicium alienatum* (Species group V, Table 3.3).

6.2. *Osteospermum rigidum* var. *rigidum*-*Pteronia incana* rocky hills subcommunity

This subcommunity is characterized by species group S and the absence of species group R. The dominant species include the succulents *Euphorbia decussata*, (species group W, Table 3.3) and *Polymita albiflora* (species group U, Table 3.3), the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), *Pteronia incana* (species group V, Table 3.3), the annuals *Zaluzianskya benthamiana* (species group W, Table 3.3) and *Cotula leptalea* (species group U, Table 3.3).

3.5 Discussion and conclusions

There appears to be some clear differences in plant communities between the communal and commercial land. The communal land contains communities 2 and 6 which are poorly represented on the commercial land, while the commercial land is dominated by community 5 which does not occur on the communal land. The two land-uses share the same communities along the river courses and on the abandoned cropland (communities 1 & 4 respectively) which are the most disturbed sites of the study area. Another community shared by the two land-uses is community 3 which occurs on the undulating plains.

An important consideration to bear in mind when comparing the vegetation on the two observatories is that land type differences do occur. Communities 2 and 6 on Paulshoek occur predominantly in the area covered by land type Ib274 which would probably classify as Kamiesberg Mountain Shrubland (Mucina and Rutherford 2006) such an underlying difference cautions against making sweeping statements on the effect of land-use.

The total number of species recorded was higher in the communal land than in the privately owned land. This agrees with many findings (Landsberg *et al.* 2002, Todd 2006) that suggest that grazing increases species richness at a local scale by providing opportunities for more species to establish. However, on a plot basis,

species richness was almost the same in both rangelands and varied with the landscape.

The sampling method used in this study could influence the final results. Plots were not chosen according to the plant community concept where the plot has to be representative of the community sampled, but they were situated north of the centre of the hectare which does not necessarily represent the floristics of the hectare or the community. Although the method used was not ideal for a phytosociological study, the data could be successfully used to classify the vegetation into distinct communities.

3.6 Appendix

List of unidentified species and their description by BIOTA task team.

- Adromischus* Flachblatt - *Adromischus* sp. 1
Androcymbium behaart - *Androcymbium* sp. 1
Androcymbium Schmalblatt - *Androcymbium* sp. 2
Albuca 5blatt = *Albuca* sp. 1
Albuca Vielblatt gestreift = *Albuca* sp. 2
Albuca Zurückgeschlagene tepalen = *Albuca* sp. 3
Antimima cf Klein - *Antimima* sp.1
Antimima Kurz Spitzblatt = *Ru robusta*? - *Antimima* sp. 2
Antimima Polster Paulshoek - *Antimima* sp. 4
Antimima *Ruschia robusta* ähnlich - *Antimima* sp. 3
Asparagus kurze Blätter - *Asparagus* sp.
Asteraceae gewelltes Pfeilblatt, rotes Köpfchen, verholzt – Asteraceae sp.
Asparagus kurze Blätter – *Asparagus* sp.
Bulbine breite Blätter, behaarter Rand - *Bulbine* sp. 3
Bulbine frutescens drüsig - *Bulbine* sp. 1
Bulbine klein bläulich – *Bulbine* sp. 2
Cephalophyllum Spitzblatt – *Cephalophyllum* sp.
Chenopodiaceae – Chenopodiaceae sp.
Chrysocoma große Blüten – *Chrysocoma* sp. 1
Crassula mini-Blätter verholzt – *Crassula* sp. 2
Crassula strauichig aufrecht - *Crassula* sp. 3
Crassula verh., rote Blätter – *Crassula* sp. 1
Drosanthemum abstehend verzweigt, schuppig – *Drosanthemum* sp. 2
Drosanthemum behaart weiss – *Drosanthemum* sp. 4
Drosanthemum fein, bläulich – *Drosanthemum* sp. 3
Drosanthemum klein weiß – *Drosanthemum* sp. 1
Fabaceae kl. 3-Blätter, Blasenfrüchte – Fabaceae sp.
Geophyt großes Blatt mit hellem Rand – Geophyte sp. 11
Geophyt heller Rand – Geophyte sp. 3
Geophyt Korkenzieher glatt - Geophyte sp. 4
Geophyt Lockenwickler – Geophyte sp. 1
Geophyt Lockenwickler gekerbt – Geophyte sp. 7
Geophyt Lockenwickler glatt – Geophyt sp. 5
Geophyt Lockenwickler hairy- Geophyte sp. 6
Geophyt Lockenwickler sukkulent – Geophyte sp. 8
Geophyt Riemenblatt – Geophyte sp.12
Geophyt Spirale sukkulent – Geophyt sp. 2

Geophyt stachlig – Geophyt sp. 9
 Geophyt welliger Rand – sp. 10
 Gras breite Blätter, behaart – Poaceae sp. 1
 Gras Langblatt – Poaceae sp. 2
Helichrysum cf. Blüten in Blattachse (, od. *Crassula*?) - *Helichrysum* sp.
Hirpicium gestreckte Achse – *Hirpicium* sp. 1
Jamesbrittenia Rundblatt – *Jamesbrittenia* sp.
Juncus klein – *Juncus* sp. 1
Juncus sp – *Juncus* sp. 2
 Keimlinge – Species 5
Lachenalia sp- *Lachenalia* sp. 4
Lachenalia Herzblatt – *Lachenalia* sp. 1
Lachenalia Zebrafuß – *Lachenalia* sp. 2
Lampranthus unordentlich/*Scopelogenia* – *Lampranthus* sp. 3
Lycium große Früchte – *Lycium* sp.
Ornithogalum 3Blatt – *Ornithogalum* sp. 3
Ornithogalum große Knolle – *Ornithogalum* sp. 1
Ornithogalum mini behaart – *Ornithogalum* sp. 2
Oxalis am Wasser – *Oxalis* sp. 2
Oxalis Fabaceae – *Oxalis* sp. 3
Oxalis Herzblatt mini – *Oxalis* sp. 1
Oxalis zusammengefaetete miniblatte – *Oxalis* sp. 4
Oxalis mini – *Oxalis* sp. 5
Pelargonium weich – *Pelargonium* sp.
Pharnaceum Basis verholzt locker – *Pharnaceum* sp.
Phyllobolus flach – *Phyllobolus* sp.
 Roggen/Hafer – species 4
Ruschia rotes Polster – *Ruschia* sp. 1
Salicornia niederliegend – *Salicornia* sp. 1
 Strauch längliche Blätter – species 1
 Strauch schmale Blätter – species 2
 Strauch spatelblättrig – species 3
Tylecodon 3 Blatt – *Tylecodon* sp. 1
Tylecodon hellgrün glatt – *Tylecodon* sp. 2

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Chapter 4

Dispersal spectra of communal versus commercial rangeland in Namaqualand, South Africa

4.1 Introduction

Dispersal is a key process in the ecological and evolutionary dynamics of a population. Dispersal plays an important role not only in range expansion of a species but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Although ecologists have long appreciated the importance of dispersal for spread and persistence of populations, the last decade has witnessed a surge of interest in how this phase of the life cycle influences community structure (Nathan and Muller-Landau 2000, Cain *et al.* 2000). Dispersal is believed to set the template from which community patterns develop (Levine and Murrell, 2003) and knowledge of seed dispersal finds applications in nature conservation and ecological restoration (Strykstra *et al.* 2002).

The persistence and distribution of any plant species is affected by many factors and the mode of dispersal of any plant species must reflect many different pressures and constraints of the environment. Every individual plant struggles to ensure that its own offspring make up as big a fraction as possible of the next generation, and for each individual plant there is an evolutionary gain to leave more surviving seedlings than its neighbour (Crawley 1993). Because natural selection must work with existing variation, and many plants have very long generation times, there are phylogenetic constraints (Willson and Traveset 2000).

In general, about 75% of the seeds produced by plants are consumed before and after dispersal. The notion of a safe site was proposed by Harper *et al.* (1965) to describe those specific conditions which permit a seed to escape all hazards of the pre-germination phase, to overcome dormancy and to establish successfully. To start a next generation in a safe site, an individual has to reach the next safe site in time as well as space through dispersal (Strykstra *et al.* 2002). An unequal distribution in habitat quality with a constant rate of dispersal results in source-sink

processes, with a net flow of individuals from rich habitats into the poor ones (Kisdi 2002, Levin *et al.* 2003).

The term dispersal is defined as the unidirectional movement of an organism away from its place of birth (Levin *et al.* 2003) and includes horizontal and vertical movement (Campos and Ojeda 1997). When studying dispersal mechanisms several criteria can be used to classify the dispersal mode. Dansereau and Lems (1957) suggested four alternative criteria: the morphological nature of the diaspore, the genetic composition of the diaspore, the presumed or observed agent of dispersal and conditions for establishment. Any one of these classification systems cannot be wholly satisfactory, since a certain structure may be adapted for dispersal in different and sometimes even antagonistic ways.

Most studies in plant community ecology in South Africa have focused on the floristic analysis of the vegetation and vegetation attributes have seldom been applied. The use of plant functional traits to describe patterns in plant communities provides us with the means to understand the mechanisms of vegetation responses to environmental change which a purely floristic approach does not accomplish. Moreover, such features lend themselves to statistical treatment in the form of spectra, which show the variety, the amplitude and the proportion of the function involved in the internal mechanics of the community (Dansereau and Lems, 1957).

Some relationships between particular dispersal methods and environmental conditions have been proposed. Stocking pressure imposes a rigorous but complex selection process on the flora by the direct grazing by herbivores, the associated trampling effects and the redistribution of nutrients through urine and faeces (Navie and Rogers 1997). Many authors (Collins and Uno 1985, Milton *et al.* 1990, Willson *et al.* 1990, Nakanishi 2000b) have suggested that epizoochores are more common in disturbed than in undisturbed habitats and that they are often also common in grazed vegetation types due to the availability of the dispersal agent (herbivorous mammals). Plant species possessing more than one type of seed differing in their dispersal mode and germination requirement (heterodiaspory) are likely to resist in unpredictable environments such as disturbed habitats given their ability to adapt to different environments (Harper 1977, Van Mölken *et al.* 2005). It could therefore be

speculated that more heterodiasporic species should be found vegetation that is heavily grazed.

Many studies (Gutterman *et al.* 1973, Johri 1984; Gutterman 1996, Gutterman & Shem-Tov 1997, Gutterman 2002) have speculated on the ecological importance of the mucilage produced by the seeds of certain desert plants upon moistening (myxospermy). The most prominent being that the mucilage: a) adheres the seed to the soil to prevent further movement, b) adheres to passing animals for long distance dispersal, c) provides a good contact between the seed and the soil surface, d) lubricates the area surrounding the seed making it easier for the root to penetrate the soil, and e) the water held by the mucilage could serve as water reservoir for germination. Ellner and Shmida (1981) characterize myxospermy as an anchorage mechanism against surface runoff and the retention of the mother site as a side effect.

The objectives of this study were to analyze and compare the dispersal spectra in a communal and commercial rangeland, and those of the different plant communities found in the study area, to improve our understanding of plant community patterns and processes.

4.2 Study area

The study site is located near Paulshoek (30°20'S, 18°15'E), one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape (Figure 2.1). Paulshoek is a remote village about 50 km east of Garies and lies on the eastern foothills of the Kamiesberg Mountain Range at an altitude of between 980 and 1 400m above sea level (Todd and Hoffman 1999). The Paulshoek commons is fenced on three sides by commercial farms. The site of the current study is a 1 km² section on the southern border of the Paulshoek commons. The study site includes another 1 km² section which extends approximately 1 km from the Paulshoek boundary into one of the neighbouring privately owned farms, Remhoogte (Southeast from Paulshoek village).

Over the last 30 years, the mean stocking density for Paulshoek has been roughly 6 ha per small stock unit, which is double the rate recommended for the region by the

South African Department of Agriculture. The stocking density on the local commercial farms remains at approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999). The grazing regime on the communal land has been characterized by heavy and continuous grazing whereas the neighboring commercial rangeland is moderately and rotationally grazed (Todd and Hoffman 1999, Petersen 2004).

Rainfall data of more than 100 years shows that the region is subject to periodic episodes of high rainfall as well as episodic droughts (Desmet and Cowling 1999a). The majority of the annual rainfall is received during the winter months (May-September). Rain occurs as a result of circumpolar frontal westerlies. The mean annual rainfall is 169.3 mm at Paulshoek (data to 2001 to 2006 for an on-site, BIOTA weather station*). The occurrence of fog in Paulshoek is relatively insignificant and is usually restricted to the high-lying western part of Kamiesberg and the low-lying valleys to the south of the village (Petersen 2004).

Winter months in Paulshoek are unpredictably cold probably because of relatively high altitudes. The mean annual temperature is 16°C (Table 3.1). The mean monthly maximum temperature reaches 30°C in the summer (February) while the mean minimum temperature falls to 3.1°C in the winter months (July) (BIOTA data).

Paulshoek is situated within the Succulent Karoo Biome (Rutherford and Westfall 1986). The study area form part of the vegetation type found in flat or gently sloping rock sheets supporting dwarf evergreen shrubs such as *Pentzia incana* and the poisonous kraalbos *Galenia Africana*. It also covers the wide plains and broad valleys with water courses. This sparse dwarf shrubland contains many succulents such as *Ruschia robusta* plants with ericoid leaves (e.g. Asteraceae), geophyte and ephemeral herbs and forms part of Acocks (1953, 1988) Namaqualand Broken Veld (VT33), or Upland Succulent Karoo (LR 56) by Low and Rebelo (1998). Mucina *et al.* (2005) recognised three vegetation types in these areas: a) the plains and broad valleys with dry water courses are described as Namaqualand Blomveld (SKn 3), b) the flat, gently sloping rock sheet is described as Namaqualand Klipkoppe Shrubland (SKn 1) and c) steep slopes of the large granite domes described as Kamiesberg Mountains Shrubland (SKn 6).

A vegetation survey of the study area revealed six plant communities (Figure 4.1). These six plant communities have been classified as follows:

- 1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water-course community
 - 1.1 *Carpobrotus edulis*-*Erodium cicutarium* water-course subcommunity
 - 1.2. *Oncosiphon suffruticosum*- *Lepidium desertorum* watercourse subcommunity
- 2 *Crassula vaillantii*-*Galenia africana* sandy valley community
- 3 *Chaetobromus dregeanus*-*Galenia africana* plains community
- 4 *Oxalis foveolata*-*Moraea serpentina* old field community
- 5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community
 - 5.1 *Anthospermum dregei* -*Polymita albiflora* rocky slope subcommunity
 - 5.2 *Pteronia ciliata*–*Eriocephalus microphyllus* rocky slope subcommunity
 - 5.3 *Cheiridopsis denticulata*-*Leipoldtia schultzei* rocky slope subcommunity
 - 5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity
6. *Antimima miersiana*-*Chrysocoma ciliata* rocky hills community
 - 6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hills subcommunity
 - 6.2 *Osteospermum rigidum* -*Chrysocoma ciliata* rocky hills Subcommunity.

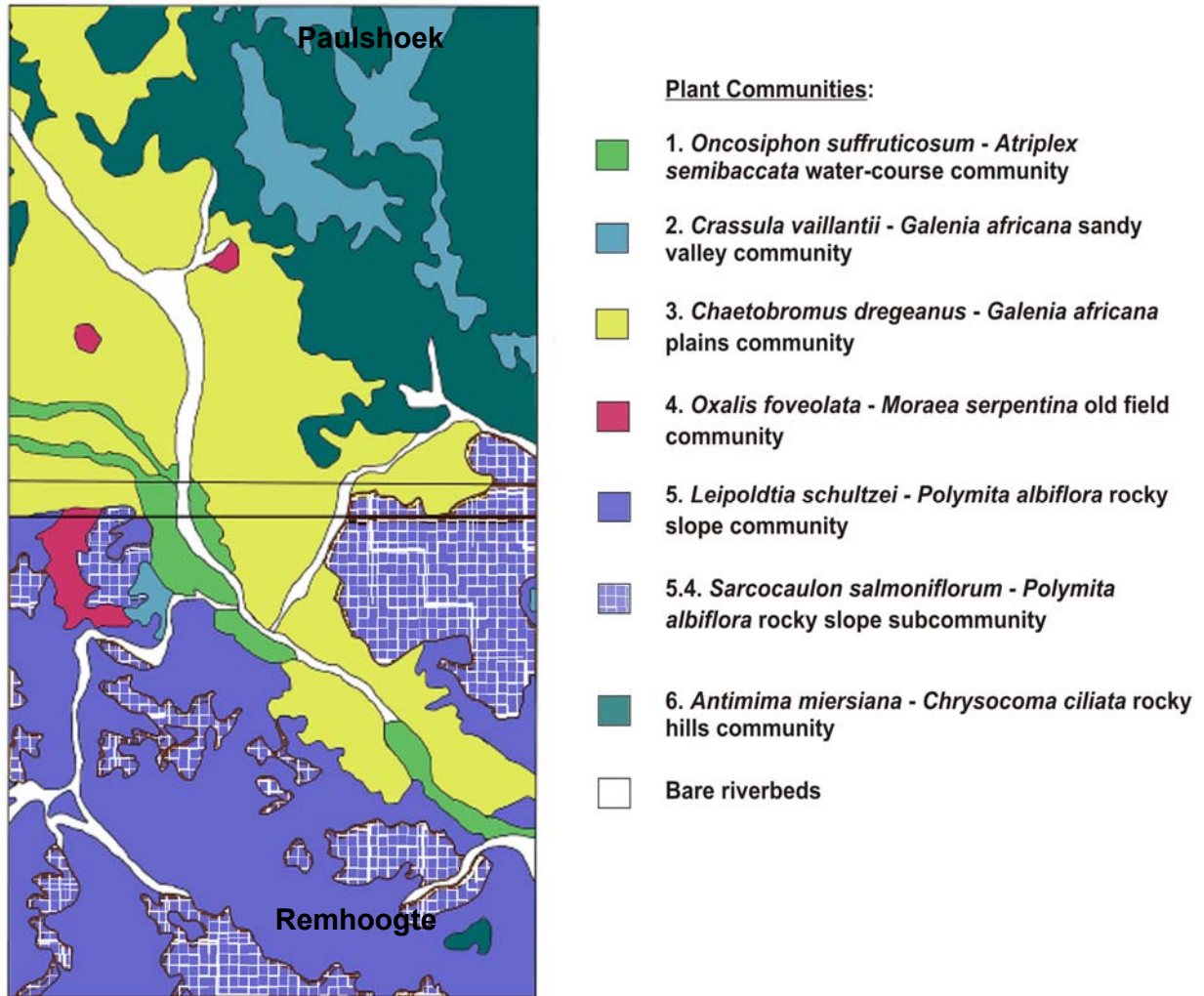


Figure 4.1 Vegetation map of the study area.

4.3 Materials and methods

Dispersal types have been assigned to each plant species recorded in the study area on the basis of apparent morphological adaptations because it requires considerable study to quantify actual dispersal vectors by field observations. There is a general consensus that the character syndromes associated with particular kinds of dispersal vectors can be identified quite reliably in the majority of species (Willson *et al.* 1990). Thus the spectra reported describe the incidence of apparent morphological traits in plants. To attribute a dispersal morphology to the species, a combination of inspection of the diaspores in the herbarium, published data concerning dispersal morphology, and field observations were used. Seventeen categories of dispersal morphology were distinguished based on the following criteria (Van Rheede van Oudshoorn and Van Rooyen 1999):

Autochory (Aut): A diaspore that is propelled explosively, e.g. a fruit that opens suddenly or by a trip-lever, this also includes hygrochasic and trypanospermic diaspores.

Balloon diaspores (Bal): Balloon diaspores contain air that increases the volume and decreases the density of the diaspore.

Dust diaspores (Dus): Small diaspores without special devices for buoyancy.

Endozoochory (End): The diaspore has a fleshy pulp or aril of a type that is associated with consumption by vertebrate frugivores to eject and disperse the seed.

Epizoochory (Epi): The diaspore has hooks, burrs, sticky hairs or other devices such that it adheres to the fur or feathers of vertebrates. Diaspores that adhere to the animals after wetting were excluded.

Heterodiaspory (Het): The production of two or more morphologically distinct types of diaspores by an individual plant.

Hygrochasy (Hyg): The diaspore is contained in a fruit that opens when wet and closes when dry.

Nautohydrochory (Nah): The diaspores are directly dispersed by water currents.

Ombrohydrochory (Omh): The direct or indirect dispersal of diaspores by rain and /or dew. In this study hygrochasic and trypanospermic diaspores are classified as ombrohydrochoric. The term indirect hydrochory has also been used to refer to this term

Myxospermy (Myx): Diaspores that produce mucilage upon wetting.

Atelochory (Ate): The diaspore has no evident morphological specialization associated with dispersal.

Plumed diaspores (Plu): The diaspore is partially covered with appendages acting like a parachute.

Synaptospermy (Syn): Two or more seeds are joined together to form a compound diaspore.

Trypanospermy (Try). The form and /or appendages of the diaspore favour burial in the soil e.g. by drilling or wedging into cracks.

Tumbleweeds (Tum): Spherical structures that consist of the entire inflorescences or even the whole plant are blown along the ground by the wind, while releasing seeds as they move.

Winged diaspores (win): The diaspore has wings that slow the rate of fall.

Woolly (Woo): The diaspore is fully covered with hair that increases air resistance.

Many species have seeds that are dispersed by more than one agent and this makes the classification of many plants species into single categories impossible (Wilson *et al.* 1990, Van Rheede van Oudtshoorn and Van Rooyen 1999). Such species contributed one case to each dispersal syndrome but only once to the total on which percentages were based.

Data analysis

The data analysis was done on a qualitative and a quantitative level. For the qualitative analysis the dispersal spectrum of each rangeland was calculated by expressing the number of species with each type of dispersal as a percentage of the total number of species present in the rangeland. For the quantitative analysis the number of individuals per species (abundance) found in the study area was taken into account to calculate the percentage. For communities the dispersal spectrum of each community was calculated by expressing the number of species/individuals with each type of dispersal as a percentage of the total number of species/individuals present in the community.

The dispersal spectra of the two rangelands, both the quantitative and qualitative analyses were further compiled in two ways. Firstly, a collective species list was compiled for each rangeland. A species was only considered as present or absent for the qualitative analysis and for the quantitative analysis the value represented the total number of individuals found in the rangeland. Secondly, the data of each relevé was considered as a repetition of the rangeland, in this case values are the mean number of species or individuals found in the 20 relevés. These two approaches will be referred as Design 1 and Design 2 respectively in the rest of the text. Design 1 only allows for the comparison of the entire spectra, whereas individual dispersal types can also be compared with Design 2. Design 1 comparisons were done by means of the T-test for independent variables and chi square test; while an One Way ANOVA was used for Design 2 comparisons. All statistical analyses were done with Statistica 7 (Statsoft Inc., Tulsa, Oklahoma).

For dispersal types within communities a One Way ANOVA and a Fisher LSD *post hoc* test were used to determine the significant difference between dispersal types in a community. The criterion for statistical significance was set at $P < 0.05$.

4.4 Results

The dispersal types consistently common in both rangelands and all communities were: ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores (Figure 4.2).

Communal versus commercial rangelands

Design 1, which compared the entire spectra found no significant difference for either the quantitative or qualitative dispersal spectra between the two rangelands (Figure 4.2A & B).

An analysis of the quantitative Design 2 revealed that endozoochory is higher on communal land than in commercial land and individuals with woolly diaspores and ombrohydrochoric diaspores were found to be significantly higher on the commercial land than in the communal land (Figure 4.3B). The qualitative Design 2 analysis

showed that the number ombrohydrochoric, myxsospermic and hydrochasic species were significantly higher on commercial land than communal land (Figure 4.3A).

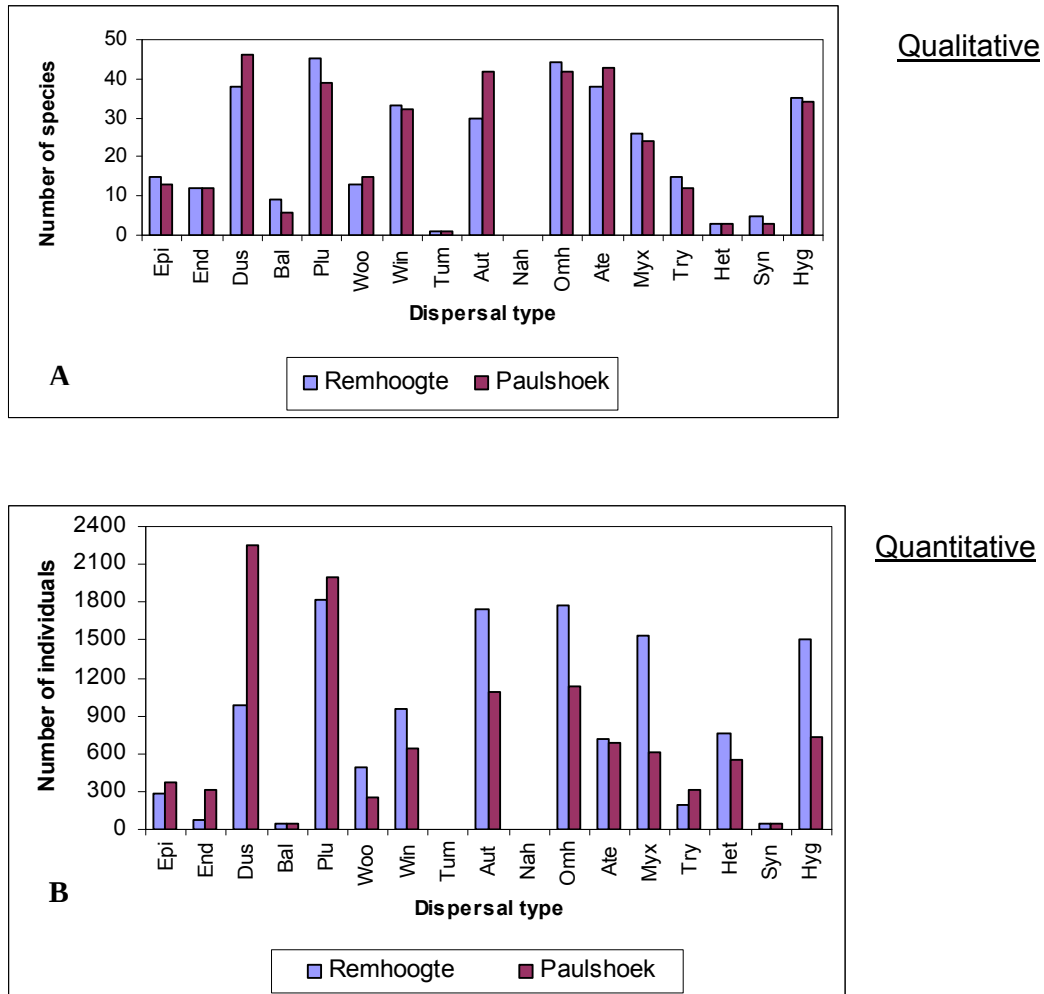
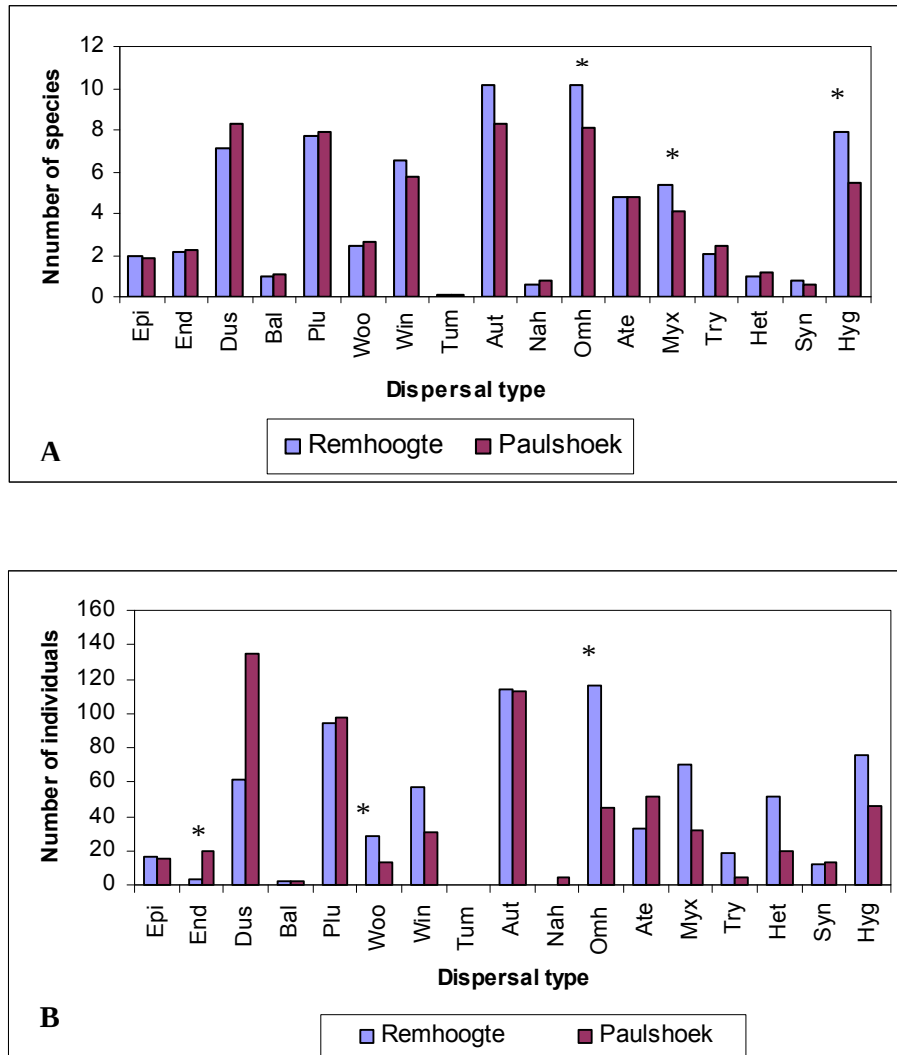


Figure 4.2 (A) Qualitative and (B) quantitative dispersal spectra of Paulshoek and Remhoogte observatories derived by evaluating a collective species list of each rangeland (Design1). Explanations of abbreviations can be found on pp.56-57.



Qualitative

Quantitative

Figure 4.3 (A) Qualitative and (B) quantitative dispersal spectra of Paulshoek and Remhoogte observatories derived by evaluating the means of 20 plots surveyed in each rangeland (Design 2). Explanations of abbreviations can be found on pp. 59-60.

Between communities

In general the dispersal spectra did not differ much between communities even though some dispersal types seemed to be more prominent in one community than others on a qualitative or quantitative basis. The comparison of dispersal types among communities is summarised in Tables 4.1 and 4.2. For qualitative data endozoochory, autochory and woolly diaspores show significant variation between

communities. Endozoochory was found to be significantly higher in the water course community (community 1) than in the plains community (community 3) and in the rocky slopes community (community 5). Woolly diaspores were found to be significantly lower in the water course community (community 1) than in the rocky hill community (community 6) (Table 4.1, Figure 4.3) and autochoric species were significantly more in the sandy valley (community 2) than in water course community.

Table 4.1 Qualitative comparisons of dispersal spectra of six plant communities of Paulshoek and Remhoogte.

Dispersal type	Community						P
	1	2	3	4	5	6	<0.05
A. Telechory							
Zoochory							
Epizoochory	3.86	4.51	3.14	2.18	4.05	6.81	0.17 ^{ns}
Endozoochory	10.81 ^b	6.46 ^{ab}	3.15 ^a	5.07 ^{ab}	3.36 ^a	5.88 ^{ab}	0.00 [*]
Anemochory							
Dust diaspores	12.89	23.57	17.86	15.53	15.40	16.94	0.07 ^{ns}
Balloon diaspores	3.07	3.50	2.40	2.44	2.36	0.25	0.13 ^{ns}
Plumed diaspores	17.47	17.03	16.69	17.05	15.49	18.74	0.91 ^{ns}
Woolly diaspores	2.45 ^a	4.24 ^{ab}	5.39 ^{ab}	6.36 ^{ab}	5.14 ^{ab}	7.64 ^b	0.00 [*]
Winged diaspores	9.12	18.24	11.68	9.93	13.86	15.75	0.06
Tumbleweeds	0.45	0.00	0.21	0.00	0.12	0.00	0.75 ^{ns}
Autochory	10.90 ^a	26.73 ^b	18.43 ^{ab}	17.00 ^{ab}	21.59 ^{ab}	19.57 ^{ab}	0.02 [*]
Hydrochory							
Nautohydrochory	0.00	0.00	0.00	0.00	0.00	0.00	1
Ombrohydrochory	13.32	25.25	20.95	19.47	20.39	17.48	0.11 ^{ns}
B. Atelechory	9.56	12.52	10.35	10.44	9.60	9.30	0.87 ^{ns}
C. Additional features (Antitelechory)							
Anchorage mechanisms							
Myxospermy	11.00	7.27	9.20	14.51	10.87	10.07	0.74 ^{ns}
Trypanospermy	2.96	2.76	5.84	3.70	4.25	4.93	0.08 ^{ns}
Reduction in dispersal potential							
Synaptospermy	2.07	1.48	1.62	0.00	1.28	2.23	0.93 ^{ns}
Heterodiaspory	4.1	3.03	2.51	2.67	1.82	1.74	0.57 ^{ns}
Restriction of dispersal in time							
Hygrochasy	13.27	16.30	15.89	11.43	14.59	11.37	0.74 ^{ns}

For quantitative data significant differences were found in the contributions of plumed, woolly, autochoric, ombrohydrochoric, and hygrochasic diaspores. The number of individuals with plumed diaspores was significantly higher in the sandy valley (community 2) than in water course community (community 1) old field community (community 4) and rocky hill community (community 6), the number of individuals with woolly diaspores were significantly lower in water course community (community 1) than in rocky hill community (community 6) and the number of ombrohydrochoric individuals was found to be significantly higher in the rocky slopes community (community 5) than in the water course community (community 1). Autochory and hygrochasy was significantly higher in the rocky slopes (community 5) than in the water-course community (community 1) (Table 4.2, Figure 4.4).

Within communities

Some dispersal types show the same trend in all the communities (Table 4.3 A&B), Figure 4.4 & 4.5). Indirect hydrochory, dust diaspores and plumed diaspores are the dominant types in most communities. Epizoochory, endozoochory, balloon diaspores tumbleweeds, synaptospermy and heterodiaspory are represented in low numbers in all communities. Qualitative analysis showed less differences than quantitative analysis.

Table 4.2 Quantitative comparisons of dispersal spectra of six plant communities of Paulshoek and Remhoogte.

Dispersal type	Community						P
	1	2	3	4	5	6	<0.05
A. Telechory							
Zoochory							
Epizoochory	2.27	0.43	5.14	0.24	2.25	2.76	0.62 ^{ns}
Endozoochory	4.52	1.40	3.54	1.09	0.51	2.01	0.09 ^{ns}
Anemochory							
Dust diaspores	7.97	41.60	21.79	17.24	15.16	24.90	0.09 ^{ns}
Balloon diaspores	0.13	0.83	0.32	0.30	0.76	0.22	0.15 ^{ns}
Plumed diaspores	14.62 ^a	43.16 ^b	24.00 ^{ab}	11.38 ^a	16.07 ^{ab}	14.82 ^a	0.02*
Woolly diaspores	0.65 ^a	0.36 ^a	4.85 ^{ab}	5.41 ^{ab}	8.10 ^b	7.15 ^b	0.02*
Winged diaspores	3.65	3.82	9.41	8.09	12.61	10.90	0.26 ^{ns}
Tumbleweeds	0.00	0.00	0.05	0.00	0.01	0.00	0.55 ^{ns}
Autochory	4.54 ^a	12.95 ^{ab}	22.58 ^{ab}	14.59 ^{ab}	32.29 ^b	22.60 ^{ab}	0.00*
Hydrochory							
Nautohydrochory	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Ombrohydrochory	3.80 ^a	5.18 ^{ab}	17.85 ^{ab}	7.50 ^{ab}	33.40 ^b	17.62 ^{ab}	0.00*
B. Atelechory	10.82	4.50	11.80	20.11	7.52	3.51	0.30 ^{ns}
C. Additional features (Antitelechory)							
Anchorage mechanisms							
Myxospermy	14.10	4.92	17.34	12.20	13.41	7.59	0.59 ^{ns}
Trypanospermy	0.67	0.45	1.10	0.25	5.40	1.44	0.44 ^{ns}
Reduction in dispersal potential							
Synaptospermy	0.48	0.98	4.95	0.00	2.95	0.93	0.82 ^{ns}
Heterodiaspory	13.22	3.2	2.94	2.63	4.40	2.50	0.24 ^{ns}
Restriction of dispersal in time							
Hygrochasy	2.68 ^a	3.19 ^{ab}	13.39 ^{ab}	10.76 ^{ab}	20.45 ^b	20.69 ^b	0.00*

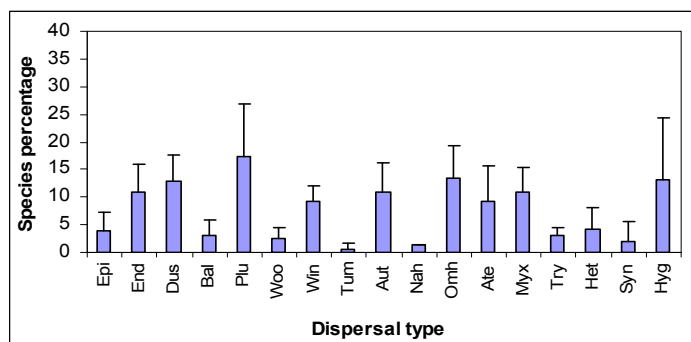
Table 4.3 Qualitative Comparisons of dispersal types within communities Within a column values with the same superscript do not differ significantly at $p < 0.05$

Dispersal type	Community					
	1	2	3	4	5	6
A Telechory						
Zoochory						
Epizoochory	3.86 ^{ab}	4.51 ^{abcd}	3.13 ^{abc}	2.18 ^{ab}	4.05 ^{abc}	6.81 ^{abcd}
Endozoochory	10.82 ^{ab}	6.49 ^{abcd}	3.15 ^{abc}	5.07 ^{abc}	3.67 ^{abc}	5.88 ^{abc}
Anemochory						
Dust diaspores	12.89 ^{ab}	23.57 ^{bcd}	17.86 ^{cd}	15.54 ^{bc}	15.40 ^{de}	16.93 ^{de}
Balloon diaspores	3.06 ^{ab}	3.50 ^{abc}	2.40 ^a	2.44 ^{ab}	2.36 ^{ab}	0.24 ^a
Plumed diaspores	17.47 ^b	17.03 ^{abcd}	16.6 ^{cd}	17.05 ^{bc}	15.49 ^{de}	18.74 ^e
Woolly diaspores	2.45 ^{ab}	4.24 ^{abcd}	5.39 ^{abcd}	6.35 ^{abc}	5.14 ^{abc}	7.65 ^{abcd}
Winged diaspores	9.10 ^{ab}	18.24 ^{abcd}	11.68 ^{abcd}	9.93 ^{bc}	13.86 ^{de}	15.75 ^{cde}
Tumbleweeds	0.45 ^a	0.00 ^a	0.21 ^a	0.00 ^a	0.12 ^a	0.00 ^a
Autochory	10.92 ^{ab}	26.73 ^d	18.43 ^{de}	17.00 ^{bc}	21.59 ^f	19.57 ^e
Hydrochory						
Nautohydrochory	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a
Ombrohydrochory	13.30 ^{ab}	25.25 ^{cd}	20.95 ^e	19.47 ^c	20.39 ^{ef}	17.48 ^{de}
B. Atelechory	9.30 ^{ab}	12.52 ^{abcd}	10.35 ^{abcd}	10.44 ^{abc}	9.59 ^{bcd}	9.29 ^{abcde}
C. Additional features (Antitelechory)						
Anchorage mechanisms						
Myxospermy	4.10 ^{ab}	7.27 ^{abcd}	9.20 ^{abcd}	14.51 ^{abc}	10.87 ^{cd}	10.07 ^{abcde}
Trypanospermy	11.00 ^{ab}	2.76 ^{abc}	5.84 ^{abcd}	3.70 ^{ab}	4.25 ^{abc}	4.93 ^{ab}
Reduction in dispersal potential						
Synaptospermy	2.96 ^{ab}	3.03 ^{abc}	2.51 ^{ab}	2.67 ^{ab}	1.82 ^a	1.74 ^{ab}
Heterodiaspores	2.07 ^{ab}	1.48 ^{ab}	1.62 ^a	0.00 ^a	1.28 ^a	2.23 ^{ab}
Restriction of dispersal in time						
Hygrochasy	13.26 ^{ab}	16.29 ^{abcd}	15.89 ^{bcd}	11.43 ^{abc}	14.59 ^{de}	11.36 ^{bcde}

Table 4.4 Quantitative comparisons of dispersal types within communities. Within a column values with the same superscript do not differ significantly at $p < 0.05$

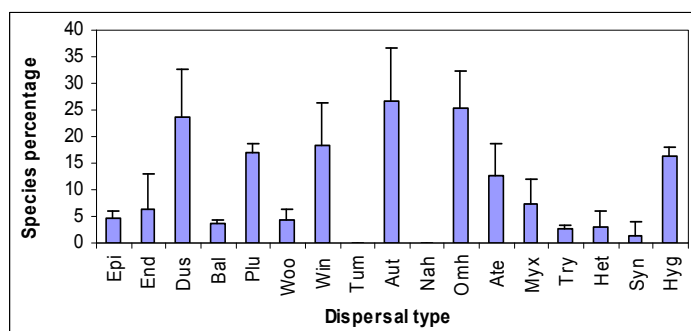
Dispersal type	Community					
	1	2	3	4	5	6
A. Telechory						
Zoochory						
Epizoochory	2.27 ^a	0.43 ^a	5.14 ^a	0.24 ^a	2.25 ^{ab}	2.76 ^{abc}
Endozoochory	4.52 ^a	1.19 ^a	3.54 ^a	1.09 ^a	0.51 ^a	2.01 ^{abc}
Anemochory						
Dust diaspores	7.97 ^{ab}	41.60 ^b	21.79 ^b	17.24 ^{ab}	15.16 ^{abc}	24.90 ^c
Balloon diaspores	0.12 ^a	0.83 ^a	0.32 ^a	0.30 ^a	0.76 ^a	0.22 ^{ab}
Plumed diaspores	14.62 ^b	43.16 ^b	24.04 ^b	11.37 ^{ab}	16.06 ^{abc}	14.81 ^{abc}
Woolly diaspores	1.09 ^a	0.36 ^a	4.85 ^a	5.41 ^a	8.10 ^{ab}	7.15 ^{abc}
Winged diaspores	3.35 ^a	3.82 ^a	9.41 ^{ab}	8.09 ^a	12.61 ^{ab}	10.90 ^{abc}
Tumbleweeds	0.09 ^a	0.00 ^a	0.05 ^a	0.00 ^a	0.01 ^a	0.00 ^a
Autochory	4.54 ^a	12.95 ^a	22.58 ^b	14.59 ^{ab}	32.29 ^c	22.60 ^{bc}
Hydrochory						
Nautohydrochory	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a
Ombrohydrochory	3.80 ^a	5.18 ^a	17.85 ^{ab}	7.49 ^a	33.39 ^c	17.62 ^{abc}
B. Atelechory	10.5 ^{ab}	4.51 ^a	11.80 ^{ab}	20.11 ^b	7.52 ^{ab}	3.51 ^{abc}
C. Additional features (Antitelechory)						
Anchorage mechanisms						
Myxospermy	10.82 ^{ab}	4.92 ^a	17.33 ^{ab}	12.20 ^{ab}	13.40 ^{ab}	7.59 ^{abc}
Trypanospermy	14.10 ^b	0.44 ^a	1.10 ^a	0.25 ^a	5.40 ^{ab}	1.44 ^{ab}
Reduction in dispersal potential						
Synaptospermy	0.67 ^a	3.20 ^a	2.63 ^a	2.63 ^a	4.40 ^{ab}	2.49 ^{abc}
Heterodiaspory	0.47 ^a	0.38 ^a	4.95 ^a	0.00 ^a	2.95 ^{ab}	0.94 ^{ab}
Restriction of dispersal in time						
Hygrochasy	2.69 ^a	3.19 ^a	13.39 ^{ab}	10.76 ^{ab}	20.45 ^{bc}	20.69 ^{abc}

a)



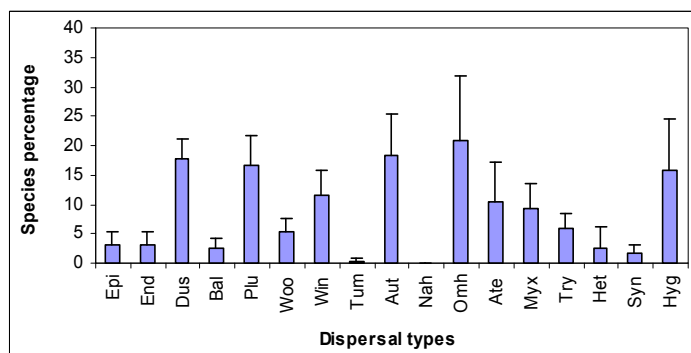
Water course community

b)



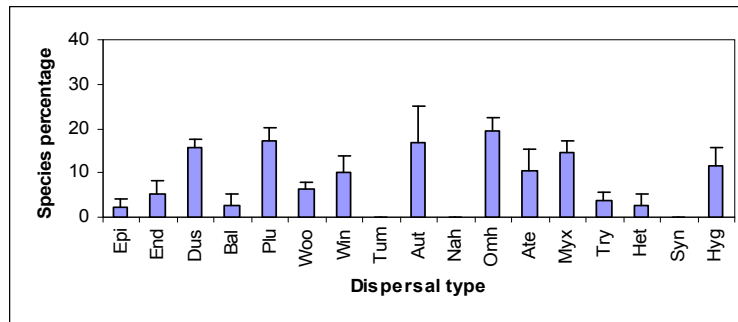
Sandy valley community

c)



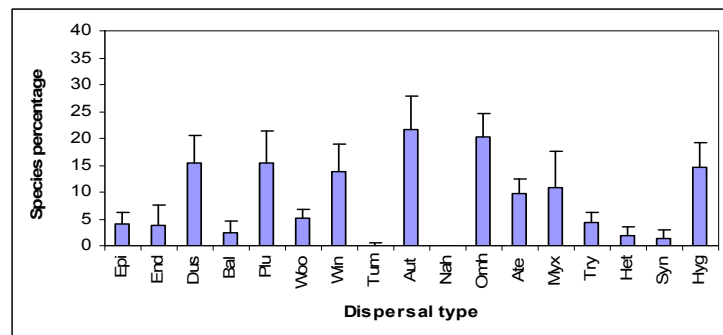
Plains community

d)



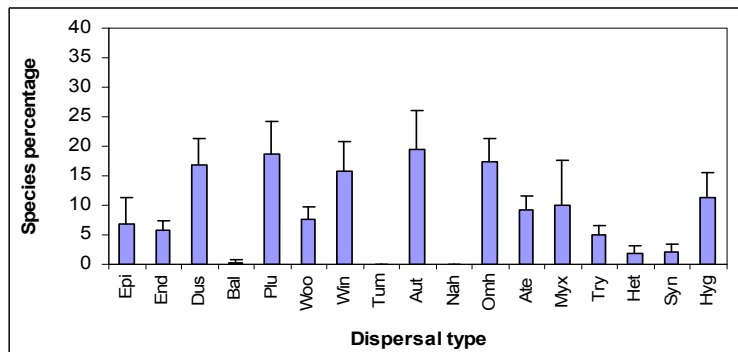
Old field community

e)



Rocky slope community

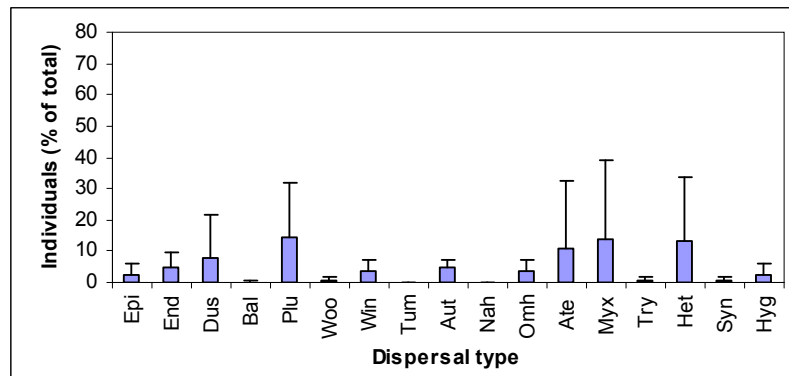
f)



Rocky hill community

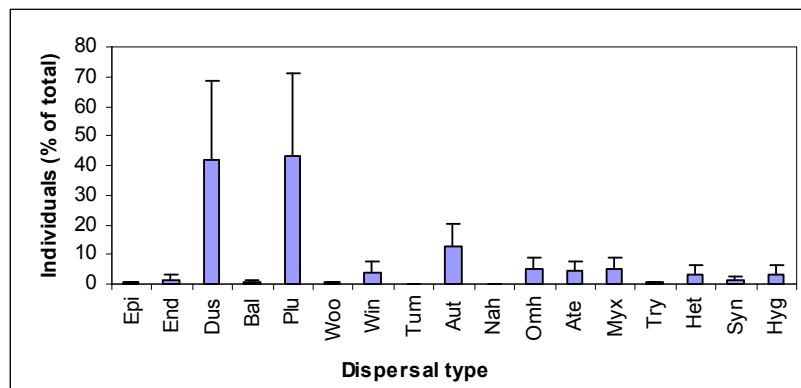
Figure 4.4 Qualitative dispersal spectra of plant communities of Paulshoek and Remhoogte. a) Water course community, b) sandy valley community, c) plains community, d) old field community, e) rocky slope community, f) rocky hill community. Abbreviations of dispersal types as defined in the text.

a)



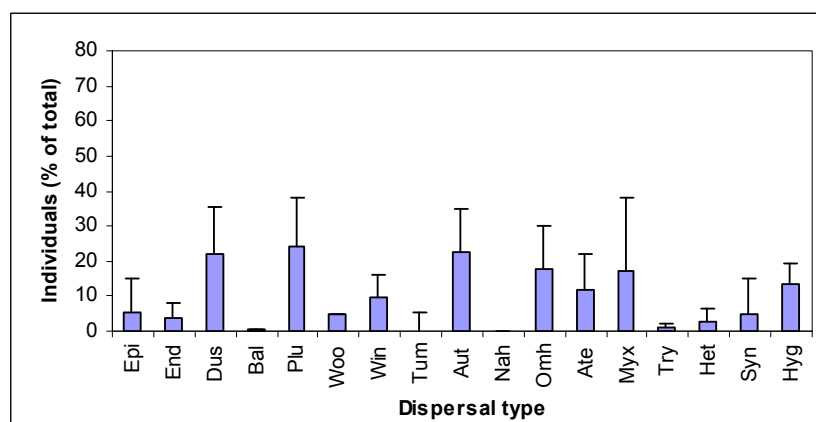
Water course community

b)



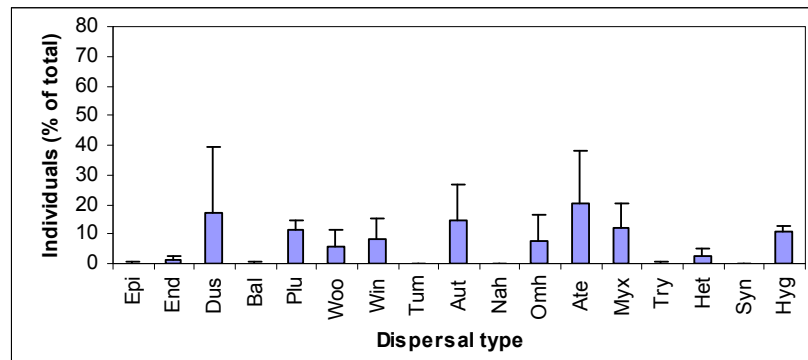
Sandy valley community

c)



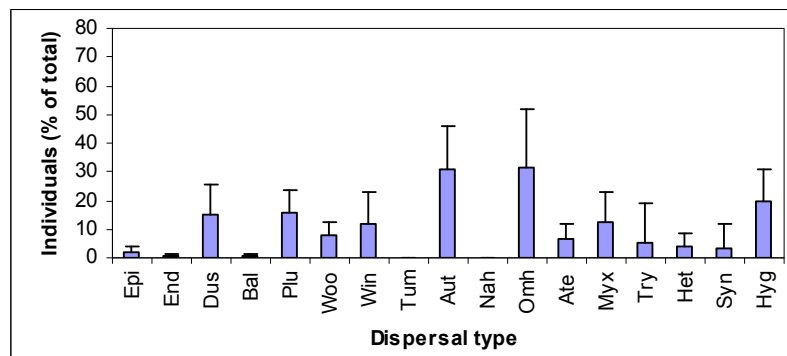
Plains community

d)



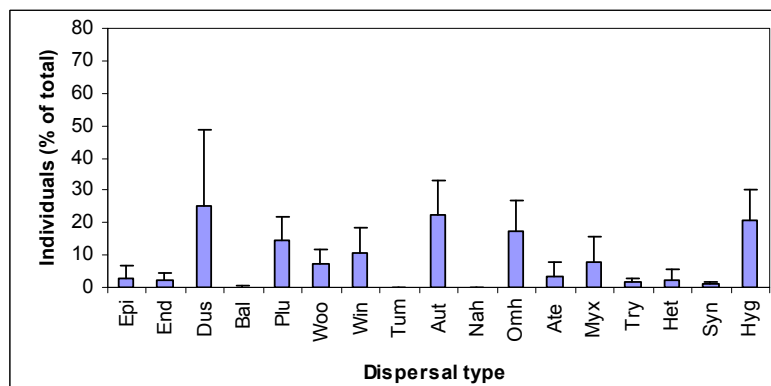
Old field community

e)



Rocky slope community

f)



Rocky hill community

Figure 4.5 Quantitative dispersal spectra of plant communities of Paulshoek and Remooghte. a) Water course community, b) sandy valley community, c) plains community, d) old field community, e) rocky slope community, f) rocky hill community. Abbreviations of dispersal types as defined in text.

4.5 Discussion

The results show clear differences between rangelands and communities for certain types of dispersal while others remain indifferent to management practices.

Retention times of seeds in the fur and in the tract of herbivores allow dispersal over long distances by zoochory (Couvreur *et al.* 2005). Zoochory in general, is a type of dispersal commonly found in forests or humid habitats (van Rooyen *et al.* 1990) and was not common in the present study. Epizoochorous plant species tend to be taxonomically diverse and rare. These plant species do not provide any means of attraction for their disseminators (Nakanishi 2000b), and have evolved in productive habitats, which support a large diversity and biomass of herbivorous mammals. This study did not support the hypothesis of many authors that epizoochory should be more prevalent in the overstocked rangeland (Collins and Uno 1985, Milton *et al.* 1990, Willson *et al.* 1990, Nakanishi 2000b), as no difference was found between the communal and commercial land.

A closer look at the dispersal spectra of the communities revealed the opposite trend with the less disturbed rocky slopes and hills (communities 5 and 6) showing high frequencies of epizoochorous species. In very arid areas epizoochoric species are generally limited to mesic sites in water courses and among rocks on ridges (Milton *et al.* 1990). This study only partially supports these findings because the riverbed and associated vegetation (community 1) did not have a large contribution by epizoochores. However the differences between the communities were not significant (Table 4.3A).

On the other hand the number of endozoochooric individuals was found to be significantly higher in communal land than in commercial land (Figure 4.3B). Herbivores can be important agents of dispersal for plants, even if they are not primarily seed eaters. Animal dung provides an ideal environment for germination of seeds and the growth of seedlings. The fibrous nature of undigested plant material means that it has good moisture retention qualities (Wilson *et al.* 1990). It is rich in nitrogen as well as organic matter which is easily broken down to inorganic nutrients by microorganisms (Dean and Yeaton 1992). Many endozoochorous seeds

germinate after a hard protective layer has been partly digested away (Stiles 1993) and these seeds are usually dispersed in large quantities increasing the probability of at least one seedling establishing. These advantages could explain the significantly higher number of endozoochorous species in the water course community (community 1) (Figure 4.4; Table 4.1) as it is one of the most grazed parts of the study area.

Dust, balloon, woolly and plumed diaspores as well as tumbleweeds, are all anemochoric mechanisms. Anemochory, although extensive, is not an essential mechanism of dispersal among seed plants, but is especially prominent among plant species of open habitats (Bansal and Sen 1981, Willson *et al.* 1990, Chambers and MacMahon 1994, Van Rheede van Oudtshoorn and Van Rooyen 1999). Van Rooyen *et al.* (1990) reported that 66.3% of the species of Namaqualand can be dispersed by wind.

Seed settling velocities vary between species, and low velocities can be very effective to promote long distance dispersal, but they are only reliable if the propagules become entrained by turbulence in convective updrafts above the vegetation canopy (Ozinga *et al.* 2004). Andersen (1992) and Redbo-Torstenson and Telenius (1995) suggested that variation in seed settling velocity may reflect difference in relative importance of dispersal life history and could be influenced by the timing of seed release relative to the seasonal periodicity of winds. Although small seeds such as dust diaspores are dispersed over long distances, larger seeds are only effectively dispersed by wind if their shape reduces the terminal velocity. Low terminal velocities have been measured for several plumed and woolly diaspores from Namaqualand (Van Rheede van Oudtshoorn and Van Rooyen 1999). However, wind dispersal along the soil surface can increase initial dispersal distances by several meters (Bakker *et al.* 1996).

According to Maddox (1985) and Bansal and Sen (1981) anemochory is regarded as a dispersal mode that developed under conditions of both climatic and biotic poverty. It is therefore not surprising that anemochory dominated the dispersal spectra of both these arid rangelands. Wind is a regular phenomenon in most desert areas and is minimally modified by vegetation acting as windbreak as is the case with a closed

habitat. The lack of significant difference found in most anemochoric dispersal modes (except woolly diaspores) between the two rangelands (Figure 4.3 A & B) is not surprising because even though the vegetation cover might be higher on the commercial land than on the communal land, the difference would not affect the wind action as desert plants are characteristically of low stature and allow wind circulation at all height levels (Arbelaez and Parrado-Rossellu 2005).

Woolly diaspores were generally not abundant in the study area. The genus *Eriocephalus* (shrubs) was the most dominant group with woolly diaspores especially the species *Eriocephalus microphyllus* var. *pubescens* (Appendix 2). High intensity grazing is said to reduce the perennial species in favor of annuals (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). The number of species with woolly diaspores on the two rangelands is more or less the same. Significantly lower number of individuals with woolly diaspores in communal rangeland can be related to the decrease of *Eriocephalus* spp. plants due to overgrazing by livestock. According to Van Rheede van Oudtshoorn and Van Rooyen (1999) diaspores entirely covered by hairs are not so well adapted to anemochory and their movement not only depends on the wind velocity but, also on the air humidity. The lowest percentage of species with woolly diaspores was found in the water course community (community 1) which occurs in the riverbed and on its banks (Figure 4.2). This relatively moist habitat could reduce the dispersal ability of woolly diaspores.

One of the simplest means of gaining access to the wind is by being extremely small with a large surface to mass ratio. These dust diaspores are usually produced in enormous numbers at the cost of fewer, larger sized seeds. Dust diaspores are characteristic of lower taxa such as fungi and mosses, but they are also found in families of higher plants such as Crassulaceae, Campanulaceae and Poaceae (Van Rheede van Oudtshoorn and Van Rooyen 1999). Gutterman (1993) suggested that the production of numerous dust-like seeds by desert plants serves as an escape strategy to prevent mass consumption of seeds. This could be one of the reasons why the number of individuals with dust diaspores was found to be higher (although not statistically significantly) in communal land than in commercial land (Figure 4.3B).

Furthermore, in this study the most dominant life forms with dust diaspores are geophytes or annuals and the unpalatable shrub *Galenia africana* (Appendix 2). Many studies (Illius and O'Connor 1999, Fynn and O'Connor 2000) have highlighted increases of annual grasses under an intensive stocking density and the stability of perennials under a low stocking density. Therefore, the higher incidence of dust diaspores on communal land could be because of the high number of annuals as they are known to be opportunistic colonizers and the dominance of the unpalatable shrub *Galenia africana* on the communal land. The rarity of tumbleweeds in the study area is supported by Ellner and Schimida (1981) who suggested that tumbleweeds are generally rare in the semi-desert and almost absent in the desert region.

The significantly higher incidence of ombrohydrochory (Figure 4.2 and 4.3) on the commercial land is attributed to the contributions of hygrochasy and trypanospermy, which are both examples of indirect hydrochory.

Trypanospermy is an anchorage mechanism caused by the presence of a long appendage on the upperside of the diaspore which is composed of two parts, a basal part which is capable of spiral twisting by a hygroscopic mechanism, and an upper part which is always straight and at right angles to the basal part. The main advantage of trypanospermy is the enhancement of water uptake due to increased seed-soil contact brought about by the burial of the diaspore. It also affords anchorage against surface runoff, while the risk of predation is decreased as soon as the diaspores are buried. It is an adaptive convergence within two distinct families, the Poaceae and the Geraniaceae. These families were poorly represented in the study area explaining the low percentage of trypanospermic species, but in general trypanospermic species are few (7%) in Namaqualand (van Rooyen *et al.* 1990). No significant differences were found in the number of trypanospermic species/individuals between the two rangelands although the Design 2 analysis seems to indicate a larger contribution by trypanospermic individuals in the commercial land (Figure 4.3).

Hygrochasy may be due to a cohesion mechanism or an imbibition mechanism or a combination of both. Cohesion mechanisms are based mainly on the water content

of the cell lumen as opposed to imbibition mechanisms that are based on the water content of cell walls. The hygrochastic mechanisms of many desert plants families have been studied in detail (Van Rheede van Oudtshoorn and Van Rooyen 1999). Hygrochasy conveys many advantages to the species. Most hygrochastic species possess a canopy seed bank from which diaspores are slowly released, depending on the amount and frequency of rainfall. This is often referred to as dispersal in time and as a result the timing of germination is also delayed and spread (Van Rheede van Oudtshoorn and Van Rooyen 1999, Nakanishi 2000a). In absolute terms the dispersal distances covered by hygrochastic diaspores are limited (Ellner and Shmida 1981, Van Rheede van Oudtshoorn and Van Rooyen 1999, Parolin 2006).

In Namaqualand the Mesembryanthemaceae (currently often included in the Aizoaceae) is the dominant family that possesses hygrochastic capsules. Some members of this family are palatable but most are not. The significantly lower number of hygrochastic species in the communal land is therefore surprising (Figure 4.3 A & B). However, if overgrazing continues long enough and no more palatable species are left, livestock have to feed on less palatable species. The reduction of these individuals could be explained by the indirect and direct effects of overgrazing on plant population dynamics. Livestock might not feed on the leaves but could consume flowers when other palatable species become rare. Overgrazing could also alter habitat conditions. If these species restrict the dispersal of their seeds in space, most seedlings might fail to establish because the environment previously favourable for the mother plant has lost some of its characteristics and is no longer favourable for the next generation. Ihlenfeldt (1983) suggested that members of this family have very narrow ecological niches because of their unique dissemination system which makes it difficult to colonize more distant suitable sites. This could also explain the significantly lower number of hygrochastic and ombrohydrochoric individuals in the severely disturbed water course (community1) (Table 4.3, Figure 4.4 & 4.5) and the significantly higher number in the less disturbed rocky slope community (community 5) which occurs on commercial land. However, Ellner and Shmida (1981) argue that persistence is not merely a matter of the re-establishment in the mother plant's site and that other nearby sites suitable for establishment can be reached without special mechanisms for long-distance dispersal, and that the superior sites are reachable

only by dispersal in time. As a result of overgrazing these superior sites might have been lost altogether.

Myxospermy, in contrast to hygrochasy, is undoubtedly classified as a mode of restriction of dispersal in space. Given the advantages conferred to the seed by the mucilage it was expected that under the adverse conditions in the communal land myxospermic species would contribute a larger percentage to the total dispersal spectrum than in the commercial land. The results showed an opposite trend (Figure 4.2 & 4.3) as the number of species was significantly higher on commercial land than in communal land. Although mucilage might therefore confer resistance to some types of disturbance it does not seem to confer resistance to overgrazing. The primary role of mucilage is linked to seed germination and seedling establishment. Myxospermy acts after rather than during the primary dispersal phase (Ellner and Schmidha 1981). It therefore has little effect on the dispersal distances achieved by primary dispersal, although it does prevent secondary dispersal.

Soil surface conditions may determine the success or failure of establishment of plants and the type of contact made by the seed with the substrate could be critical in determining whether a seed germinates or not. Seeds may interact with variations in soil microtopography or soil crust to determine the abundance and proportion of different species becoming established (Harper *et al.* 1965, Harper and Benton. 1966, Zaady *et al.* 1997). In grazed areas, trampling may cause physical destruction or soil crumbling and loosening of the soil surface (Chambers and MacMahon 1994, Zaady *et al.* 2001). These changes of the soil microtopography might influence germination patterns of mucilaginous species.

Autochorous species are well represented in all communities except in community 1 (Figure 4.4 & 4.5). One ecological constraint for autochorous species is the seed size and the plant height, because neither very heavy nor very light seeds can be projected effectively. Hygroscopic movement occurs over a range of relative humidities and increase with time (Lacey 1980). The higher number of autochorous species in commercial rangelands and lower number in the water course community (community 1) largely reflect the contribution of hygrochasy as this mechanism is considered to be autochorous. Autochorous species do not disperse their seed over

a long distance and consequently there is a possibility of competition among siblings when the natural resources available are limited.

Flowing water as an agent of dispersal is primarily important for plants in or close to water. In deserts and arid shrublands nautohydrochory is accidental (Van Rheede van Oudtshoorn and Van Rooyen 1999). No nautohydrochorous species were found in this study area. Furthermore, to be a successful hydrochore it is not necessary for a species to have well-developed morphological adaptations for water dispersal. This emphasizes that classifying dispersal mechanisms strictly according to morphology can lead to false predictions on the dispersal capacity of a species (Johansson *et al.* 1996). The lack of nautohydrochory can be related to the landscape, for species inhabiting the rocky hills and slopes there would be no advantage if their seeds were to be carried by water currents from the hills to end up in the flat areas.

Heterodiaspory in plants is often linked with physiological polymorphism in some germination requirements. It typically occurs in annual, weedy species of variable, unpredictable environments such as frequently disturbed habitats in arid and semi-arid environments. Heterocarpy enhances the ability of a species to survive in a highly variable environment (Harper 1977, Venable and Levin 1985). This could explain the higher (although not significant) number of heterocarpic individuals in the communal land (Figure 4.2 & 4.3). When unsuitable environmental conditions arise, species with more than one type of dispersal are more likely to survive because different seed morphs usually differ in their dispersal mode and germination requirement, dormancy and competitive performance (Venable and Levin 1985, Beneke *et al.* 1992, Zhang 1994, Van Mólken *et al.* 2005). Plants grown from dispersed diaspores are usually more vigorous and produce more seeds than plants grown from non-dispersed diaspores, when conditions are favourable. Plants grown from the non-dispersed seeds, however are more stress tolerant and can produce some seeds in extreme conditions when others cannot (Beneke *et al.* 1992, Van Mólken *et al.* 2005).

Seed germination and seedling establishment are both crucial steps in the life cycle of a plant. The success of a species depends on every step of the life cycle; the interruption of one step might affect the survival negatively (Levine and Murell 2003).

Livestock grazing may affect the plant biomass and the reproductive capacity of plants and long-term grazing may affect the seed bank (Zaady *et al.* 2001). Most herbivores do not consume seeds, however, they feed on flowers, thus reducing seed production. Furthermore, Schupp and Fuentes (1995) argue that the best site for seed survival may not be best for germination; the best for germination may not be best for seedling growth or best for juvenile growth and survival. It is to be noted that the unequal number of relevés in each community could possibly influence the dispersal spectra, but we do believe that the difference could be minor as the percentage of dispersal types found on each community could be related to the level of disturbance and the position on the landscape.

4.6 Conclusions

Livestock grazing is commonly considered a disturbance that affects ecological systems, especially if the grazing pressure is high. It may also affect the abiotic environment for example nutrient and water flow and loosening or compaction of the soil. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands.

The high percentage of dust diaspores and heterocarpic species in the communal land is proof of the effect of grazing on the dispersal types and community structure. Dust diaspores can be easily dispersed by wind on soil that is compact or bare as a result of trampling and heterocarpic species can persist in spite of disturbance because of the different strategies displayed by the different seeds types on the same plant. A higher percentage contribution by epizoochorous species was expected in the communal land given the large number of livestock but no significant difference was found between the two land-uses. The lower number of hydrochastic species in the communal land could be the result of indirect effects of grazing on plant fitness and maybe on the soil microtopography. Many myxospermic species are highly palatable and their low number could be a direct result of grazing.

Plumed diaspores and ombrohydrochory are the dominant dispersal types in the study area. The most open community (community 2), was dominated by species with dust diaspores emphasizing the high activity of wind in this area. Water

definitely influences the spread of woolly species as they cannot be easily blown by wind when wet.

4.7 Appendix

Dispersal mode (or plant traits) of plants species found in the study area. Values in the last two columns indicate the total of individuals per species in the different land-uses

	Zoochory	Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals					
	Epizoochory Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Acanthopsis carduifolia</i>										x	x			x		20.33	10.67
<i>Adromischus alstonii</i>		x														2.00	0.00
<i>Adromischus filicaulis</i> ssp. <i>filicaulis</i>		x														7.67	9.67
<i>Adromischus</i> sp.		x														1.67	0.00
<i>Adromischus marianiae</i> var. <i>immaculatus</i>		x														0.33	1.67
<i>Aizoon canariense</i>									x					x		11.22	133.33
<i>Albuca</i> sp. 1							x									0.00	8.33
<i>Albuca cooperi</i>							x									40.52	62.00
<i>Albuca longipes</i>							x									0.33	0.00
<i>Albuca</i> sp. 2							x									0.00	3.33
<i>Albuca viscosa</i>							x									3.00	13.33
<i>Albuca</i> sp. 3							x									0.33	2.00
<i>Aloe krapohlana</i>							x									1.00	0.00
<i>Amellus microglossus</i>				x												16.00	0.00
<i>Amsinckia calycina</i>								x								175.00	0.00
<i>Anacampseros karamontana</i>							x									0.67	0.00
<i>Anacampseros filamentosa</i> ssp. <i>namaquensis</i>							x									345.67	5.00
<i>Androcymbium</i> sp. 2								x								0.00	0.67
<i>Androcymbium</i> sp. 3								x								1.00	0.00
<i>Androcymbium</i> sp. 1								x								2.67	10.33
<i>Anisodonteia triloba</i>								x								0.67	0.00
<i>Anthospermum dregei</i> ssp. <i>dregei</i>			x													6.67	0.00
<i>Antimima</i> sp. 1									x	x				x		21.33	0.00
<i>Antimima</i> sp. 2									x	x				x		0.00	1.00
<i>Antimima</i> sp. 4									x	x				x		0.00	0.67
<i>Antimima</i> sp. 3									x	x				x		2.00	3.67
<i>Antimima clavipes</i>									x	x				x		5.33	0.00
<i>Antizoma miersiana</i>	x															0.67	0.00
<i>Aptosimum indivisum</i>									x					x		2.00	88.67
<i>Aptosimum spinescens</i>									x					x		0.00	0.67
<i>Arctotheca calendula</i>						x										2.00	4.33
<i>Arctotis acaulis</i>						x										5.00	0.33
<i>Arctotis laevis</i>						x	x									0.00	22.33
<i>Aridaria noctiflora</i> ssp. <i>noctiflora</i>									x					x		5.67	0.67
<i>Asclepias</i> sp.			x													0.00	0.33
<i>Asparagus capensis</i>	x															4.92	4.67
<i>Asparagus</i> sp.1	x															0.33	0.00
<i>Atriplex semibaccata</i>	x															2.67	89.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty					Total number of individuals		
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Atriplex lindleyi</i> ssp. <i>inflata</i>		x	x															2.00	0.33
<i>Avonia papyracea</i> ssp. <i>namaensis</i>								x										12.00	0.00
<i>Avonia quinaria</i> ssp. <i>quinaria</i>								x										0.33	0.00
<i>Babiana attenuata</i>																		0.83	15.33
<i>Ballota africana</i>									x									1.67	3.33
<i>Berkheya onobromoides</i>	x			x														0.67	4.00
<i>Bromus japonicus</i>	x																	167.00	0.00
<i>Brunsvigia boesmaniae</i>						x												1.00	1.33
<i>Bulbine</i> sp. 3								x										10.01	1.67
<i>Bulbine frutescens</i>								x										0.00	5.33
<i>Bulbine</i> sp.1								x										3.33	26.00
<i>Bulbine</i> sp. 2								x										15.67	9.00
<i>Bulbine praemorsa</i>								x										2.67	0.00
<i>Carpobrotus edulis</i>		x																2.67	15.33
<i>Cephalophyllum rigidum</i>										x							x	14.00	0.00
<i>Cephalophyllum</i> sp										x	x						x	0.00	3.33
<i>Chaetobromus dregeanus</i>	x			x						x	x			x	x			22.00	22.67
<i>Cheilanthes capensis</i>			x															15.00	0.00
<i>Cheiridopsis denticulata</i>										x	x						x	113.44	0.00
<i>Cheiridopsis imitans</i>										x	x						x	54.67	60.67
<i>Cheiridopsis namaquensis</i>										x	x						x	139.89	6.67
<i>Chenopodiaceae</i> sp			x															0.00	3.33
<i>Chenopodium album</i>			x															0.00	1.67
<i>Chlorophytum undulatum</i>								x										41.33	26.00
<i>Chrysocoma ciliata</i>					x													108.56	194.67
<i>Chrysocoma</i> sp. 1					x													0.00	0.00
<i>Conicosia elongata</i>								x	x									2.44	1.67
<i>Conophytum calculus</i> ssp. <i>vanzeylii</i>										x	x						x	0.00	1.00
<i>Cotula barbata</i>			x											x				45.00	0.00
<i>Cotula coronopifolia</i>			x											x				0.00	1.33
<i>Cotula leptalea</i>			x											x				220.33	43.33
<i>Cotyledon papillaris</i>			x															0.00	3.00
<i>Crassula atropurpurea</i>			x															5.33	2.33
<i>Crassula cotyledonis</i>			x															0.33	40.67
<i>Crassula deceptor</i>			x															0.00	3.00
<i>Crassula hemisphaerica</i>			x															3.67	1.67
<i>Crassula pyramidalis</i>			x															0.00	1.00
<i>Crassula umbellata</i>			x															0.00	1.00
<i>Crassula vaillantii</i>			x															4.67	355.33

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty					Total number of individuals	
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Naurohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Crassula columnaris</i> ssp. <i>prolifera</i>			x														23.67	3.67
<i>Crassula</i> sp. 2			x														1.33	0.00
<i>Crassula muscosa</i> var. <i>muscosa</i>			x														8.67	4.33
<i>Crassula muscosa</i> var. <i>obtusifolia</i>			x														69.33	16.33
<i>Crassula sericea</i> var. <i>sericea</i>			x														6.67	66.00
<i>Crassula</i> sp. 3			x														0.00	16.67
<i>Crassula subaphylla</i> var. <i>subaphylla</i>			x														0.00	14.67
<i>Crassula subaphylla</i> var. <i>virgata</i>			x														22.11	6.67
<i>Cyphia longiflora</i>								x									9.00	5.67
<i>Diascia batteniana</i>			x														0.17	0.00
<i>Diascia rudolphii</i>			x														0.44	3.33
<i>Dicerotheramnus rhinocerotis</i>					x												0.00	12.67
<i>Dimorphotheca polyptera</i>								x					x				0.00	1.00
<i>Dimorphotheca sinuata</i>								x					x				1.33	0.00
<i>Dorotheanthus</i> sp. 5										x	x				x		11.67	34.67
<i>Drosanthemum</i> sp. 1										x	x				x		0.00	1.33
<i>Drosanthemum globosum</i>										x	x				x		0.67	1.33
<i>Drosanthemum hispidum</i>										x	x				x		0.00	10.00
<i>Drosanthemum</i> sp. 2										x	x				x		0.00	0.33
<i>Drosanthemum</i> sp. 4										x	x				x		5.50	11.00
<i>Drosanthemum</i> sp. 3										x	x				x		0.00	1.33
<i>Drosanthemum</i> sp.5										x	x				x		11.00	0.00
<i>Duvalia caespitosa</i>								x									7.67	4.00
<i>Ehrharta barbinodis</i>					x												102.00	92.33
<i>Ehrharta calycina</i>					x												6.67	9.33
<i>Eriocephalus africanus</i>								x									7.67	38.33
<i>Eriocephalus microphyllus</i> var. <i>pubescens</i>								x									413.17	156.00
<i>Eriospermum alicorne</i>								x									0.33	2.00
<i>Eriospermum paradoxum</i>								x									0.00	0.33
<i>Eriospermum</i> sp.								x									24.11	1.33
<i>Erodium cicutarium</i>					x					x					x		36.67	34.67
<i>Euphorbia decussata</i>													x				58.33	33.33
<i>Euphorbia mauritanica</i>													x				1.33	64.67
<i>Euphorbia muricata</i>													x				0.33	0.00
<i>Euryops dregeanus</i>								x									0.00	1.33
<i>Euryops multifidus</i>								x									2.00	0.00
<i>Felicia brevifolia</i>					x												1.00	9.33
<i>Felicia filifolia</i>					x												3.67	0.67
<i>Felicia merxmulleri</i>					x												43.33	2.00
<i>Fockea comaru</i>								x									0.67	2.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty		Total number of individuals					
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Galenia africana</i>			x															58.89	504.33
<i>Galenia fruticosa</i>		x	x															1.00	0.33
<i>Galenia meziana</i>			x															2.75	58.00
<i>Galenia sarcophylla</i>			x															1.00	23.00
<i>Galium spurium-aparine</i>	x																	0.00	1.33
<i>Gazania lichtensteinii</i>					x								x					137.97	119.00
<i>Gazania othonnites</i>					x								x					2.00	2.00
<i>Gazania tenuifolia</i>					x								x					20.56	26.67
<i>Gethyllis sp.</i>		x																1.67	0.00
<i>Gnidia scabra</i>									x									3.33	0.00
<i>Gomphocarpus fruticosus ssp. fruticosus</i>					x													0.00	9.67
<i>Grielum humifusum</i>	x							x							x			3.67	0.00
<i>Hallianthus planus</i>										x						x		7.67	0.00
<i>Hermannia amoena</i>									x									1.00	7.00
<i>Helichrysum sp</i>					x													3.33	0.00
<i>Helichrysum cylindriflorum</i>					x													0.33	0.33
<i>Helichrysum leontonyx</i>					x													246.67	529.67
<i>Heliophila variabilis</i>													x					258.44	77.33
<i>Hermannia meyeriana</i>									x									13.33	0.00
<i>Hermannia cuneifolia var. cuneifolia</i>									x									32.67	23.67
<i>Hermannia cuneifolia var. glabrescens</i>									x									1.00	1.33
<i>Hirpicium alienatum</i>					x													107.33	30.67
<i>Hirpicium sp1</i>					x													0.33	0.00
<i>Hyobanche sanguinea</i>			x															1.67	668.67
<i>Hypertelis salsoloides</i>			x															3.83	65.67
<i>Jamesbrittenia sp</i>									x									0.00	2.33
<i>Juncus acutus</i>									x				x					0.00	3.33
<i>Juncus sp. 1</i>									x				x					0.00	333.33
<i>Juncus sp. 2</i>									x				x					0.00	6.67
<i>Lachenalia carnosia</i>									x									1.33	5.33
<i>Lachenalia sp. 1</i>									x									0.00	1.67
<i>Lachenalia mutabilis</i>									x									0.00	3.00
<i>Lachenalia sp. 3</i>									x									1.67	3.00
<i>Lachenalia sp. 2</i>									x									0.00	1.00
<i>Lampranthus godmaniae</i>										x					x			5.33	2.00
<i>Lampranthus meyeriana</i>										x					x			2.00	0.00
<i>Lampranthus sp.</i>										x					x			0.00	45.67
<i>Larryleachia cactiformis</i>							x											1.33	0.00
<i>Lasiospermum brachyglossum</i>							x											24.33	12.00
<i>Lebeckia multiflora</i>												x						67.67	9.00
<i>Leipoldtia schultzei</i>										x						x		322.59	0.00

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals						
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Lepidium desertorum</i>													x					183.33	58.33
<i>Lessertia capitata</i>				x														3.67	0.67
<i>Lessertia diffusa</i>				x														0.00	5.33
<i>Leysera tenella</i>					x								x					657.94	409.67
<i>Limeum africanum</i>								x										0.00	0.33
<i>Limonium dregeanum</i>								x										0.00	6.67
<i>Limonium sp.</i>								x										0.00	12.00
<i>Lotononis falcata</i>				x														13.83	37.33
<i>Lotononis oligocephala</i>				x														12.67	0.33
<i>Lotononis sp.</i>				x														3.33	0.00
<i>Lycium sp.</i>		x																0.00	2.00
<i>Lycium cinereum</i>		x																37.94	44.00
<i>Manochlamys albicans</i>		x																6.22	0.00
<i>Manulea cheiranthus</i>			x															12.00	3.67
<i>Massonia depressa</i>								x										2.67	8.33
<i>Melolobium adenodes</i>														x				2.00	0.00
<i>Melolobium candicans</i>														x				0.33	0.00
<i>Mentha longifolia ssp. capensis</i>								x										0.00	8.67
<i>Mesembryanthemum guerichianum</i>										x						x		8.78	78.00
<i>Microloma sagittatum</i>						x												0.33	1.67
<i>Moraea bifida</i>								x										3.56	15.00
<i>Moraea fugax</i>								x										4.33	3.33
<i>Moraea serpentina</i>								x										167.28	116.00
<i>Oedera sedifolia</i>							x											0.00	4.00
<i>Oncosiphon grandiflorum</i>							x						x					45.67	32.67
<i>Oncosiphon suffruticosum</i>							x						x					194.33	7.00
<i>Orbea namaquensis/Quaqua mammilaris</i>						x												3.56	1.00
<i>Ornithogalum sp. 3</i>							x											3.33	0.00
<i>Ornithogalum maculatum</i>							x											5.00	0.00
<i>Ornithogalum sp. 1</i>							x											0.33	0.00
<i>Ornithogalum sp. 2</i>							x											0.00	1.00
<i>Ornithogalum pruinosum</i>							x											1.67	0.00
<i>Ornithogalum secundum</i>							x											0.00	13.00
<i>Ornithogalum unifolium</i>							x											0.00	2.00
<i>Ornithoglossum viride</i>								x										8.89	3.00
<i>Osteospermum pinnatum</i>	x								x									13.33	0.33
<i>Osteospermum rigidum var. rigidum</i>	x								x									0.33	5.67
<i>Othonna arbuscula</i>				x									x					5.00	0.00
<i>Othonna hederifolia</i>				x									x					4.00	0.33
<i>Othonna protecta</i>				x									x					2.22	0.33
<i>Othonna retrosa</i>				x									x					2.00	1.67

	Zoochory		Anemochory					Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals						
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Oxalis</i> sp. 3											x						46.00	24.67
<i>Oxalis foveolata</i>											x						108.72	46.00
<i>Oxalis</i> sp. 1											x						0.00	58.67
<i>Oxalis</i> sp. 5											x						0.00	5.00
<i>Oxalis</i> sp. 4											x						0.00	6.67
<i>Oxalis obtusa</i>											x						11.78	102.67
<i>Oxalis</i> sp. 2											x						0.00	1.00
<i>Pelargonium carnosum</i>	x				x					x			x				37.17	12.67
<i>Pelargonium</i> sp. 2	x				x					x			x				4.00	4.33
<i>Pelargonium praemorsum</i>	x				x					x			x				0.00	0.33
<i>Pelargonium</i> sp.	x				x					x			x				0.50	0.00
<i>Pelargonium triste</i>	x				x					x			x				0.67	0.00
<i>Pelargonium</i> sp. 1	x				x					x			x				0.33	2.00
<i>Peliostomum virgatum</i>								x									2.33	8.33
<i>Pentzia incana</i>								x		x			x				57.89	56.67
<i>Pentaschistis airoides</i> ssp. <i>airoides</i>										x				x			24.33	16.67
<i>Polygonum aviculare</i>								x									0.00	1.00
<i>Polygonum kitaibelianum</i>								x									0.00	41.67
<i>Psilocaulon leptarhron</i>										x						x	0.67	0.33
<i>Pteronia ciliata</i>					x												25.33	0.00
<i>Pteronia divaricata</i>					x												1.17	0.00
<i>Pteronia glomerata</i>					x												2.00	3.67
<i>Pteronia incana</i>					x												17.33	39.00
<i>Pteronia mucronata</i>					x												0.00	0.33
<i>Pteronia camphorata</i> var. <i>camphorata</i>					x												0.00	2.67
<i>Pharnaceum exiguum</i>			x														0.00	166.70
<i>Rhus undulata</i>		x															0.00	2.33
<i>Rhynchosidium pumilum</i>					x												56.67	120.00
<i>Ruschia aggregata</i>										x						x	43.61	0.00
<i>Pharnaceum</i> sp.			x						x								7.33	0.33
<i>Pharnaceum croceum</i>			x						x								0.00	25.67
<i>Pharnaceum dichotomum</i>			x						x								6.67	1.33
<i>Phyllobolus congestus</i>											x	x			x		0.00	3.00
<i>Phyllobolus</i> sp. 2											x	x			x		9.00	3.33
<i>Phyllobolus</i> sp. 1											x	x			x		0.00	4.00
<i>Phyllobolus spinuliferus</i>											x	x			x		0.33	0.00
<i>Phyllobolus trichotomus</i>											x	x			x		1.00	3.33
<i>Polymita albiflora</i>											x	x			x		457.33	65.00
<i>Ruschia centrocapsula</i>											x	x			x		0.00	0.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty				Total number of individuals		
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Nautohydrochory	Ombrohydrochory	Autochory	Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Ruschia goodiae</i>										x	x				x		72.00	3.67
<i>Ruschia grisea</i>										x	x				x		35.78	0.00
<i>Ruschia robusta</i>										x	x				x		78.56	0.67
<i>Ruschia</i> sp. 1										x	x				x		11.33	0.00
<i>Ruschia viridifolia</i>										x	x				x		72.00	119.67
<i>Salicornia</i> sp.1								x									0.00	22.00
<i>Sarcocaulon crassicaule</i>				x						x				x			4.78	0.00
<i>Sarcocaulon salmoniflorum</i>				x						x				x			10.33	0.33
<i>Sceletium exalatum</i>										x	x				x		0.00	18.00
<i>Schismus barbatus</i>			x														269.67	139.00
<i>Selago namaquensis</i>			x					x									6.67	3.00
<i>Selago divaricata</i>			x					x									0.33	1.00
<i>Senecio abruptus</i>					x								x				0.00	3.33
<i>Senecio arenarius</i>					x								x				1.67	0.00
<i>Senecio bulbinifolius</i>					x								x				0.33	0.00
<i>Senecio cinerascens</i>					x								x				0.33	0.00
<i>Senecio muricatus</i>					x								x				5.67	1.00
<i>Senecio niveus</i>					x								x				0.00	5.33
<i>Senecio radicans</i>					x								x				0.33	0.00
<i>Senecio rowleyanus</i>					x								x				1.00	1.33
<i>Senecio sisymbriifolius</i>					x								x				0.00	0.33
<i>Septulina glauca</i>		x															11.78	3.67
<i>Sonchus oleraceus</i>					x												0.00	1.33
<i>Spergularia media</i>								x									0.00	1.33
<i>Stachys rugosa</i>									x								0.00	1.00
<i>Stipagrostis brevifolia</i>	x				x					x	x			x			6.67	0.00
<i>Stipagrostis dregeana</i>	x				x					x	x			x			23.33	219.00
<i>Stipagrostis namaquensis</i>					x					x	x			x			27.33	2.33
<i>Sutherlandia frutescens</i>				x											x		0.33	0.00
<i>Tetragonia fruticosa</i>								x							x		20.33	19.00
<i>Thesium lineatum</i>		x															3.00	1.67
<i>Trachyandra falcata</i>									x								0.67	0.33
<i>Trachyandra tortilis</i>									x								32.67	13.67
<i>Tribolium utriculosum</i>	x								x								0.00	3.33
<i>Trichogyne lerouxiae</i>			x														50.33	842.00
<i>Trichogyne polycnemoides</i>			x														46.11	55.33
<i>Tripteris aghillana</i>								x					x				0.00	0.33
<i>Tripteris amplexens</i>								x					x				0.67	0.00
<i>Tripteris hyoseroides</i>								x					x				12.33	0.00

	Zoochory	Anemochory	Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals
	Epizoochory Endozoochory	Dust Balloon Plumed/Hairs Tumbleweed Woolly Winged		Nautohydrochory Ombrohydrochory		Heterodiaspory Myxospermy Trypanospermy Synaptospermy Hygrochasy	Remhoogte Paulshoek
<i>Tripteris sinuata</i> var. <i>sinuata</i>			x			x	71.22 11.33
<i>Tulbaghia dregeana</i>			x				4.33 1.67
<i>Tylecodon</i> sp. 1		x					1.33 0.00
<i>Tylecodon</i> sp. 2		x					0.00 0.33
<i>Tylecodon reticulatus</i>		x					3.67 4.00
<i>Tylecodon wallichii</i>		x					0.00 0.33
<i>Ursinia nana</i> ssp. <i>nana</i>			x			x x	93.56 144.00
<i>Urtica</i> sp				x			0.00 5.00
<i>Wahlenbergia androsacea</i>		x					0.00 12.00
<i>Wahlenbergia divergens</i>		x					3.33 40.00
<i>Wahlenbergia oxyphylla</i>		x					12.00 0.67
<i>Wiborgia monoptera</i>			x				11.33 2.67
<i>Zaluzianskia benthamiana</i>		x					57.33 56.00
<i>Zygophyllum foetidum</i>				x			0.00 3.00
<i>Zygophyllum retrofractum</i>				x			212.44 2.33
<i>Zygophyllum sessilifolium</i>				x			9.00 8.67
<i>Zygophyllum spinosum</i>				x			1.67 0.33

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Chapter 5

Germination strategies of some mucilaginous seeds from Namaqualand:

Temperature and light requirements

5.1 Introduction

Seed germination and seedling establishment are the most remarkable and critical stages during a plant's life cycle. Germination is a risky transition, especially under arid climates, between the most drought tolerant stage and the weakest point in plant development (Guttermann 1993). It marks the end of a period of relative safety rendered by dormancy mechanisms, hard seed testas and the protection by soil. Germination is considered as a major environmental sieve controlling the population dynamics of a species (Harper 1977). Therefore, selection favours environmental cueing mechanisms that decrease the probability of encountering unacceptable growth conditions following germination.

Determining what controls the timing of seed germination in the field requires information on the seed, environmental conditions in the habitat, and how the two interact from the time of seed maturation to germination (Baskin and Baskin 1998). Factors such as temperature, moisture, light, oxygen, nutrients as well as combinations of all, play a major part in breaking dormancy and can inhibit, delay, or promote germination. The response to these factors depends on environmental and maternal influences during seed maturation. This response in turn determines the germination traits of a species (Guttermann 1993, Fenner 2000). The knowledge of these traits and understanding of the underlying processes controlling germination are of vital importance in understanding life history patterns among different plant species in a community.

The abiotic and biotic environmental factors of arid regions influence the adaptations and survival strategies of plants growing there. Arid areas or habitats are characterized by temperature fluctuations often extending beyond the limiting temperatures for germination, by recurrence of moisture deficiency and sometimes by deficiencies of nutrients in the soil. In addition, rainfall is unpredictable, and

precipitation at the beginning of the growing season will not always be followed by enough rainfall for plants to complete their life cycles (El-Sharkawi *et al.* 1989, Philippi 1993).

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Factors influencing the germination of these seeds are poorly known. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems.

5.2 Materials and methods

Diaspores (referred to as seeds henceforth) of 23 mucilaginous species (24 seed types) were collected in spring or early summer from natural populations in the Namaqualand Klipkoppe Shrubland and Namaqualand Blomveld which form part of the Namaqualand Hardeveld Bioregion (Mucina and Rutherford 2006). Seeds were stored in brown paper bags at room temperature for a period of six months at the University of Pretoria, before commencing with germination trials.

Species used in this investigation included the following annuals: *Cotula barbata* DC., *Cotula thunbergii* Harv., *Foveolina dichotoma* (DC.), *Gazania lichtensteinii* Less Källersjö, *Heliophila lactea* Schltr., *Heliophila seselifolia* Burch. ex DC., *Heliophila thunbergii* (Eckl. & Zeyh) Steud var. *thunbergii*, *Heliophila variabilis* Burch. ex DC., *Heliophila* sp.1, *Heliophila* sp.2, *Oncosiphon grandiflorum* (Thunb.) Källersjö, *Senecio arenarius* Thunb., *Senecio cardaminifolius* DC., *Tripteris amplexens* Harv., *Tripteris hyoseroides* DC., *Ursinia calenduliflora* (DC.) N.E.Br. and *Ursinia cakilefolia* D.C. (dark and white achenes).

The following perennial species were investigated: *Gazania leiopoda* (DC.) Roessler, *Pentzia incana* (Thunb.) Kuntze, *Salvia dentata* Aiton, *Senecio niveus* (Thunb.) Willd. *Tripteris oppositifolia* (Aiton) B.Nord. and *Tripteris sinuata* DC.

Seeds were germinated in either 50 mm or 90 mm Petri dishes containing two layers of filter paper to which approximately 4 cm³ or 6 cm³ distilled water was added respectively. Germination tests were conducted in incubators and each treatment consisted of four replicates of 50 seeds for each species. To determine the effect of light and different temperature regimes on germination, tests were conducted in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 mol. m⁻² s⁻¹) and dark at six constant temperatures (7°C, 12°C, 17°C, 22°C, 27°C, 32°C) and one alternate temperature regime (12°C/22°C; 12h/12h). Petri dishes of the dark treatment were placed in cardboard boxes and sealed with aluminum foil to prevent light from penetrating. Germination of dark replicates was counted under a green safety light.

Trials continued over a 30 day period. Petri dishes were examined every day during the first seven days of germination and every two days the following weeks. Germination was considered to have occurred when the radicle protruded.

The optimal temperature for germination (T_o) of a specific species was calculated as:

$$T_o = \sum tp / \sum p,$$

where p is the percentage germination at temperature t (Kochankov *et al.* 1998, De Villiers 2000).

The mean germination time (MGT) of each treatment and species was calculated using the equation:

$$MGT = \sum Dn / \sum n$$

where n is the number of seeds which germinate on day D and D is the number of days counted from the beginning of the test (De Villiers 2000).

All data were analyzed using an analysis of variance (ANOVA) of the STATISTICA 7 computer program (Statsoft, Tulsa). The least significant difference (LSD) *post hoc* test was used to determine significant differences ($P \leq 0.05$) in germination percentages and mean germination time between different treatments within a species. The LSD multifactor ANOVA was used to determine significant differences between light and dark and temperature treatment at a $P \leq 0.05$ level.

A principal coordinates analysis (PCoA) in the computer program Syn-Tax 2000 (Podani 2001) was used on mean germination percentages at different temperatures to find patterns in the germination behaviour among species.

5.3 Results

The temperature and light requirements for germination of the 23 mucilaginous species of Namaqualand (24 seed types) investigated, are presented in Tables 5.1, 5.2, and 5.3. Species and seed types were grouped according to their optimum temperature, mean germination time as well as to their responses to light conditions

Significantly higher germination percentages in dark treatments were obtained for seven species (30% of species investigated) (Table 5.1). The majority of these species are annuals except the perennial *Salvia dentata*, and they all have a low ($\leq 17^{\circ}\text{C}$) optimal germination temperature. In general, their germination percentages are higher than 50% in the temperature range from 12-17°C in the dark (Table 5.1).

Almost half (11 species) of the species investigated required light for optimum germination and all of these species were annuals except the perennial *Tripteris oppositifolia*, (Table 5.1). They can be classified into three groups according to their optimum germination temperature: species with optimum temperature (T_{opt}) in the light $\leq 17^{\circ}\text{C}$, those with T_{opt} in light $> 17-20^{\circ}\text{C}$ and finally species with $T_{\text{opt}} > 20^{\circ}\text{C}$.

The majority of the perennial species (four species) investigated and two annuals were not significantly affected by light (26% of the total number of species). As light requiring species, they could also be divided into three groups according to their optimum germination temperature.

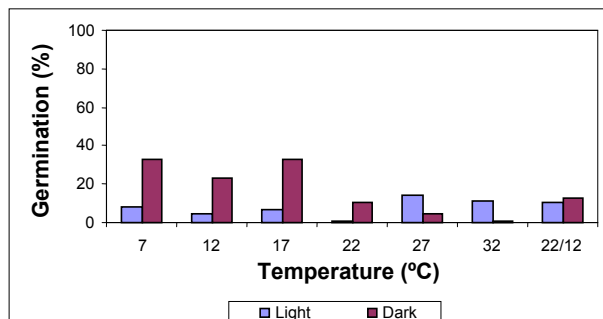
Table 5.1 Mean germination percentage of 23 myxospermic plant species of Namaqualand, at different temperature treatment under light and dark conditions. Within each species values followed by the same letter are not significantly different at $p \leq 0.05$

	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	P-value
Species where mean germination percentages were significantly higher in the dark than in the light															
Species with low optimum temperature in dark $T_{opt} \leq 17^\circ\text{C}$															
<i>Heliophila lacteal</i> (A)	8.0 ^{bc}	4.5 ^b	6.5 ^{bc}	1.0 ^a	14.5 ^{cd}	11.5 ^c	10.5 ^c	32.5 ^d	23.5 ^f	33.0 ^g	10.5 ^c	4.5 ^b	1.0 ^a	13.0 ^{cd}	0,001
<i>Ursinia cakilefolia</i> (dark) (A)	36.0 ^e	6.5 ^{abccc}	44.0 ^g	12.0 ^d	5.0 ^{abcc}	4.5 ^{abcc}	4.0 ^{ab}	53.5 ^f	11.0 ^d	56.0 ^h	9.5 ^{abccc}	7.0 ^{abccc}	2.0 ^a	26.5 ^e	0,000
<i>Heliophila</i> sp. 1 (A)	79.5 ^{ef}	74.0 ^{ef}	41.2 ^{cd}	34.5 ^{bc}	24.5 ^b	1.0 ^a	32.0 ^{bc}	88.0 ^j	79.5 ^{ef}	67.5 ^e	32.5 ^{bc}	21.0 ^d	2.0 ^a	70.5 ^e	0,000
<i>Heliophila</i> sp. 2 (A)	34.0 ^{cd}	61.0 ^{ef}	61.5 ^{ef}	65.0 ^f	30.0 ^{bc}	5.0 ^a	33.0 ^c	58.0 ^{def}	67.5 ^f	61.0 ^{ef}	71.0 ^f	39.0 ^{cde}	6.0 ^{ab}	62.0 ^{ef}	0,000
<i>Heliophila variabilis</i> (A)	72.0 ^g	72.0 ^g	62.0 ^{ef}	44.0 ^c	52.0 ^{cde}	14.0 ^a	53.0 ^{cde}	82.0 ^g	80.0 ^g	72.0 ^g	51.0 ^{cd}	56.0 ^{de}	26.0 ^b	71.0 ^g	0,000
<i>Heliophila thunbergii</i> var. <i>thunbergii</i> (A)	11.0 ^{def}	6.5 ^{bcd}	6.6 ^{bcd}	1.0 ^a	1.0 ^a	0.0 ^a	4.0 ^{abc}	12.5 ^{ef}	12.5 ^{ef}	12.0 ^{def}	8.4 ^{cde}	3.0 ^{ab}	0.0 ^a	16.0 ^f	0,000
<i>Salvia dentate</i> (P)	45.0 ^{bc}	66.5 ^{cde}	61.5 ^{cde}	42.0 ^b	42.6 ^b	10.0 ^a	8.0 ^a	67.0 ^{de}	89.5 ^a	54.7 ^{bcd}	40.7 ^d	42.7 ^{bc}	6.7 ^a	49.6 ^{bcd}	0,000
Species where mean germination percentages were significantly higher in the light than in the dark															
Species with low optimum germination temperature in light ($T_{opt} \leq 17^\circ\text{C}$)															
<i>Tripteris oppositifolia</i> (P)	34.0 ^{cd}	50.5 ^e	43.3 ^{de}	30.8 ^c	16.0 ^b	1.5 ^a	20.0 ^b	18.5 ^b	35.5 ^{cd}	33.3 ^{cd}	16.0 ^b	10.5 ^{ab}	0.5 ^a	9.5 ^{ab}	0,000
<i>Senecio cardaminifolius</i> (A)	36 ^f	31.0 ^f	36.0 ^f	23.5 ^e	16.5 ^d	4.5 ^{abc}	22.0 ^e	19.5 ^{ad}	7.0 ^{bc}	8.5 ^c	2.0 ^{ab}	2.5 ^{ab}	0.0 ^a	2.0 ^{ab}	0,000
<i>Cotula barbata</i> (A)	100.0 ^f	100.0 ^f	91.5 ^{ef}	98.0 ^{ef}	84.0 ^{de}	59.5 ^c	100.0 ^f	100.0 ^f	72.0 ^{cd}	75.5 ^d	22.5 ^b	6.5 ^a	12.5 ^{ab}	16.5 ^{ab}	0,000
<i>Ursinia cakilefolia</i> (white) (A)	54.0 ^f	26.0 ^f	51.5 ^{gh}	28.0 ^f	19.5 ^{cdef}	2.0 ^a	20.5 ^{def}	43 ^f	16.5 ^{bcd}	54.0 ^h	25.5 ^{ef}	15.5 ^{bcd}	9.0 ^{ab}	11.0 ^{ab}	0,000
Species with intermediate optimum germination temperature in light ($17 < T_{opt} \leq 20^\circ\text{C}$)															
<i>Cotula thunbergii</i> (A)	94.0 ^{ef}	87.5 ^{de}	93.5 ^{ef}	92.5 ^{ef}	97.5 ^f	81.5 ^d	93.5 ^{ef}	64.0 ^c	67.0 ^c	29.5 ^b	9.0 ^a	9.5 ^a	5.0 ^a	6.0 ^a	0,000
<i>Foveolina dichotoma</i> (A)	29.5 ^d	30.0 ^d	23.5 ^g	17.0 ^{de}	10.5 ^{bcd}	19.5 ^{ef}	16.0 ^{de}	28.0 ^d	10.0 ^{bcd}	12.0 ^{cd}	3.5 ^{ab}	2.5 ^a	1.5 ^a	5.5 ^{abc}	0,000
<i>Heliophila seselifolia</i> (A)	50.0 ^f	32.5 ^{de}	46.5 ^f	33.0 ^e	30.5 ^{de}	21.5 ^c	45.0 ^f	64.5 ^d	25.5 ^{cde}	24.0 ^{cd}	12.0 ^b	3.5 ^a	0.0 ^a	17.5 ^{bc}	0,000
<i>Oncosiphon grandiflorum</i> (A)	19.0 ^{cde}	23.5 ^{def}	37.0 ^g	17.5 ^{bcde}	28.0 ^f	12.0 ^b	25.5 ^{ef}	16.0 ^{bc}	5.0 ^a	3.0 ^a	2.5 ^a	0.0 ^a	1.5 ^a	0.5 ^a	0,000
<i>Ursinia calenduliflora</i> (A)	44.5 ^{ef}	51.0 ^{gh}	66.0 ^g	47.5 ^{ef}	31.0 ^d	16.0 ^b	41.0 ^e	21.0 ^{bc}	32.5 ^d	29.5 ^{cd}	21.0 ^{bc}	15.5 ^d	1.0 ^a	23.5 ^{bcd}	0,000
Species with high optimum germination temperature in light ($T_{opt} \geq 20^\circ\text{C}$)															
<i>Senecio arenarius</i> (A)	30.5 ^{cd}	11.5 ^{ab}	22.5 ^{bc}	41.0 ^{de}	67.0 ^f	46.5 ^e	33.5 ^{cd}	25.5 ^c	3.0 ^a	6.6 ^a	2.0 ^a	3.0 ^a	1.5 ^a	3.0 ^a	0,000
<i>Tripteris amplexens</i> (A)	2.0 ^a	13.0 ^{cd}	26.0 ^e	63.0 ^g	40.0 ^f	21.0 ^{de}	37.0 ^f	2.5 ^{ab}	12.0 ^{bcd}	8.0 ^{abc}	10.0 ^{abc}	8.5 ^{abc}	4.0 ^{abc}	4.0 ^{abc}	0,000
Species where mean germination percentages were not significantly different between light and dark															
Species with low optimum germination temperature ($T_{opt} \leq 17^\circ\text{C}$)															
<i>Senecio niveus</i> (P)	79.0 ^{bcd}	83.0 ^{bcd}	82.0 ^{bcd}	90.0 ^{cde}	86.0 ^{bcd}	70.5 ^{abc}	91.5 ^{de}	100.0 ^e	84.5 ^{bcd}	59.0 ^a	83.0 ^{bcd}	75.5 ^{abcd}	80.5 ^{bcd}	69.5 ^{abc}	0,140
Species with intermediate optimum germination temperature in light ($17 < T_{opt} \leq 20^\circ\text{C}$)															
<i>Gazania leiopoda</i> (P)	70.0 ^{ef}	65.0 ^{cdef}	62.0 ^{cdef}	48.5 ^a	51.0 ^{ab}	48.5 ^a	57.5 ^{abc}	61.5 ^{cde}	72.0 ^f	72.5 ^f	59.5 ^{bcd}	47.0 ^a	47.0 ^a	67.5 ^e	0,0000
<i>Gazania lichtensteini</i> (A)	25.5 ^{cdef}	27.5 ^{cde}	19.5 ^{bcd}	19.0 ^{bcd}	25.0 ^{cdef}	14.0 ^{ab}	19.5 ^{bcd}	26.0 ^{ef}	35.0 ^d	17.5 ^b	16.5 ^b	18.5 ^{bc}	9.5 ^a	13.0 ^{ab}	0,0000
<i>Tripteris sinuata</i> (P)	59.0 ^d	59.0 ^d	59.0 ^{cd}	55.0 ^{cd}	38.0 ^b	18.0 ^a	56.0 ^d	47.5 ^d	60.0 ^d	47.5 ^d	45.2 ^{cd}	50.0 ^c	19.5 ^a	5.07 ^d	0,000
Species with high optimum germination temperature in light ($T_{opt} > 20^\circ\text{C}$)															
<i>Pentzia incana</i> (P)	0.0 ^a	0.5 ^{ab}	4.0 ^{abc}	2.0 ^{ab}	9.0 ^c	1.0 ^{ab}	3.0 ^{ab}	0.0 ^a	2.5 ^{ab}	3.0 ^{ab}	5.5 ^{bc}	2.8 ^{ab}	2.0 ^{ab}	1.5 ^{ab}	0,040
<i>Tripteris hyoseroides</i> (A)	0.0 ^a	0.0 ^a	7.0 ^{bcd}	7.5 ^{cd}	10.0 ^d	2.5 ^b	4.5 ^{abc}	1.5 ^a	1.0 ^a	6.5 ^{bcd}	6.5 ^{bcd}	2.5 ^{ab}	1.0 ^a	3.0 ^{bcd}	0,000

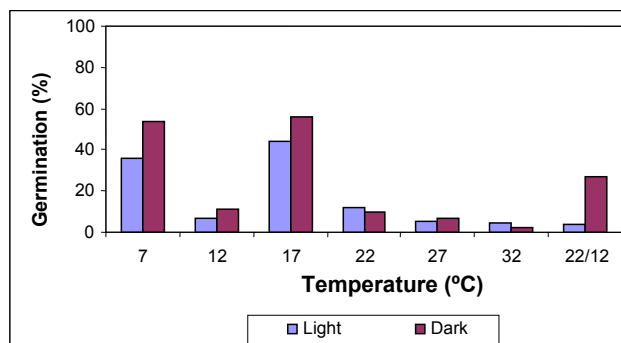
A-Annual

-Treatment not used for this species/seed type

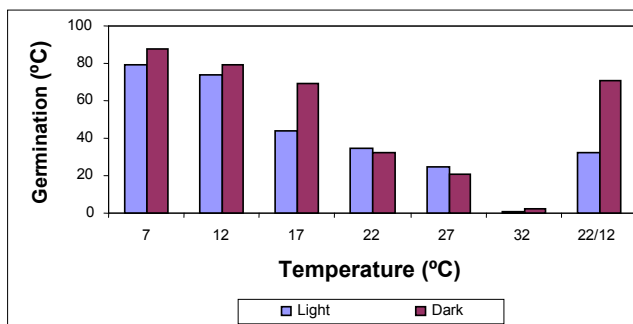
P-Perennial



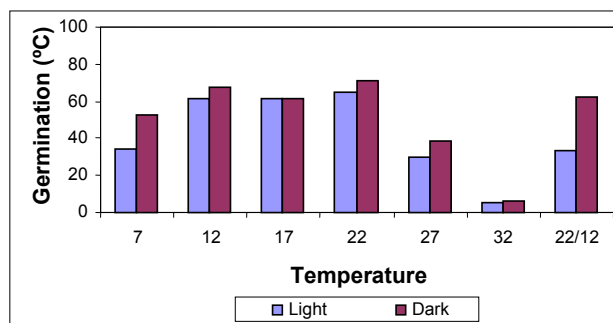
Heliophila lactea



Ursinia cakilefolia (black achenes)

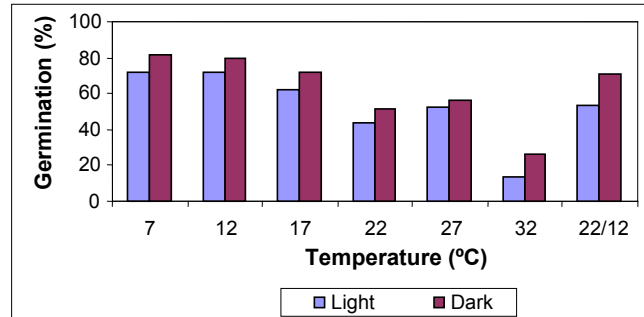


Heliophila sp. 1

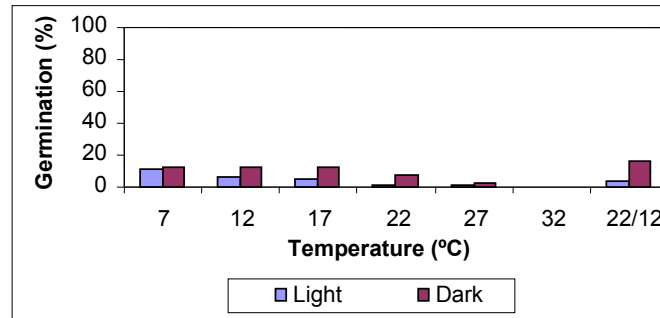


Heliophila sp. 2

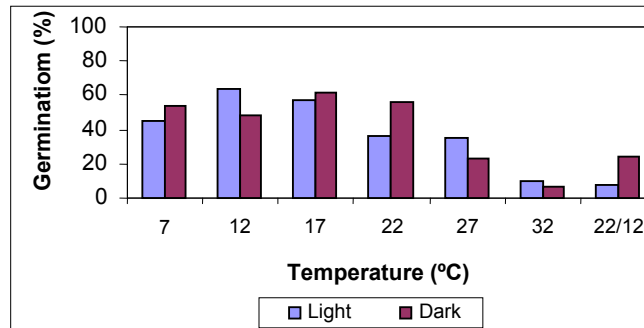
Figure 5.1 Germination percentages of 23 myxospermic species in light and dark at different temperatures. Order follows that in Table 5.1.



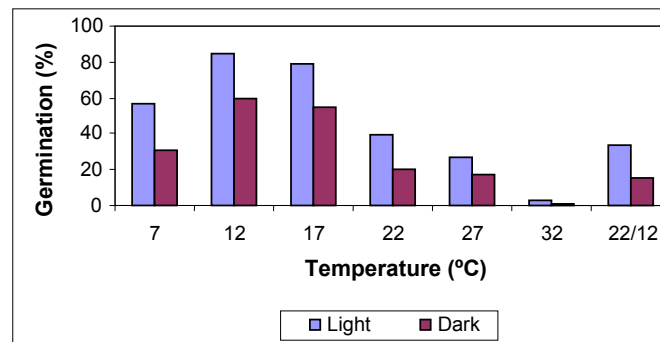
Heliophila variabilis



Heliophila thunbergii var. *thunbergii*

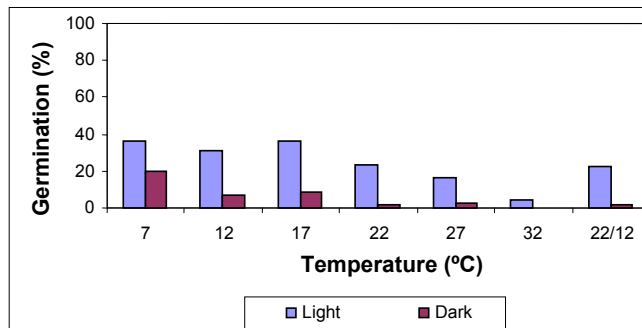


Salvia dentata

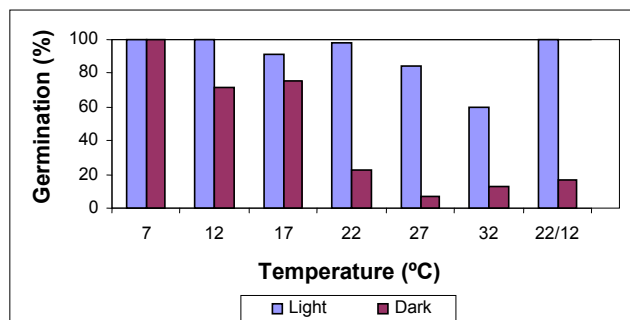


Tripteris oppositifolia

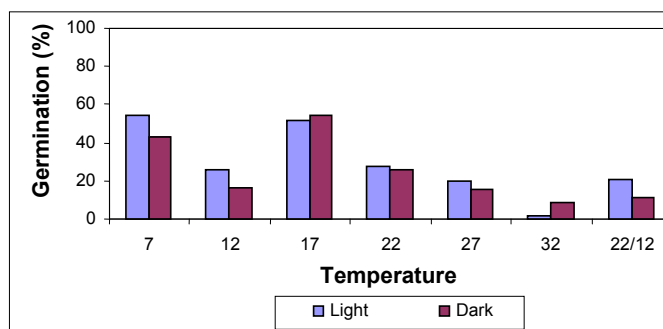
Figure 5.1 (Continued)



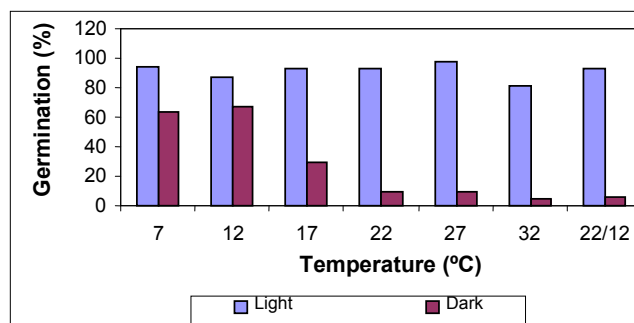
Senecio cardaminifolius



Cotula barbata

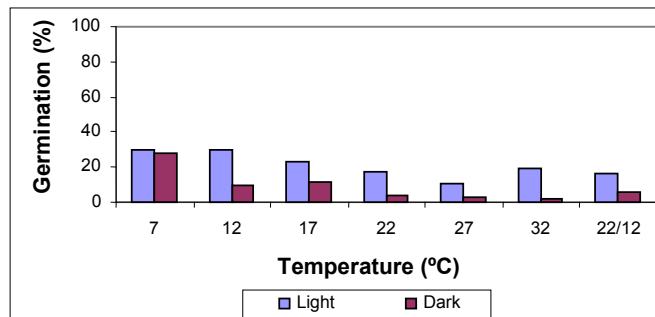


Ursinia cakilefolia (white achenes)

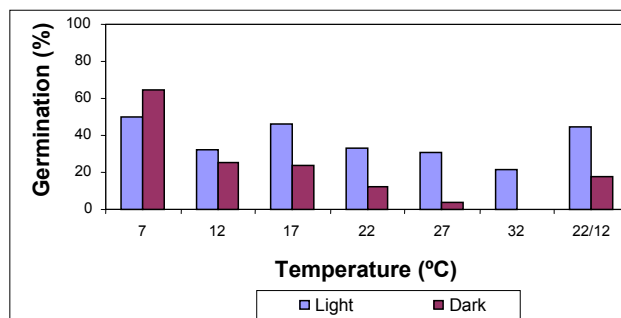


Cotula thunbergii

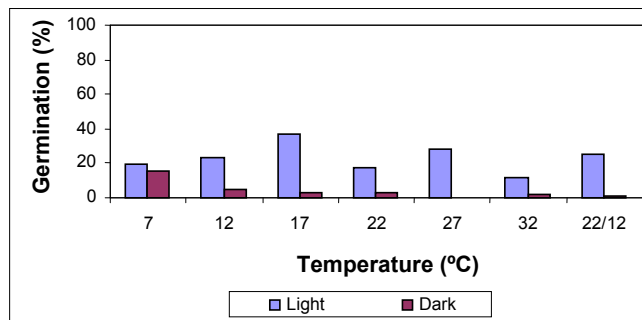
Figure 5.1 (Continued).



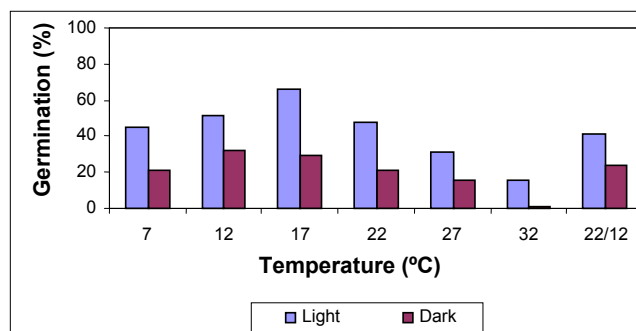
Foveolina dichotoma



Heliophila seselifolia

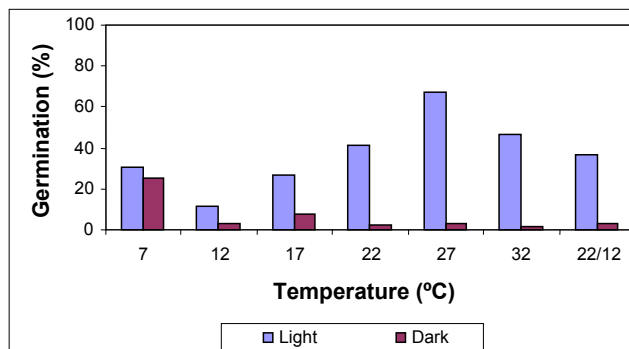


Oncosiphon grandiflorum

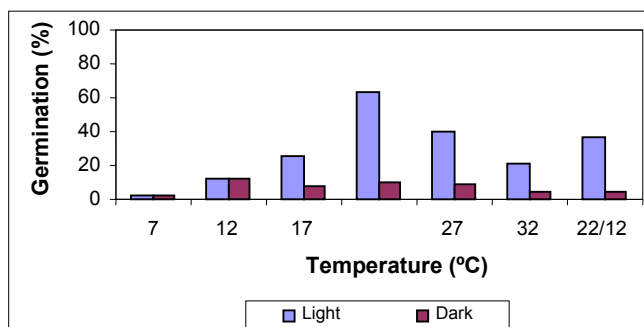


Ursinia calenduliflora

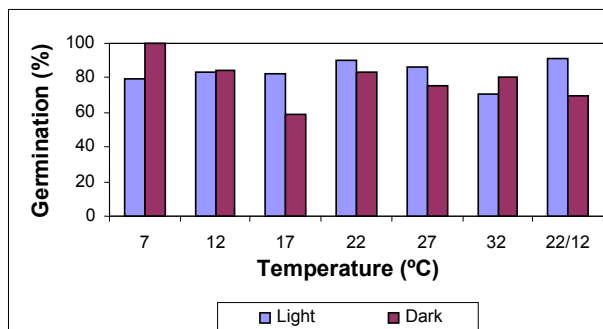
Figure 5.1 (Continued).



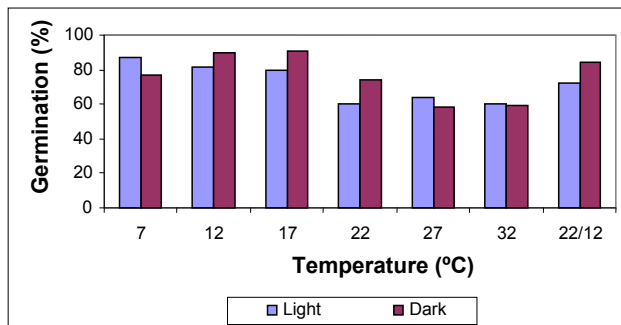
Senecio arenarius



Tripteris amplexans

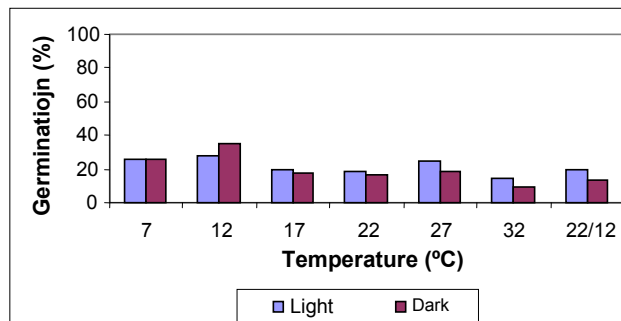


Senecio niveus

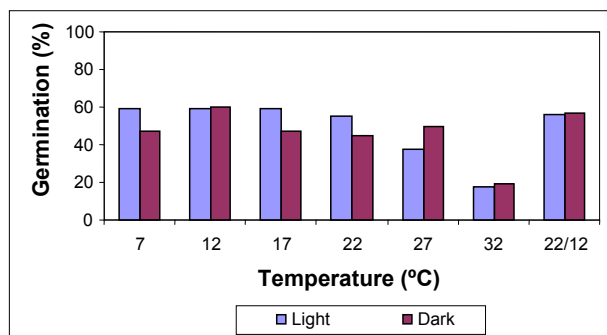


Gazania leiopodia

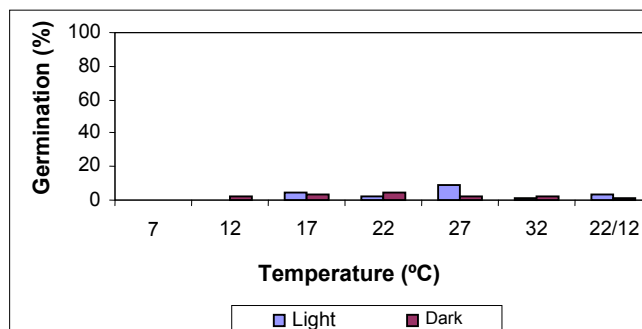
Figure 5.1 (Continued).



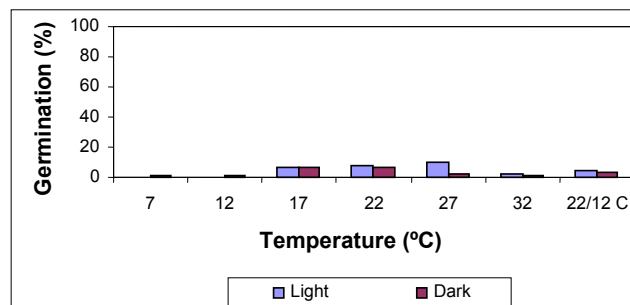
Gazania lichtensteinii



Tripteris sinuata



Pentzia incana



Tripteris hyoseroides

Figure 5.1 (Continued).

Table 5.2 Mean time to germination (days), of 23 myxospermic plant species of Namaqualand, at different temperature treatments under light and dark conditions. Within each species, values followed by the same letter are not significantly different at $p \leq 0.05$

	Light							Dark							Temp	Dark/light
	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C		
Mean time to germination was significantly shorter in light than in dark																
<i>Cotula thunbergii</i> (A)	12.4 ^g	7.1 ^{abcd}	5.3 ^{ab}	4.9 ^a	4.9 ^a	7.2 ^{abcd}	5.6 ^{ab}	14.0 ^g	9.7 ^{def}	10.0 ^{ef}	88.4 ^{1cde}	6.21 ^{abc}	20.7 ⁱ	7.8 ^{bcd}	0,000	0,000
<i>Foveolina dichotoma</i> (A)	8.9 ^{abc}	7.1 ^{ab}	5.5 ^a	5.8 ^a	6.7 ^{ab}	5.6 ^a	5.8 ^a	10.6 ^{bc}	13.0 ^c	12.7 ^c	10.1 ^{bc}	7.6 ^{ab}	6.3 ^{ab}	12.7 ^c	0,100	0,002
<i>Cotula barbata</i> (A)	11.9 ^{df}	6.7 ^{bc}	5.9 ^{abc}	5.5 ^{abc}	9.2 ^d	10.1 ^{de}	4.1 ^a	15.2 ^f	7.5 ^c	7.5 ^c	5.5 ^{ab}	11.5 ^{ef}	12.0 ^f	5.9 ^{abc}	0,000	0,000
<i>Gazania lichtensteinii</i> (A)	17.8 ^d	7.5 ^{ab}	5.9 ^a	7.6 ^{ab}	8.2 ^{ab}	10.2 ^{bc}	9.9 ^b	21.7 ^e	13.8 ^c	11.1 ^{bc}	7.8 ^{ab}	6.9 ^{ab}	7.4 ^{ab}	10.1 ^b	0,000	0,022
<i>Heliophila seselifolia</i> (A)	5.6 ^f	3.9 ^{de}	3.0 ^{cd}	2.9 ^{ab}	3.0 ^b	2.9 ^{ab}	4.3 ^a	6.3 ^g	3.7 ^{cd}	3.0 ^b	2.8 ^{ab}	2.3 ^a	-	3.3 ^{bc}	0,000	0,000
<i>Oncosiphon grandiflorum</i> (A)	7.6 ^{cd}	4.7 ^{abc}	4.5 ^{abc}	4.9 ^{abc}	5.6 ^{abc}	9.3 ^{de}	4.4 ^{ab}	7.1 ^{bcd}	7.4 ^{cd}	7.5 ^{cd}	10.7 ^e	-	14.0 ^f	4.0 ^a	0,002	0,040
<i>Senecio arenarius</i> (A)	6.7 ^b	5.1 ^{ab}	7.7 ^{bc}	5.3 ^{ab}	4.5 ^a	4.3 ^a	5.1 ^{ab}	6.8 ^b	4.8 ^a	7.5 ^{bc}	11.5 ^d	8.3 ^c	6.7 ^b	3.7 ^a	0,486	0,020
<i>Senecio niveus</i> (P)	10.6 ^e	6.1 ^{bc}	5.7 ^{ab}	5.1 ^{ab}	4.9 ^a	14.6 ^f	5.4 ^{ab}	9.9 ^{ade}	5.7 ^{ab}	5.6 ^{ab}	4.9 ^a	6.8 ^c	14.5 ^f	8.8 ^d	0,000	0,004
<i>Ursinia calenduliflora</i> (A)	10.2 ^{bcd}	7.6 ^{abc}	6.1 ^{ab}	6.3 ^{ab}	5.1 ^a	14.5 ^{ade}	7.6 ^{abc}	16.6 ^e	6.1 ^{ab}	10.0 ^{bcd}	9.4 ^{abc}	10.5 ^{cd}	16.0 ^a	7.7 ^{abc}	0,006	0,023
Mean time to germination was significantly shorter in dark than in light																
<i>Gazania leiopoda</i> (P)	10.1 ^g	7.1 ^{cde}	5.8 ^b	8.0 ^{df}	7.6 ^{de}	8.2 ^f	6.2 ^{bc}	9.2 ^{fg}	5.3 ^{ab}	4.6 ^a	4.5 ^a	6.7 ^{bcd}	7.8 ^a	5.2 ^{ab}	0,000	0,000
<i>Heliophila sp.2</i> (A)	7.5 ^d	7.2 ^d	3.6 ^{ab}	4.1 ^{abc}	5.4 ^c	3.0 ^{cb}	2.8 ^a	7.0 ^b	3.2 ^{ab}	3.4 ^{ab}	4.2 ^{ab}	3.1 ^{ab}	4.0 ^{abc}	3.1 ^{ab}	0,000	0,026
Mean time to germination not significantly affected by light or dark																
<i>Heliophila variabilis</i> (A)	5.0 ^e	3.3 ^{cd}	3.0 ^{bcd}	3.1 ^{bcd}	2.1 ^{ab}	2.6 ^{abc}	2.4 ^{ab}	4.7 ^a	3.7 ^d	2.3 ^{ab}	2.1 ^a	2.1 ^a	3.5 ^d	2.5 ^{ab}	0,000	0,464
<i>Tripteris hyoseroides</i> (A)	-	-	7.6 ^{ab}	6.7 ^{ab}	6.6 ^{ab}	19.6 ^c	8.7 ^{ab}	24.7 ^d	13.0 ^{bc}	11.1 ^{abc}	9.6 ^{ab}	8.5 ^{ab}	5.0 ^a	10.7 ^{abc}	0,663	0,327
<i>Pentzia incana</i> (P)	0.0	19.0 ^f	11.1 ^{cdef}	9.3 ^{bcd}	3.9 ^a	14.0 ^{ef}	16.0 ^{ef}	0.0	12.3 ^{def}	8.0 ^{abcd}	5.2 ^{ab}	6.3 ^{abc}	12.0 ^{def}	8.3 ^{abcd}	0,242	0,082
<i>Tripteris amplexens</i> (A)	16.0 ^c	10.0 ^{ab}	5.1 ^a	4.8 ^a	4.5 ^a	4.9 ^a	5.9 ^a	14.3 ^{bc}	8.8 ^{ab}	6.2 ^a	5.4 ^a	5.1 ^a	6.8 ^a	5.5 ^a	0,042	0,404
<i>Heliophila sp.1</i> (A)	5.5 ^e	3.2 ^c	2.6 ^a	2.5 ^a	3.1 ^{ab}	7.0 ^a	2.44 ^a	6.1 ^f	4.1 ^d	2.5 ^a	2.5 ^a	2.4 ^a	15.5 ^h	3.1 ^{bc}	0,092	0,729
<i>Ursinia cakilefolia black</i> (A)	6.4 ^{cde}	5.5 ^{abcde}	3.3 ^{ab}	2.9 ^{bca}	6.6 ^{de}	6.1 ^{bcd}	3.5 ^{abc}	6.3 ^{cde}	8.8 ^a	4.1 ^{abcd}	4.2 ^{abcd}	4.0 ^{abcd}	5.0 ^{abcd}	4.3 ^{abcd}	0,014	0,810
<i>Salvia dentata</i> (P)	16.7 ^{cd}	7.4 ^a	7.9 ^a	9.4 ^{ab}	14.9 ^{bcd}	19.6 ^d	8.6 ^a	14.8 ^{bcd}	10.5 ^{ab}	6.9 ^a	8.4 ^a	10.9 ^{bcd}	14.4 ^{bcd}	7.9 ^a	0,000	0,443
<i>Tripteris oppositifolia</i> (P)	15.6 ^a	8.5 ^{bc}	5.3 ^a	8.7 ^{bc}	12.2 ^d	8.5 ^{bc}	7.6 ^{abc}	12.4 ^d	8.7 ^{bc}	6.8 ^{ab}	6.83 ^{ab}	7.3 ^{abc}	10.0 ^{cd}	8.2 ^{bc}	0,000	0,095
<i>Tripteris sinuata</i> (P)	5.8 ^d	3.7 ^{abc}	2.3 ^a	3.1 ^{abc}	4.2 ^c	12.6 ^f	3.4 ^{abc}	6.5 ^a	3.7 ^{abc}	2.3 ^a	2.3 ^a	2.8 ^{abc}	8.9 ^a	2.7 ^{ab}		
<i>Senecio cardaminifolius</i> (A)	7.5 ^c	5.6 ^{abc}	3.4 ^a	4.3 ^{ab}	6.4 ^{abc}	3.5 ^a	4.9 ^{abc}	7.5 ^c	4.4 ^{ab}	4.8 ^{abc}	3.5 ^a	7.0 ^{bc}	-	4.5 ^{ab}	0,001	0,164
<i>Heliophila thunbergii</i> var <i>thunbergii</i> (A)	6.7 ^d	4.0 ^{abc}	3.8 ^{abc}	2.0 ^a	2.0 ^a	-	2.5 ^a	6.9 ^d	4.7 ^{bcd}	2.8 ^a	2.8 ^a	5.6 ^{bcd}	-	2.6 ^a	0,000	0,095
<i>Ursinia cakilefolia (white)</i> (A)	6.3 ^{cde}	5.6 ^{abcde}	3.2 ^a	6.6 ^{de}	6.2 ^{bcd}	8.5 ^{de}	4.2 ^{abcd}	6.4 ^{cde}	5.6 ^{abcde}	4.2 ^{abcd}	4.1 ^{abcd}	4.0 ^{abcd}	5.0 ^{abcd}	4.3 ^{abcd}	0,041	0,082
<i>Heliophila lactea</i> (A)	5.7 ^{eg}	4.2 ^{cd}	4.9 ^{de}	5.0 ^{de}	4.1 ^{bcd}	2.9 ^a	6.9 ^f	6.4 ^f	3.5 ^{abc}	3.8 ^{abc}	2.9 ^a	5.7 ^{ef}	3.0 ^{bab}	3.4 ^{abc}	0,000	0,118

- Treatment not used for this species.

A - Annual

P-Perennial

Table 5.3 Optimum germination temperatures (°C) calculated for 24 myxospermic species of Namaqualand

Species /seed type	Temperature(°C)	
	Light	Dark
Low temperature in light and dark		
<i>Heliophila</i> sp.1 (A)	14,20	14,00
<i>Heliophila thunbergii</i> var <i>thunbergii</i> (A)	11,80	14,60
<i>Cotula barbata</i> (A)	15,45	12,80
<i>Senecio niveus</i> (P)	15,25	13,97
<i>Ursinia cakilefolia</i> (black achenes) (A)	15,00	13,80
<i>Senecio cardaminifolius</i> (A)	15,88	12,06
Intermediate temperatures in light & low temperatures in dark		
<i>Oncosiphon grandiflorum</i> (A)	18,75	11,60
<i>Heliophila seselifolia</i> (A)	17,60	11,80
<i>Foveolina dichotoma</i> (A)	17,29	12,39
<i>Cotula thunbergii</i> (A)	19,60	12,87
<i>Gazania lichtensteinii</i> (A)	18,24	16,80
<i>Salvia dentata</i> (P)	16,18	14,89
Intermediates temperaures in light and dark		
<i>Ursinia calenduliflora</i> (A)	17,34	16,12
<i>Ursinia cakilefolia</i> (White achenes) (A)	15,31	16,42
<i>Heliophila</i> sp.2 (A)	16,32	16,59
<i>Tripteris sinuatum</i> (P)	17,14	17,65
<i>Gazania leiopoda</i> (P)	18,30	18,38
<i>Tripteris oppositifolia</i> (P)	15,31	15,27
High temperatures in light & low temperature in dark		
<i>Senecio arenarius</i> (A)	22,42	12,11
<i>Heliophila lactea</i> (A)	21,70	13,90
High temperatures in light & intermediate temperature in dark		
<i>Tripteris hyoseroides</i> (A)	23,50	19,76
<i>Tripteris amplexens</i> (A)	22,76	19,40
<i>Pentzia incana</i> (P)	20,10	19,60

A- Annual

P- Perennial

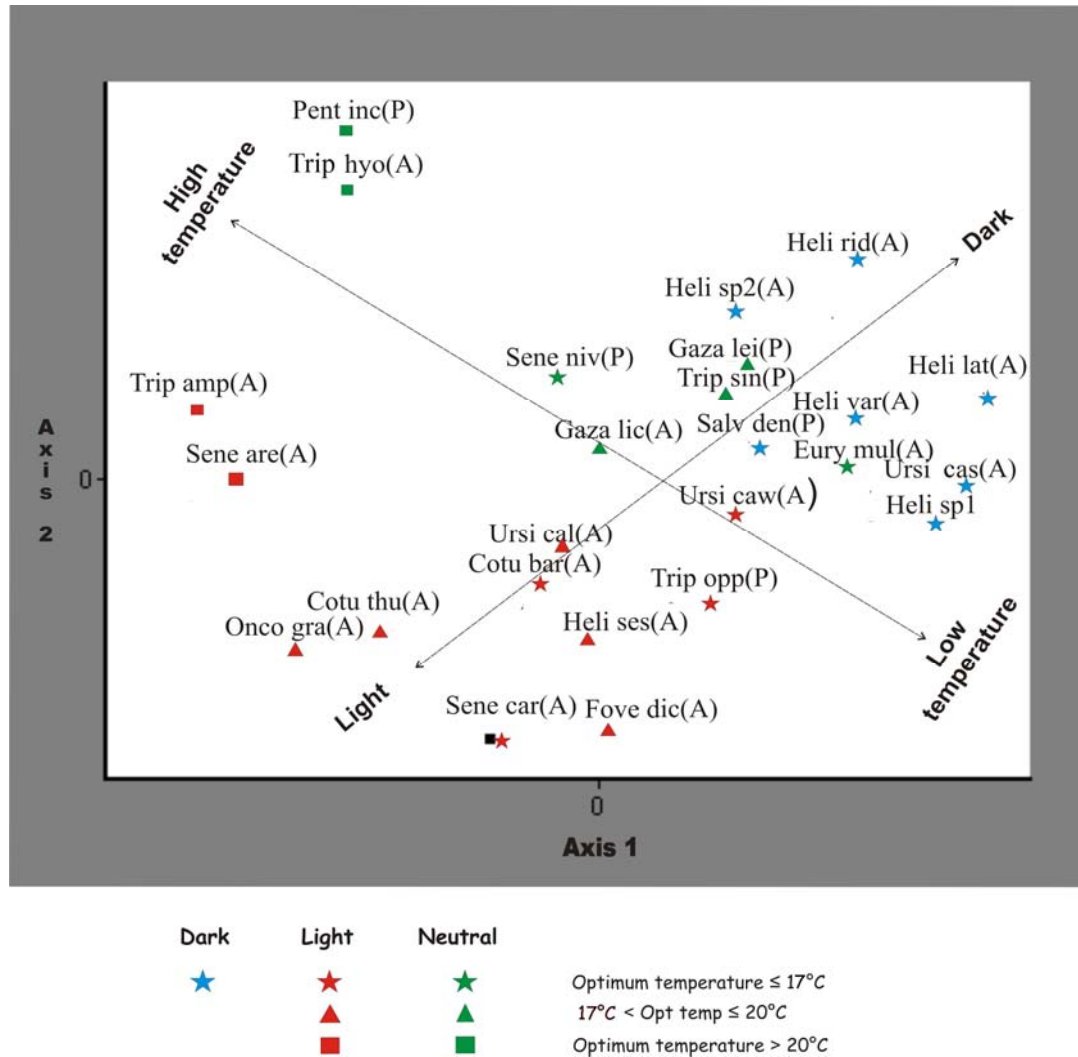


Figure 5.2 Ordination diagram based on a Principal Coordinate Analysis of the species germination percentages data with respect to two environmental variables (temperature, light/dark).

Nine species, mostly annuals, obtained significantly shorter mean germination times (days) in light than in the dark (Table 5.2), of which four also had the highest germination percentage in light. Four of these species obtained their shortest mean germination time (MTG) at intermediate temperature conditions (Table 5.2). The only perennial species in this group was *Senecio niveus* (Table 5.2).

Two of the species investigated obtained significantly shorter MTG in the dark (Table 5.2), of which the annuals *Heliophila* sp. 2 obtained the highest germination percentage in the dark. The germination percentage of the perennial *Gazania leiopoda* was not significantly different in light and dark (Table 5.2).

Mean germination time was not significantly affected by light in more than 50% of the species. This group included approximately a half of all annual as well as most of the perennial species investigated.

The alternating temperature did not show a particular trend in this study. Alternating temperatures did not significantly improve the mean germination percentages (Table 5.2) and the mean germination times of the species investigated above those at constant temperatures.

The principal coordinates analysis (PCoA) separated species according to their light and temperature requirements for optimal germination (Figure 5.2). Both factors had significant effects on seed germination, but the light requirement appears to be the dominant factor especially for annual species. Nevertheless the species with high temperature requirements can be differentiated from those with low and intermediate temperatures irrespective of the light requirement. But there is no clear separation between species that require low and intermediate temperature for optimum germination.

5.4 Discussion

Specific germination requirements can provide fine temporal niche partitioning, because these requirements are often far more restrictive than requirements for vegetative growth and reproduction (Bazzaz 1979). Overall desert plants from arid environments also require a high water availability for germination (Facelli *et al.* 2005) and have adaptations that allow them to time their germination to the most favourable, and often more predictable, part of the year (Baskin *et al.* 1993, Claus & Venable 2000).

Temperature requirements

Most species, both perennials and annuals in this study obtained their highest germination percentages and shortest mean germination time within the temperature range of 12-22°C (Table 5.1 & 5.2). The mean optimal germination temperature of 80% of species investigated occurred in the temperature range of 12-20°C in either light or dark. Many studies on seed germination and survival in the Succulent Karoo have found similar results (De Villiers *et al.* 2002a, Milton 2005).

Namaqualand is an arid winter rainfall region (Desmet and Cowling 1999). Annual species in an arid environment depend largely on seed germination during periods when the environment is suitable for completion of their life cycle (Van Rooyen 1999, Guterman 2002). After maturation seeds of winter annuals become conditionally dormant and undergo the process of afterripening during the hot and dry summer months (De Villiers *et al.* 2002b, Van Rooyen and De Villiers 2004). High temperature and low soil moisture conditions during summer promote loss of dormancy (Baskin and Baskin 1998). Occasional rainfall during this period does not induce germination, but as soon as the growing season approaches, the afterripening requirement has been satisfied and there is available moisture and suitable temperatures and germination can take place (De Villiers *et al.* 2002a, Van Rooyen and De Villiers 2004).

Additionally, winter annuals have developed phenological characters that prevent their seeds from germinating during summer because the maximum temperatures at which seeds can germinate are below those occurring in the habitat. Seeds germinate in autumn and early winter because at this season the temperatures are lower and conditions are relatively humid (De Villiers *et al.* 2002a, Milton 1995).

Most perennial species investigated in this study germinated over a wide range of temperatures and did not require light for germination (Table 5.1). They probably do not accumulate a persistent seed bank. This is supported by the findings of De Villiers (2000) on his study of some plants species of the Strandveld Succulent Karoo and by Smith *et al.* (1997) who reported that the seeds of some perennial species of other warm deserts have no dormancy and germinate in a wide range of low and intermediate temperatures. In the Succulent Karoo, where summer humidity is low and soil surface temperatures reach 64°C, selection has evidently favoured species whose germination is inhibited by high temperatures (Milton 1995). However, a high temperature reduces the percentage of seeds that remain in primary dormancy after their maturation, while germination in late autumn or winter would facilitate establishment during the moist winter period (Went 1949, Smith *et al.* 1996)

Although under natural conditions most seeds will germinate at low or intermediate temperatures, a reduced percentage of seeds might be able to germinate with late spring rains (Escudero *et al.* 1999). This might be the case with *Pentzia incana* that obtained its highest germination percentage at high temperatures.

Seeds of many species with low germination capacity at constant temperatures are stimulated by alternating temperatures (Baskin and Baskin 1998, Myers and Cooper 1989). Temperature fluctuation can act as a strong germination trigger, as diurnal fluctuation may be more important than light as environmental signal in sensing proximity to the soil surface because temperature, unlike light, is not attenuated as effectively by soil (Benvenuti *et al.* 1999). Alternating temperatures could also act as a season-sensing mechanism (Van Assche and Vanderberghe 1989). Sensitivity to periodic temperature fluctuation constitutes an important sensory system allowing plants to respond to daily variations in soil surface temperature. Alternating

temperatures interact with other environmental factors, including light, nitrate, substrate moisture level, oxygen concentration and level of active phytochrome to control germination (Gul and Weber 1999, Bewley and Black 1994). In other species, including those of this study, alternating temperatures had no positive effect on germination (Went 1979). The mucilage of the species investigated in this study largely prevent them from penetrating the soil, thus they do not face the problem of germinating from a great depth. In addition, temperature fluctuations during the winter season would be reduced.

Some species have mechanisms that insure that seed germination is spread over time, often over a period of years so called bet hedging (Venable and Lawlor 1980, Adondakis and Venable 2004). This is also found among heterocarpic species. The production of different types of seeds by one species is a common phenomenon found in unpredictable environments and arid environments to increase the chance of regeneration in the future (El-Keblawy and Al-Rawai 2006). The black seeds of *Ursinia cakilefolia* germinated better in the dark, while white seeds germinate better in light, but both obtained their highest germination percentages at low temperatures.

Light requirement

Non-dormant seeds of many species germinate equally well in light and darkness, others germinate to higher percentages in light than in darkness, and those of relatively few germinate to higher percentages in dark than in light (Baskin and Baskin 1998).

Light promoted germination of most annual species in this study. On the PCoA ordination species with a light requirement are clearly separated from the others. Various studies have demonstrated that light is one of the most important environmental signals in response to which seed germination is regulated (Guterman 1993, Zheng *et al.* 2005, Flores *et al.* 2006). In arid and semi-arid environments, sandy soils can modify the photon flux and light quality underground according the type of sand and soil moisture. Thus light can be relevant for triggering germination of desert plant seeds (Flores *et al.* 2006)

Seeds of many species are known to undergo a transition from primary to secondary dormancy during the burial period and then develop a light requirement to trigger germination (Gul and Weber 1999). The plant pigment phytochrome is the physiological sensor of light in seeds, and light-controlled seed germination is associated with this pigment. Another trait influencing the responsiveness to light is seed size (Baskin and Baskin 1998). Small seeds delay their germination until they are brought to the surface by soil disturbing agents to avoid fatal germination at depth in the soil (Schütz and Rave 1999).

Light sensitive seeds that are stimulated positively by light (positive photoblastic) and are situated on the soil surface may be exposed not only to light, but also to rapid dehydration after a rainfall that may stimulate their germination. However, the seeds of the mucilaginous species investigated, adhere to the soil surface which prevents them from being blown into dark cracks in the soil crust, thus conferring an advantage for species with a light requirement. The good contact between the soil and mucilage enables the seed to absorb the water in the surrounding soil and lubricate the area around the seed, thus making it easier for the root to penetrate the soil (Guttermann 2000).

Most perennial and a few of the annual species investigated acted indifferently towards light or dark, but on the PCoA ordination are closely associated with species that obtain their highest germination percentage and the shortest mean in the absence of light. Negative photoblasty implies that seeds require dark conditions and therefore need to be covered by sand in order to germinate (Guttermann 2002). The photo-inhibition mechanism can be considered to be an adaptation against surface seedling establishment in harsh habitats (Bell 1993). This group was mainly dominated annual species, particularly the genus *Heliophila*. Seeds with the potential to germinate in darkness at certain temperatures are induced into secondary dormancy if they are kept in darkness for prolonged periods of time at inappropriate temperatures for germination (Baskin and Baskin 1998).

5.5 Implications for management and conservation

The optimal management for increasing germination and seedling establishment differed among species, but in general most species obtained their highest germination percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons. Only a few species are inhibited by light. Most required light and others acted indifferent to light. For species with light requirements, the burial of seeds caused by the movement of sand or fauna may reduce their germination (Martinez-Sanchez *et al.* 2006).

Heavy grazing has been demonstrated to promote seed germination in tropical environments by removal of the relatively dense canopy (Derigibus *et al.* 1994). The vegetation in arid regions is less dense and should allow ample opportunities for light demanding species to germinate. The soil surface in arid regions however, is unstable and the presence of grazing animals could increase the instability. Keeping livestock on the field during summer months prior to autumn germination could promote the germination of some species because animal movement might bury seeds with negative photoblasty, however, it could also reduce germination of positive photoblastic seed by their burial.

Most of the species examined in this study have a relatively short mean germination time and are therefore fast germinators (Escuadero *et al.* 1997). It has been suggested by Van Rheede van Oudtshoorn and Van Rooyen (1999) that heavy dew falls, fog or small rainfall events that are not sufficient to cause germination, may produce conditions that induce a priming effect on mucilaginous seeds, which are then able to germinate immediately when there is sufficient water. It has been proposed that mucilaginous seeds in dormant seed banks have an advantage over non-mucilaginous seeds because the viability and longevity of the mucilaginous species is promoted by their prolonged wetting by dew (Van Rheede van Oudtshoorn and Van Rooyen 1999). This implies that if these seeds are deeply buried, their longevity will be reduced because the quantity of water produced by dew or fog could not penetrate the soil.

In concordance with what has been suggested in the preceding paragraph, with increasing climate change, conserving these species will be a difficult task, because the decrease in rainfall, dew and fog will affect the expansion of mucilage during late spring and early summer thus most seed would be carried by wind into depressions and few seeds might remain viable till the next growing season. Temporal wetting of the soil surface after seed maturation could be a possibility to maintain the seed bank.

Mucilaginous seeds have the same germination requirement as most desert seed, but their adhesion to the soil (often near the mother plants) provides them with the ability to germinate in a suitable environment. The germination and the establishment of seeds dispersed by water are uncertain because most of them will end up in depressions and be covered by soil.

5.6 References

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Chapter 6

Anatomical investigation of the mucilaginous diaspores of selected species of Namaqualand, South Africa

6.1 Introduction

Plants have developed many functional traits that allow them to adapt and survive in different environments. Seed dispersal is an important functional trait that influences the population structure and the spatial and temporal turnover of a plant community. The seed coat of some species has features that assist in seed dispersal. For example, the testa of seeds that are eaten by animals and man may be resistant to digestive processes and permit the seed to pass through the intestinal tract without damage (Fahn 1990).

Myxospermy is a functional trait where the epidermis of the diaspore (seed/fruit) contains mucilaginous cells, which swell and become sticky when in contact with water (Gutterman and Shem-Tov 1997, Van Rheede van Oudtshoorn and Van Rooyen 1999). According to Johri (1984) the mucilage-forming substance consists of secondary walls swelling after hydration.

There are many divergent ideas about the ecological importance of myxospermy, and it probably fulfills various functions. When wet, myxospermic diaspores adhere to the soil or to animals, and after drying out again remain glued to soil particles and thus resist being carried to unfavourable locations by wind. The good contact between the mucilage layer and the soil surface increases water absorption for germination and the water held by the mucilage could also serve as a water reservoir for seedling establishment (Gutterman *et al.* 1967, Van Rheede van Oudtshoorn and Van Rooyen 1999). Furthermore, the adherence of the seed to the soil by the mucilage prevents massive collection by seed predators and the repeated wetting of mucilaginous seeds during many nights with dew may affect the repair mechanisms of the DNA, cell membranes and organelles, thereby enhancing seed viability for many years (Van Rheede van Oudtshoorn and Van Rooyen, 1999). Mucilage may also control the germination process by excluding the passage of oxygen when the

moisture is in excess and could damage the emerging seedling (Gutterman *et al.* 1967, 1973, Gutterman 1996, Tamara *et al.* 2000). Little attention has thus far been given to the origin and chemical composition of mucilage of mucilaginous diaspores. Therefore, in this study the origin and the chemical composition of the mucilage of selected plant species of Namaqualand (South Africa) are investigated.

6.2 Background of species of which diaspores have been investigated

ACANTHACEAE

***Acanthopsis horrida* Nees.**

It is a dwarf perennial shrub up to 0.3 m high. The basal leaves are hairy, obovate and tapering into the leafstalk, with short spines on the margins. The flowerheads in which dense flowers are borne has very spiny bracts. It is found at altitudes of 460 to 500 m above sea level. It is an endemic species confined to the Northern Cape (Germishuisen *et al.* 2006).

***Blepharis furcata* (L.f.) Pers.**

It is a dwarf shrub of 0.1 to 0.5 m height. The flowers are in spikes with spiny bracts. It is found at altitudes of 200 to 1020 m above sea level in the Northern Cape (Germishuisen *et al.* 2006).

ASTERACEAE

***Cotula barbata* DC.**

A tufted annual herb growing 90 to 180 mm tall. The very hairy leaves are deeply divided and about 40 mm long. The flowerheads with only yellow disc florets are about 10 mm in diameter, and borne singly on a slender, hairless stalk. The involucre bracts are almost round and papery with a transparent margin. It is found in sandy places in the Richtersveld and Namaqualand klipkoppe (Le Roux 2005).

***Tripteris hyoseroides* DC.**

It is a glandular-hairy, aromatic annual herb of up to 0.5 m tall. The leaves are elliptical and irregularly toothed. The flowerheads are 30 to 50 mm in diameter, dark purplish in the center with orange ray florets surrounded by two series of bracts with membranous margins. Diaspores are three winged and are 7 to 8 mm long. It is

found in stony and rocky places throughout Namaqualand and also in other dry parts of the Northern, Western and Eastern Cape (Manning, 2003).

***Othonna cylindrica* (Lam.) DC.**

It is a shrub growing 0.5 to 1 m tall with narrow succulent leaves of 20 to 40 mm long. The flowerheads are about 20 mm in diameter and are borne in loose groups above the leaves. Each flowerhead contains about 10 green-veined, yellow ray-florets. The involucral bracts are in one row and joined at the base. It is found throughout Namaqualand and in the Western Cape and Namibia (Le Roux 2005).

***Senecio arenarius* (Thunb.)**

An annual herb growing about 0.4 m tall. The leaves with glandular hairs are up to 70 mm long and lobed into broad segments. The flowerheads are 25 to 30 mm in diameter with magenta-pink ray florets and yellow disc florets. The involucral bracts are free and in a single row (Le Roux 2005).

***Ursinia cakilefolia* DC.**

An annual herb growing up to 0.25 m tall. The leaves are up to 6 cm long, toothed and doubly-lobed into very narrow segments. The flowerheads are borne singly and are 25 to 35 mm in diameter. The ray florets are orange and disc florets are black. The involucral bracts are in many rows and the innermost bract is the largest with a conspicuous transparent tip. It is found in sandy places throughout Namaqualand and in the northern part of the Western Cape (Le Roux 2005).

***Pentzia incana* (Thunb.) Kuntze:**

An erect, densely-branched shrub growing up to 0.50 m high. The leaves are deeply divided, 2 to 6 mm long and covered with white hairs. The flowerheads have yellow discflorets only, are 6 mm in diameter and borne on leafless stalks. The involucral bracts are arranged in four rows and have membranous margins. An unpalatable plant to stock that grows on flats in the Richtersveld, Namaqualand klipkoppe and other arid regions in South Africa (Le Roux 2005).

***Oncosiphon grandiflorum* (Thunb.) Källersjö.**

A loosely-branched, annual herb growing 0.1 to 0.4 m tall. The leaves with a pungent smell are finely dissected, and up to 6 cm long. The flowerheads with yellow disc florets only are 7 to 10 mm in diameter and borne on a short, stout stalk. The involucre bracts are arranged in four rows with membranous margins. It is an unpalatable plant to stock. It is found in sandy places, often on ploughed land throughout Namaqualand, the Western Cape and in Namibia. (Le Roux, 2005).

***Foveolina dichotoma* (DC.) Källersjö.** An annual herb growing 0.2 to 0.3 m tall, branching mainly from the base. The leaves are doubly-lobed, sparsely covered with minute hairs and up to 2 cm long. The flowerheads have only yellow disc florets, are almost round, 5 to 7 mm in diameter, and borne singly on thin leafless stalks. The involucre bracts with membranous margins are in four rows. It is an unpalatable plant to stock. Found throughout Namaqualand and other dry parts of the Northern, Western and Eastern Cape (Le Roux 2005).

BRASSICACEAE

Heliophila thunbergii* (Eckl. & Zeyh.) Steud var. *thunbergii

This plant name has changed from *Heliophila latisiliqua*. The genus is native to South Africa, contains 70 species of annuals, perennials and subshrubs belonging to the cabbage family of which 26 occur in Namaqualand. *Heliophila thunbergii* var. *thunbergii* is an annual herb of 0.15 to 0.35 m tall. The leaves are simple or lobed. The four-petalled flowers are borne on racemes and are white, producing a colourful display in spring. It is found in sandy and rocky soils often on slopes in Namaqualand (Germishuisen *et al.* 2006).

LAMIACEAE

***Salvia dentata* Aiton**

A much branched shrub growing up to 1 m tall. The greyish leaves are up to 20 mm long and 10 mm wide and usually with toothed margins. The blue flowers are in groups on the ends of the branches and are up to 25 mm long. The calyx has rounded lobes and minute hairs. It is an unpalatable plant to stock, and is found along drainage lines and on rocky slopes in the Richtersveld and Namaqualand (Le Roux 2005).

6.3 Materials and Methods

Scanning electron microscopy

Dry seeds/achenes (henceforth referred to as seeds) were mounted on a stub and made conductive with RuO₄ vapour (Van der Merwe and Peacock 1999). For wet samples, seeds of each species were soaked in water for 24 hours before fixation. They were then fixed in 2.5% glutaraldehyde in 0.075 M phosphate buffer, pH 7.4, for one hour and rinsed three times (five minutes each) in 0.075 M phosphate buffer and dehydrated in an ethanol series with the respective concentrations of 30%, 50%, 70%, 90% and 100%. This was followed by critical point drying in liquid CO₂ and mounted on a stub and made conductive with RuO₄ vapour. Samples were viewed with the use of a JSM 840 scanning electron microscope (JEOL, Tokyo, Japan) and photographs were taken with the computer program Orion 6.60.4 (Belgium).

Light microscopy

Further studies were done on seeds or achenes where the origin of the mucilage could not clearly be establish with the scanning electron microscope. Dry samples were fixed in 4% (v/v) formaldehyde in 50% (v/v) ethanol (FAA) to prevent mucilage release (Tamara *et al.* 2000). The wet samples were immersed in water for 24 hours. Wet samples were fixed in 2.5% glutaraldehyde in 0.075 M phosphate buffer, pH 7.4 for 1 hour and rinsed three times (five minutes each) in 0.075 M phosphate buffer and dehydrated in an ethanol series with the respective concentrations 30%, 50%, 70%, 90% and 100%. Samples were then infiltrated over two days with pure LR-White, polymerised at 65°C for 24 to 36 hours. Sections were cut with a Reichert Ultracut E microtome. Each section was stained with toluidine blue (0.2% in 0.5% NaCO₃), mounted in immersion oil and viewed with a Nikon Optiphot light microscope (Tokyo, Japan). Photographs were taken with the Nikon Digital camera DXM 1200 (Tokyo, Japan) and the computer program Nikon ACT-1 (Tokyo, Japan).

Staining methods

Diaspore staining was done according to various manuals of microscopic staining (McClean and Ivimey Cook 1941, O'Brien and McCully 1981, Lawton and Ettridge 1986) the details of which are given in Table 6.1.

Table 6.1 Stains used for various compounds and expected results

Stain	Compound	Expected results
Methylene blue	Cellulose	Blue
Ruthenium red	Pectic substances	Red
Toluidine Blue	Polysaccharides	Pink –purple
Sudan 4	Lipids	Yellow
Phloroglucinol	Lignin	Pink
Aniline blue	Callose	Blue
Biuret solution	Protein	Violet

6.4 Results and discussion

The results suggest three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the outer cell wall of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs.

6.4.1 Epidermal mucilage

***Heliophila thunbergii* var. *thunbergii* (Brassicaceae)**

Scanning electron microscopy of dry seeds of *Heliophila thunbergii* var. *thunbergii* (Brassicaceae) reveals a circular seed (Figure 6.1A). The epidermal layer (e) consists of circular cells with a raised margin and a cavity in the centre (Figure 6.1B). The outermost layer (ol) seems to be filled with spongy content, probably mucilage (Figure 6.1C). The thin section of the dry seeds also reveals epidermal cells filled with mucilage (m) (Figure 6.1G). Once wet, the seed is covered by a gelatinous film (Figures 6.1D&E). The section of the wet seed reveals the epidermis with ruptured cells from which filaments of mucilage (m) emerge (Figure 6.1F). This is also visible in the thin section of the wet seed seen with the light microscope (Figure 6.1H). Upon wetting the mucilage swells and the epidermal cells become incapable of containing the excess mucilage and therefore rupture.

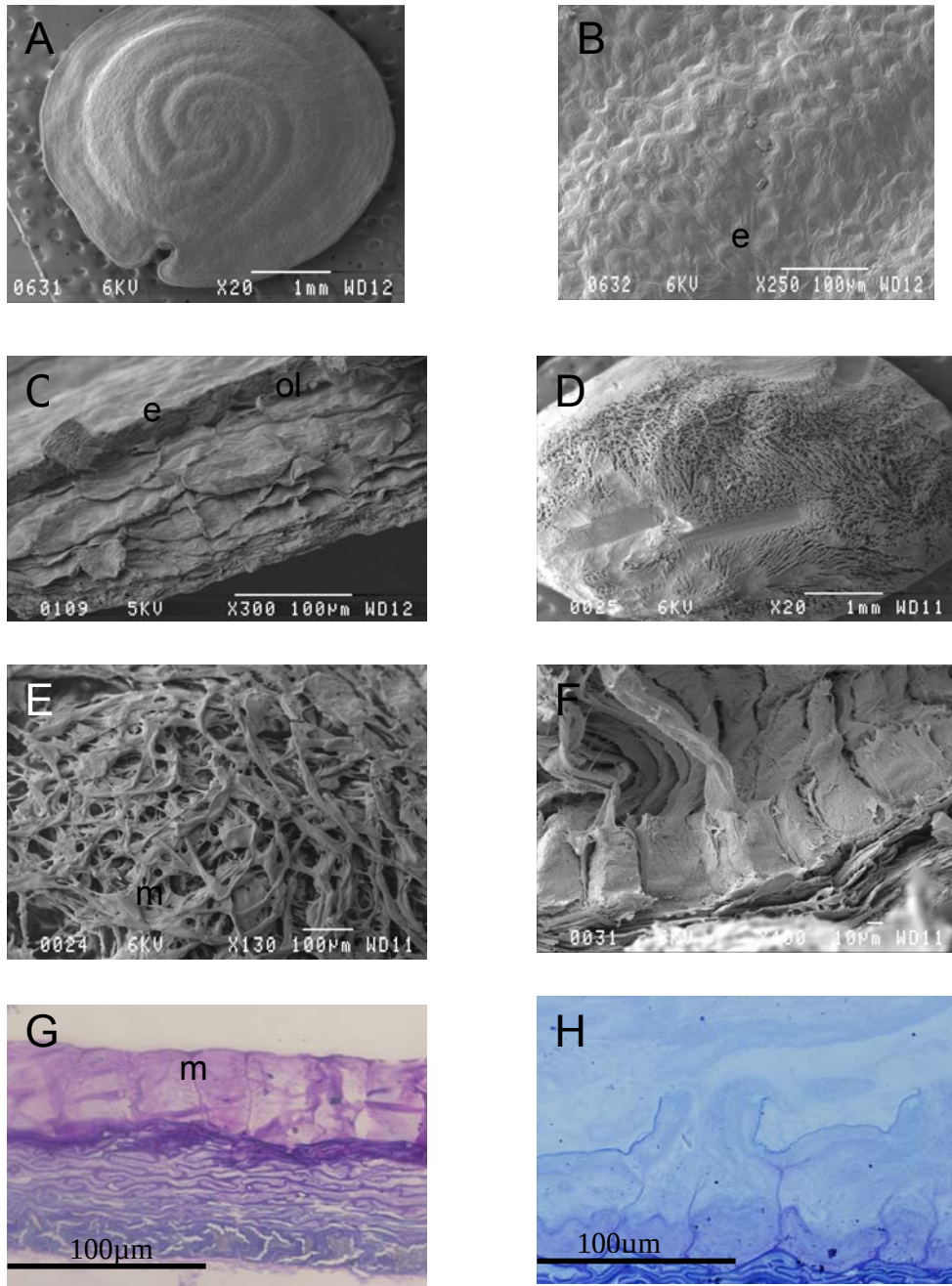


Figure 6.1 Scanning microscope (A-F) and light microscope (G-H) images of seeds of *Heliophila thunbergii* var. *thunbergii* : (A) Entire dry seed (scale bar = 1 mm); (B) high magnification of dry epidermis; (scale bar = 100 µm); (C) section of the dry seed (scale bar = 100 µm); (D) entire wet seed (scale bar = 1 mm); (E) high magnification of wet seed surface (scale bar = 100 µm); (F) section of wet seed (scale bar = 10 µm); (G) section of the dry seed (scale bar = 100 µm); (H) cross section of wet epidermis (scale bar = 100 µm). e = epidermal layer, m = mucilage, ol = outermost layer.

***Cotula barbata* (Asteraceae)**

In the dry state, the achene of this species does not have the same structure on both sides, the upper side is smooth (Figure 6.2 B) while the lower side is undulated (6.2.A) The phenomenon observed in *Cotula barbata* (Figure 6.2) is similar to the one of *H. thunbergii* var. *thunbergii*. When *C. barbata* achenes come in contact with water, the epidermal cells burst across the entire outer surface (Figure 6.2F) and not only the centre of the cell as in the case of *H. thunbergii* var. *thunbergii* (Figure 6.1H). This could be the reason for the mucilage appearing multi-layered (Figure 6.2E).

***Salvia lanceolata* (Lamiaceae)**

The scanning electron micrographs of the dry seed of *S. lanceolata* do not clearly reveal the structure of the mucilage in the epidermal cells (Figure 6.3A-C). The light microscopy cross section shows the epidermis filled and covered with mucilage (Figure 6.3G). After wetting the seed is covered with a thick mucilage layer (Figure 6.3D & E). Once in contact with water the outer layer of the epidermis absorbs water quickly, the epidermis cells swell, the cuticle ruptures and the contents are excreted in the shape of long, continuous threads. This is clearly visible on the wet sectioned seed (Figure 6.3F) and the thin cross section of the wet seed (Figure 6.3H).

Foveolina dichotoma*, *Oncosiphon grandiflorum* and *Pentzia incana

These three species are taxonomically related, all previously belonged to the genus *Pentzia*. Apparently these species have the same way to produce mucilage. The scanning electron microscopy shows that the epidermis of the dry achene of *F. dichotoma* consists of parallel longitudinal cells (Figure 6.4A & D). The epidermis of *O. grandiflorum* (Figure 6.4 B & E) and *P. incana* (Figure 6.4C & F) also reveals an epidermis that consists of longitudinal, more or less hexagonal, cells. Following wetting and freeze drying, the seeds are covered with a gelatinous film but the wings remain unchanged (Figure 6.5G, H, J). Light microscope sections show that the epidermal cells of the dry seeds are filled with mucilage (Figure 6.4K & L), which is released when the cells burst open upon swelling in contact with water (Figure 6.4 M).

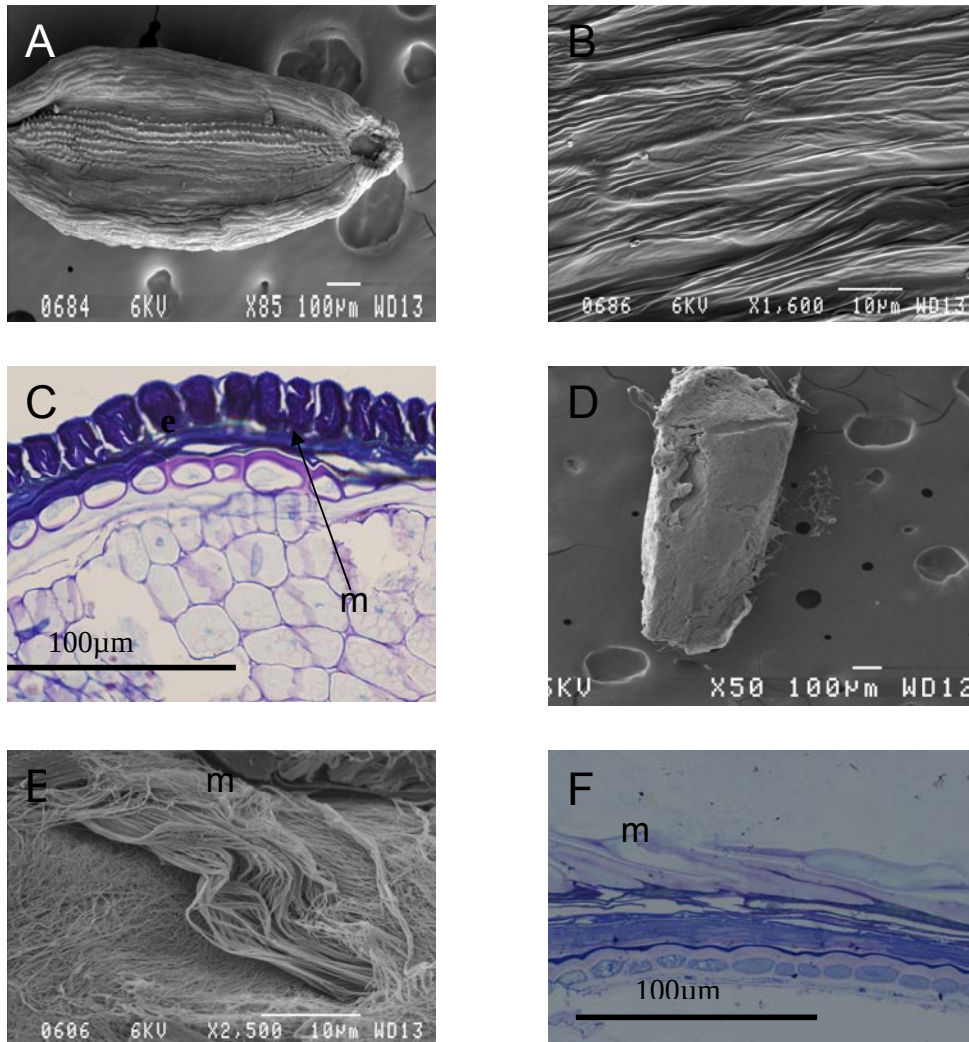
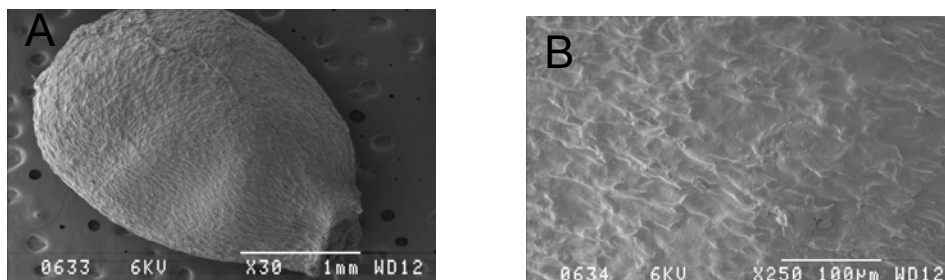


Figure 6.2 Scanning microscope (A- B, D, E) and light microscope (C, F) images of achenes of *Cotula barbata*: (A) Entire dry seed (scale bar = 100 µm); (B) high magnification of the epidermis (scale bar = 10 µm); (C) cross section of the dry seed coat (scale bar=100 µm) , with mucilage (arrow) retained in the epidermal layer; (D) entire wet seed (scale bar = 100 µm); (E) high magnification (scale bar = 10 µm) of wet epidermis covered with a thick layer of mucilage; (F) cross section of the wet epidermis of which the outer layer has burst, releasing mucilage from the epidermal cells (scale bar = 100 µm). e = epidermis; m = mucilage.



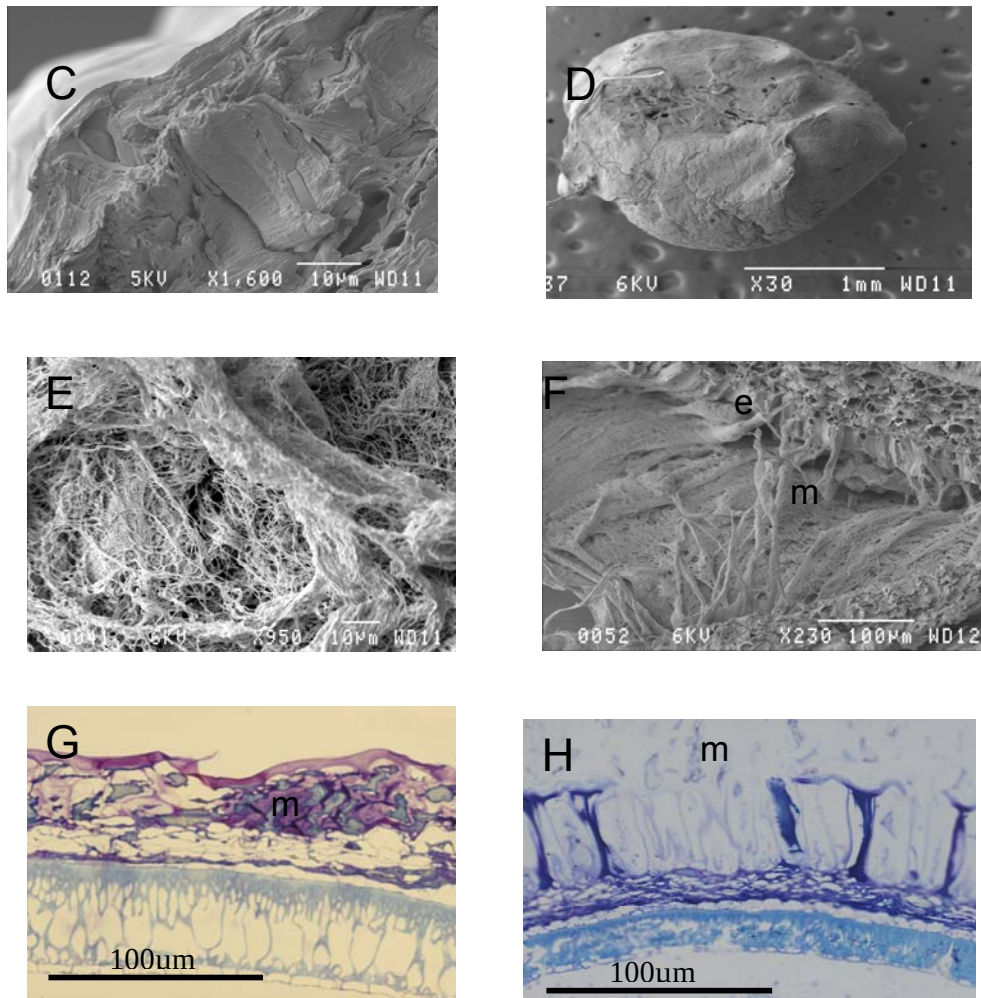
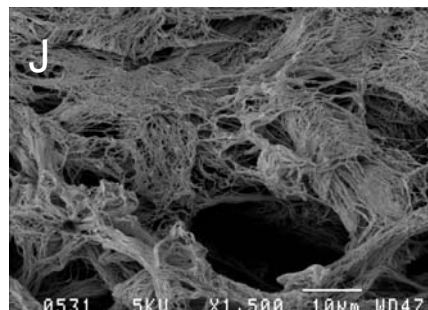
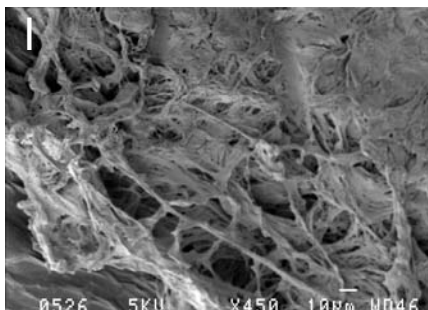
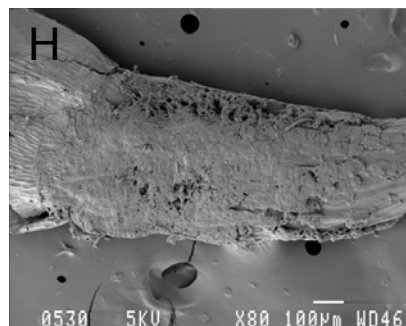
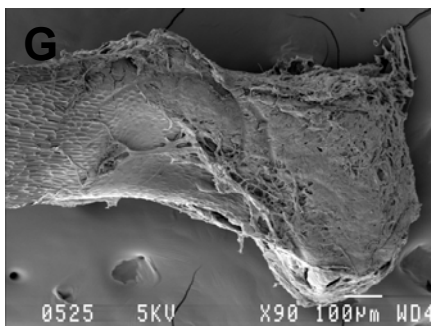
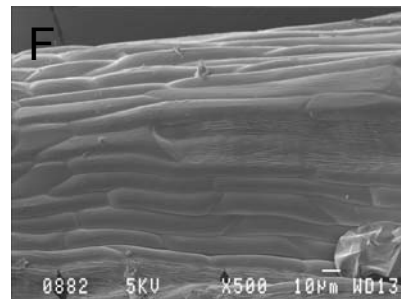
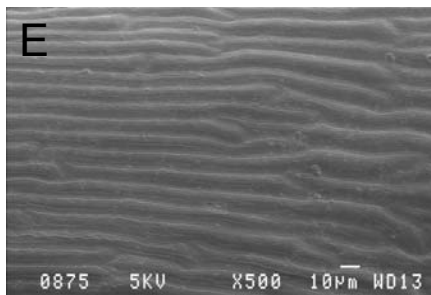
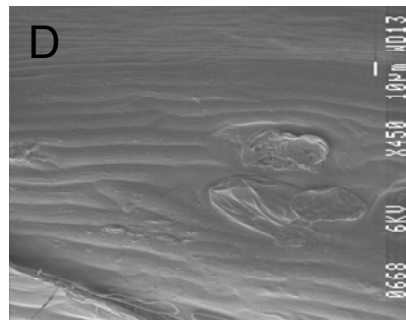
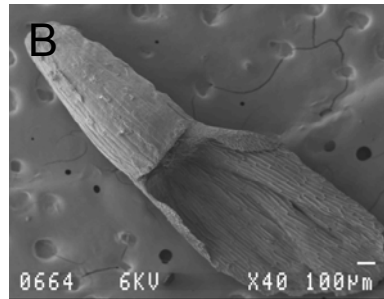
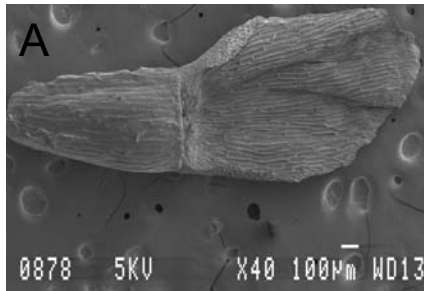


Figure 6.3 Scanning microscope (A-F) and light microscope (G,H) images of seeds of *Salvia lanceolata*: (A) Entire dry seed (scale bar = 1 mm); (B) high magnification of the dry epidermis filled with mucilage (scale bar = 100 μ m); (C) section of the dry seed (scale bar = 10 μ m); (D) entire wet seed covered with mucilage (scale bar = 1 mm); (E) high magnification of the wet epidermis covered with mucilage (scale bar = 10 μ m); (F) section of the wet seed with long strands of mucilage (scale bar = 100 μ m); (G) thin cross section of the dry seed with epidermal cells filled with mucilage (scale bar = 100 μ m); (H) thin cross section of the wet epidermis with an open cell that liberate mucilage (scale bar = 100 μ m), m = mucilage.



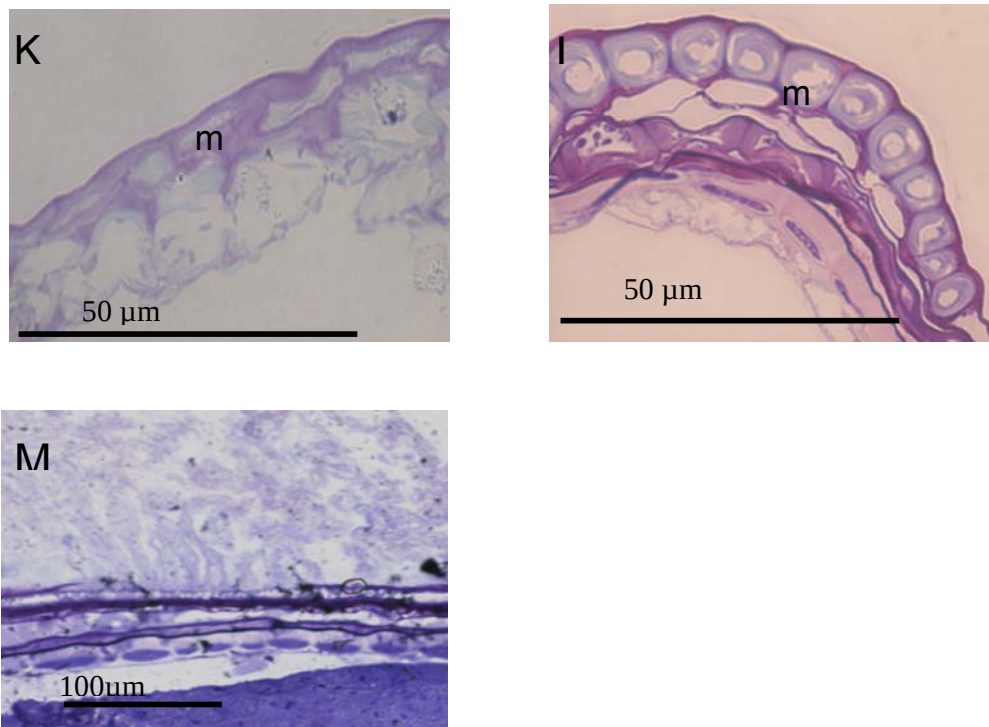


Figure 6.4: Scanning microscope (A-J) and light microscope (K-L) images of achenes of *Foveolina dichotoma*, *Oncosiphon grandiflorum* and *Pentzia incana*. (A) entire seed of *F. dichotoma* (scale bar = 100 µm); (B) entire dry achene of *O. grandiflorum* (scale bar = 100 µm); (C) entire dry achene of *P. incana* (scale bar = 1 mm); (D) high magnification of the epidermis *F. dichotoma* (scale bar = 10 µm); (E) high magnification of the epidermis of *O. grandiflorum* (scale bar = 10 µm); (F) high magnification of the epidermis of *P. incana* (scale bar = 10 µm); (G) entire wet achene of *F. dichotoma* (scale bar = 100 µm); (H) entire wet achene of *P. incana* (scale bar = 100 µm); (I) high magnification of the mucilage of *F. dichotoma* (scale bar = 10 µm); (J) high magnification of the epidermis of *P. incana* (scale bar = 10 µm); (K) thin cross section of dry epidermis of *F. dichotoma* (scale bar = 50 µm); (L) thin cross section of dry epidermis of *O. grandiflorum* (scale bar = 50 µm), and (M) thin cross section of wet epidermis of *O. grandiflorum* (scale bar = 100 µm) with broken epidermal cells that liberate mucilage.

6.4.2 Mucilaginous wings

Ursinia cakilefolia

Dry achenes of *Ursinia cakilefolia* (Asteraceae) have a winged pappus (Figure 6.5A), consisting of a single layer of radially elongated cells with helically thickened cell walls (Figures 6.5B & C). When the pappus comes into contact with water, the cells separate at the middle lamellae and the helical thickenings uncoil to form long strands of mucilage (Figures 6.5D & E). The different steps through which the pappus uncoils are clearly visible under the scanning electron microscope (Figure 6.5F).

Tripteris hyoseroides

Achenes of *Tripteris hyoseroides* (Asteraceae) are three-winged. The epidermis of the seed bearing part of the achene is undulate and does not become mucilaginous (Figure 5.6A). The section of the wings show hexagonally shaped cells completely filled with mucilage and separated by thick cell walls (Figure 6.6B). Upon wetting, the cells separate and the wings become completely mucilaginous (Figures 6.6C & D) and the long mucilage strands remain attached to the achene (Figure 6.6E).

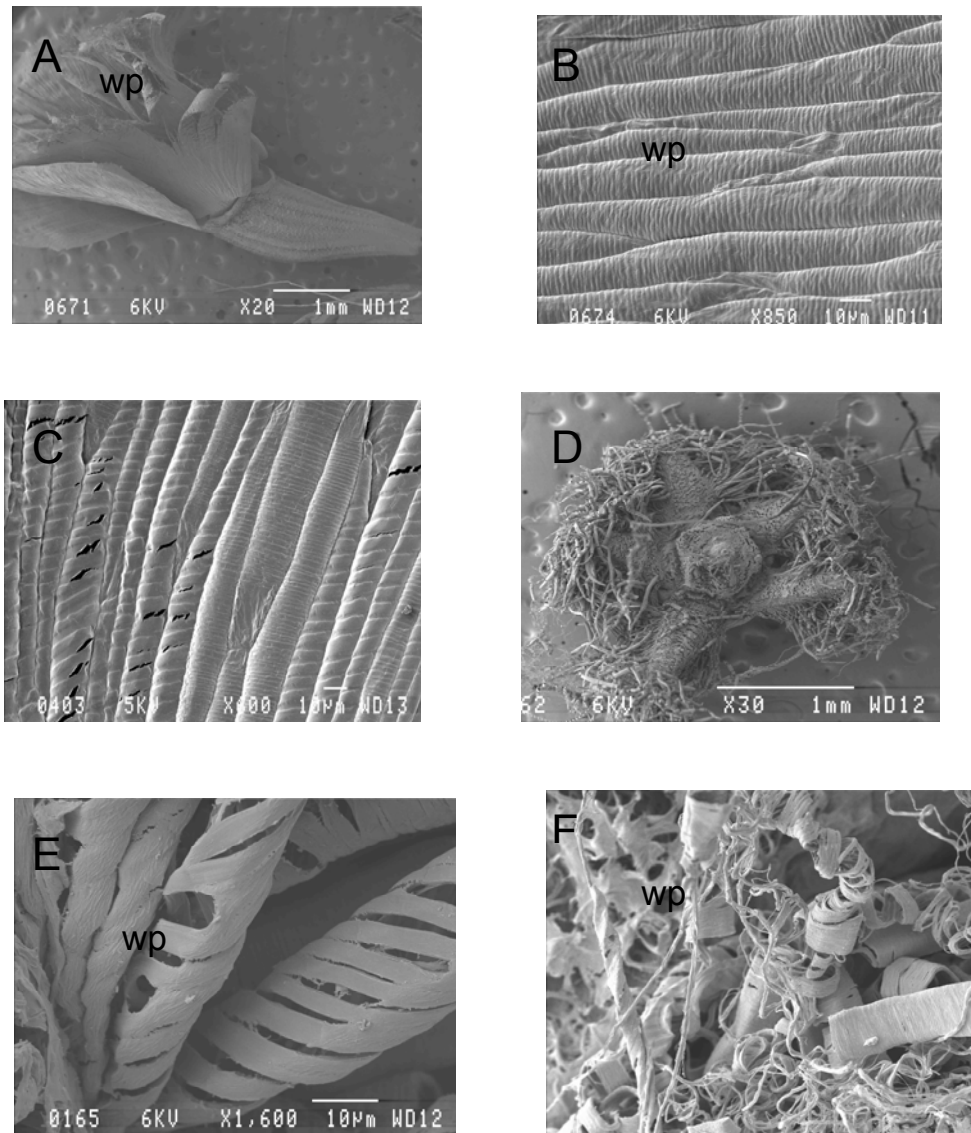


Figure 6.5 Scanning electron micrographs of the achenes of *Ursinia cakilefolia*. (A) Entire dry achene with wing pappus (scale bar = 1 mm); (B & C) High magnification of the dry winged pappus consisting of radially elongated cells (scale bar = 10 µm); (D) entire wet achene with uncoiled winged pappus (scale bar = 1 mm); (E) high magnification of wet winged pappus (scale bar = 10 µm); (F) long strands of uncoiled mucilage (scale bar = 10 µm), wp = winged pappus.

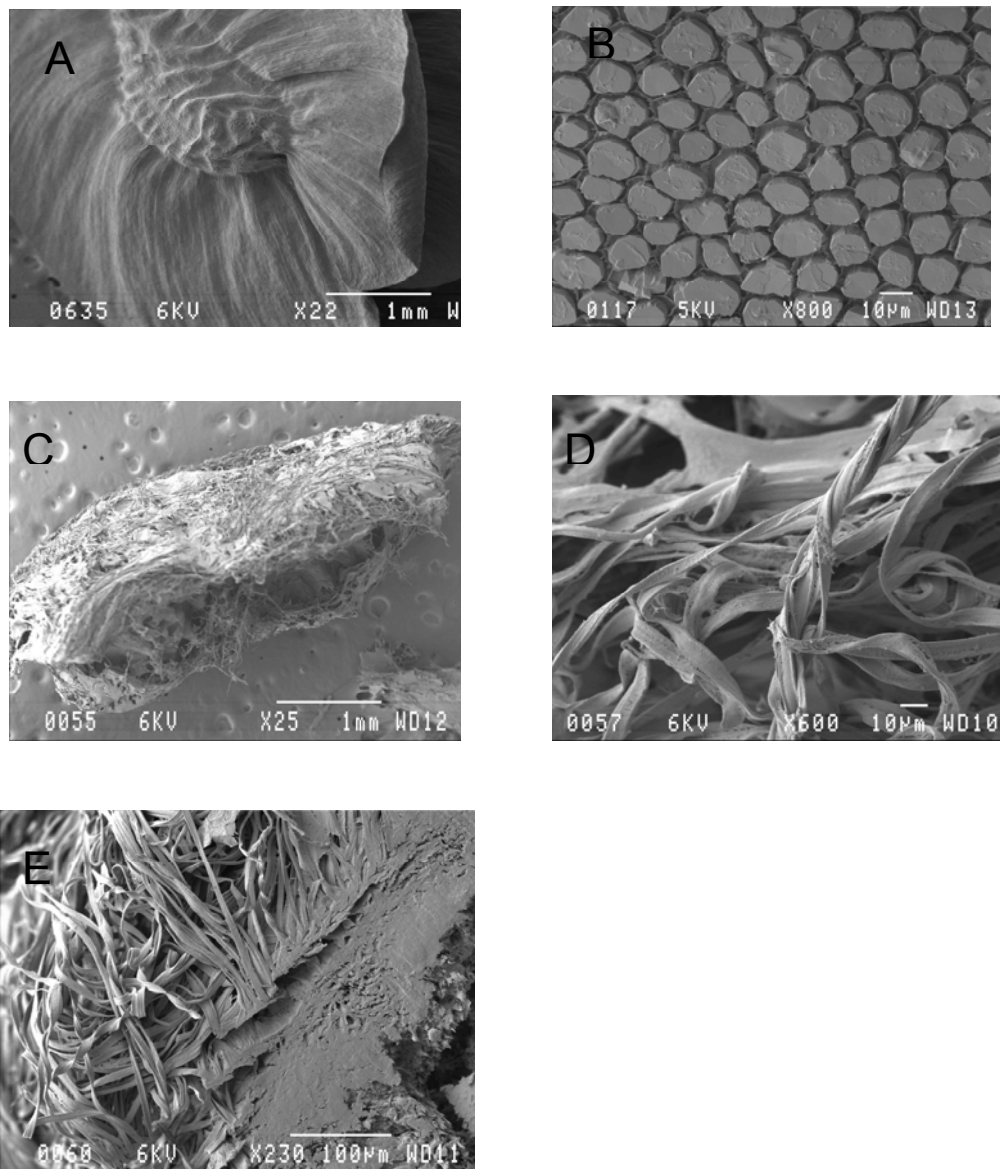


Figure 6.6 Scanning electron micrographs of the achenes of *Tripteris hyoseroides*. (A) Entire dry achene (scale bar = 1 mm); (B) high magnification of a section of the wings (scale bar = 10 μm); (C) entire wet achene with disintegrated wing (scale bar = 1 mm); (D) high magnification of long strands of mucilage (scale bar = 10 μm); (E) section of the wet seed with disintegrated wings (scale bar = 100 μm).

6.4.3 Mucilaginous hairs

Senecio arenarius

In the dry condition, the shiny white hairs, lie against the achene (Figure 6.7A) and have a finger-like shape. The interior of the hair seems to be filled with a coiled thread as seen at high magnification (Figure 6.7B & C). In the wet condition the hairs are orientated more or less perpendicular to the achene. Apparently, when the mucilaginous hairs absorb water the threads uncoil and become thin and long (Figure 6.7D). Under the light microscope, the hairs consist of two elongated cells attached to the epidermis (Figure 6.7F).

Othonna cylindrica

The dry achenes of *O. cylindrica* are covered with long white hairs (Figure 6.8A & B). When wet the tips of the hairs disintegrate to release an amorphous mucilaginous mass (Figure 6.8D). Apparently the hairs of *O. cylindrica* are covered and filled with a mucilage which, when in contact with water forms a firm gel (Figure 6.8E) that remains attached to the hair and produces long strands of mucilage that separate from the rest of the hair (Figure 6.8F). The bottom of the hair remains intact and firmly attached to the epidermis (Figure 6.8G).

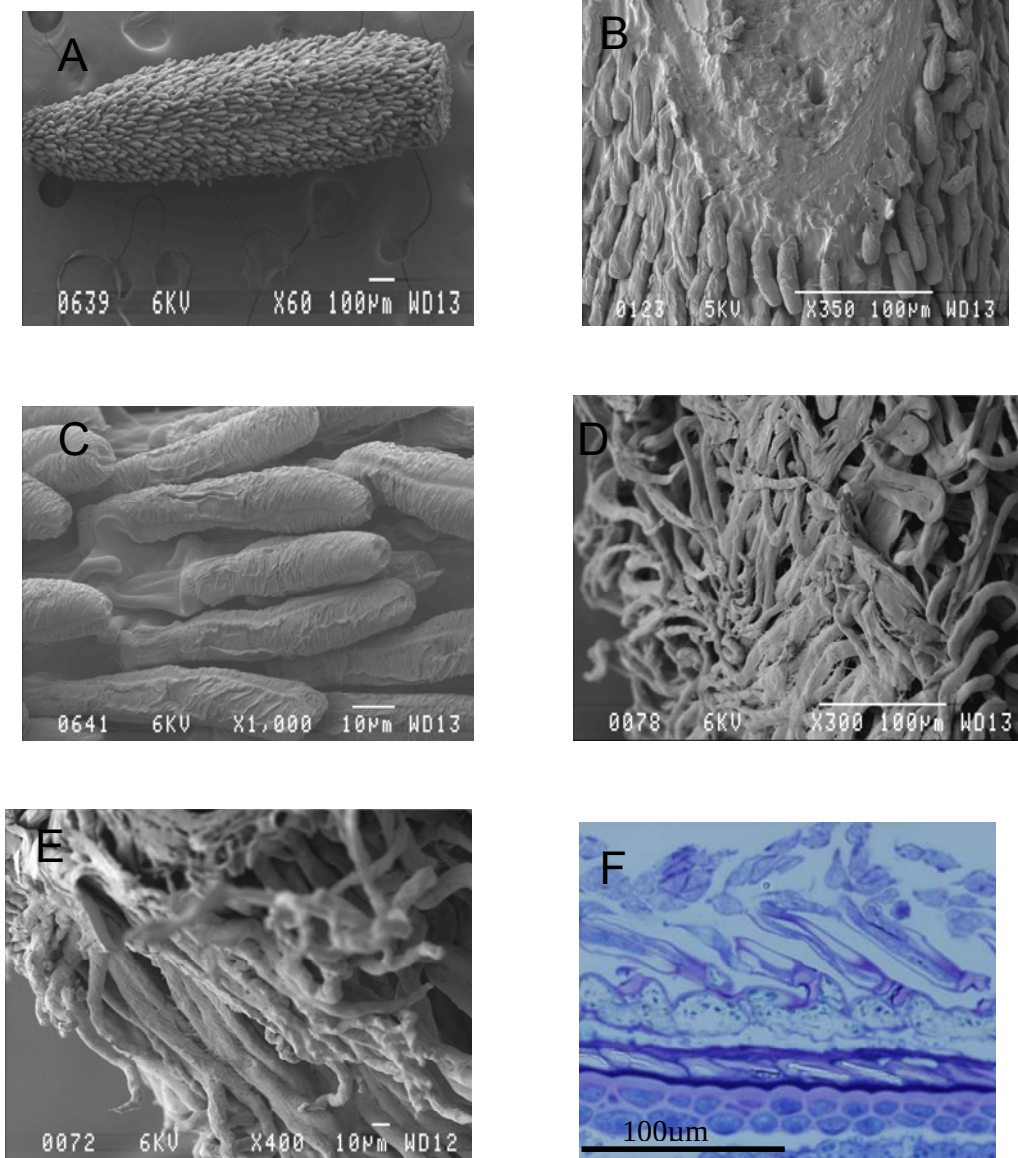


Figure 6.7 Scanning microscope (A-E) and light microscope (F) images of the achenes of *Senecio arenarius*: (A) Entire dry achene (scale bar = 100 µm); (B) dry section of the achene with hair lying against it (scale bar = 100 µm); (C) high magnification of hairs (scale bar = 10 µm); (D) entire wet achene (scale bar = 100 µm); (E) high magnification of wet achene with elongated hairs (scale bar = 10 µm); (E) cross section of wet achene with elongated bicellular hairs (scale bar = 100 µm).

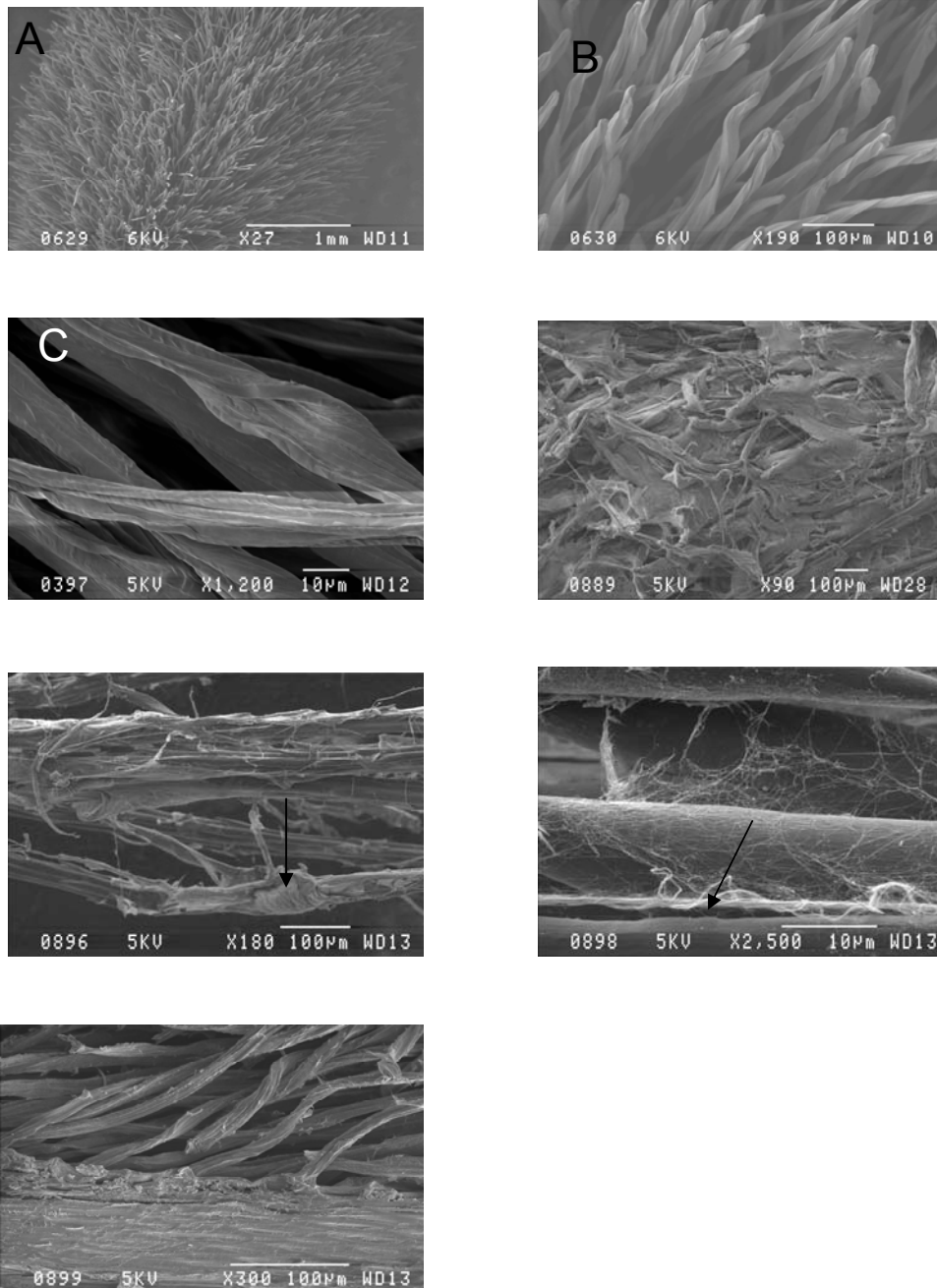
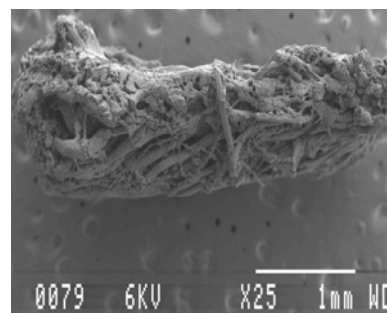
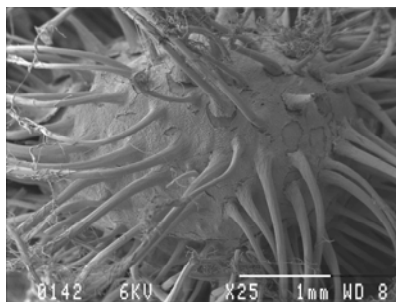
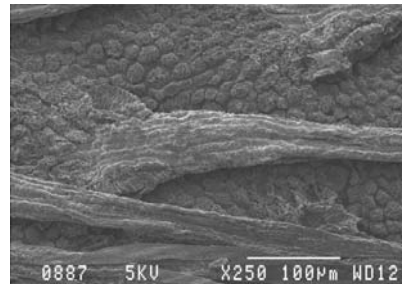
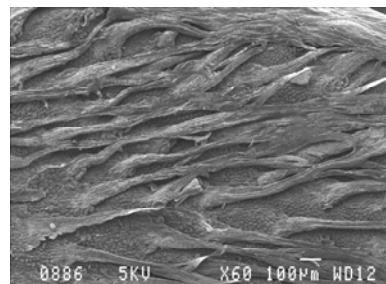
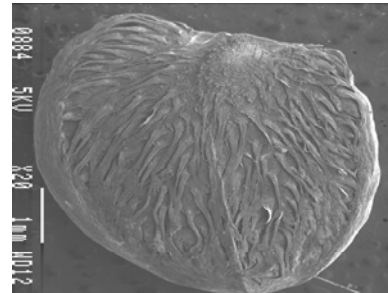
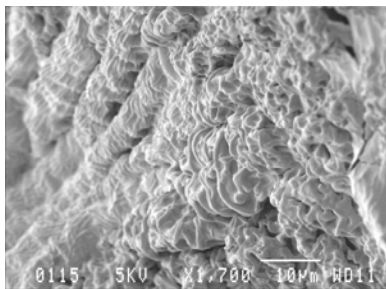
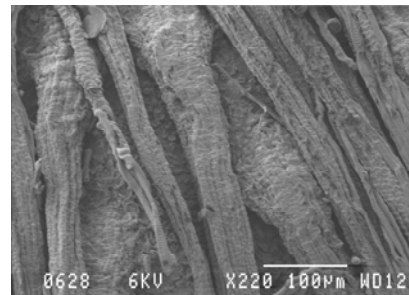
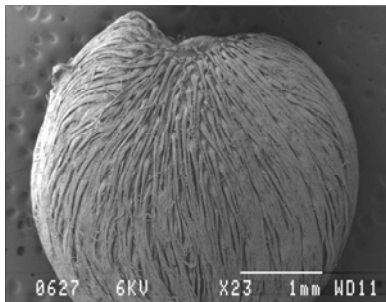


Figure 6.8 Scanning electron micrograph of achenes of *Othonna cylindrica*: (A) Entire dry achene (scale bar = 1 mm); (B) dry hair in high magnification (scale bar = 100 μ m); (C) dry hair (scale bar = 10 μ m); (D) entire wet achene (scale bar = 100 μ m); (E) hairs covered with mucilage (arrow) (scale bar = 100 μ m); (F) high magnification of wet hair with mucilage strand (arrow) (scale bar = 10 μ m); (G) section of wet seed with the bottom of the hair attached to the epidermis (scale bar = 100 μ m), m = mucilage.

***Acanthopsis horrida* and *Blepharis furcata* (Acanthaceae)**

In the dry condition the hairs on the seed surface of *Acanthopsis horrida* (Figure 6.9 A & B) and *Blepharis furcata* (Figure 6.9D & E) are tightly appressed to the seed coat and are covered with a thick deposit (Figure 6.9C & F). At high magnification it can be seen that these hairs contain coiled spirals (Figure 6.9 B). Once in contact with water the thick deposit expands, the hairs become swollen and orientate perpendicular to the seed coat (Figure 6.9G-I). The tips of the hair break open and release a multitude of strands of mucilage (Figures 6.9K-M). The bases of the hairs remain intact (Figure 6.9J).



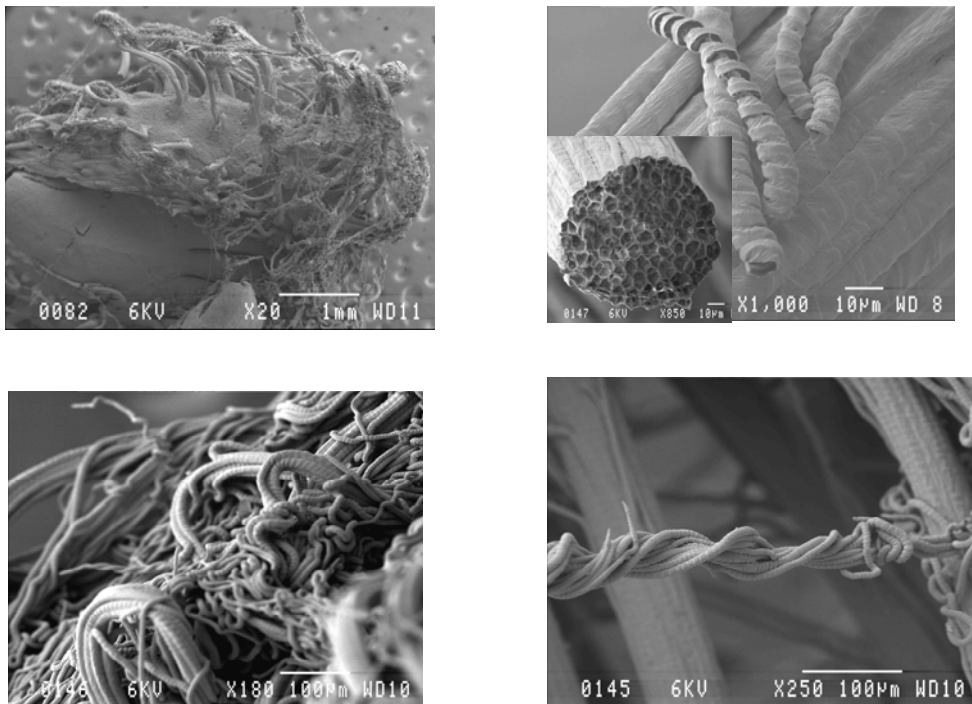


Figure 6.9 Scanning electron micrographs of seeds of *Acanthopsis horrida* and *Blepharis furcata*. (A) Entire dry seed of *A. horrida* (scale bar = 1 mm); (B) hairs of *A. horrida* (scale bar = 100 μm); (C) dry epidermis of *A. horrida* covered with thick deposit (scale bar = 10 μm); (D) entire dry seed of *B. furcata* (scale bar = 1 mm); (E) hairs of *B. furcata* (scale bar = 100 μm); (F) dry epidermis of *B. furcata* covered with thick deposit (scale bar = 100 μm); (G) wet seed of *A. horrida* (scale bar = 1 mm); (H & I) wet seed of *B. furcata* (scale bar = 1 mm); (J) bottom of a single wet hair of *A. horrida* made up of many strands (scale bar = 10 μm); (K) swollen hairs of *A. horrida* (scale bar = 10 μm); (L & M) uncoiled strands of mucilage of *A. horrida* (scale bar = 100 μm).

6.4.4 Staining

A positive reaction was only found with three stains: methylene blue for cellulose, ruthenium red for pectic substances and toluidine blue for polysaccharides. The rest of the stains did not react with the mucilage (see Appendix 1)

Table 6.1 Reaction of staining with the mucilage of each species

	Methylene blue	Ruthenium red	Toluidine blue
<i>Heliophila thunbergii</i> var. <i>thunbergii</i>	++	+	-
<i>Cotula barbata</i>	+	+++	++
<i>Salvia dentata</i>	+	+++	+
<i>Foveolina dichotoma</i>	+++	++	+
<i>Ursinia cakilefolia</i>	+++	++	+
<i>Tripteris hyoseroides</i>	+++	++	++
<i>Othonna cylindrica</i>	+++	+	+
<i>Senecio niveus</i>	++	+++	+++
<i>Acanthopsis horrida</i>	+++	+++	+++
<i>Blepharis furcata</i>	+++	+++	++

+ the number of symbol indicate the intensity of the reaction

Cellulose is the most abundant plant polysaccharide found in the form of microfibrils in cell walls and mucilage. It is a linear polymer of β -(1-4)-D- glucopyranose units. Different types of cellulose are found depending on the hydrogen bonding and hydrophobic properties. Dry amorphous and fibrous cellulose can absorb considerable amounts of water and becomes soft, flexible and viscous. Some cellulose is water-soluble and does not form a gel but forms open helical coils. Pectin is a heterogeneous grouping of acidic structural polysaccharides with the main molecules being the D-galacturonic acid residues. They do not possess exact structures and are complex. As for cellulose, pectin is a water binder, highly viscous and can form a firm gel when in contact with water (www.lsbu.ac.uk/water/hypec.html).

In all cases, the mucilage of these diaspores contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. This could be due to the presence of microfibrils of cellulose embedded in the pectin compounds forming a complex matrix. However, pectic substances and cellulose are also known to be the main component of the cell wall. In contact with water, hydrolytic enzymes such as pectinase, degrade the cell walls by breaking polymers into small subunits or breaking crosslinks. The reaction to the stains could partly be ascribed to the cell walls being present in the mucilage. There was no relationship between the structural origin of the mucilage and its chemical composition.

6.5 Conclusions

The structural origin and the chemistry of mucilage produced by diaspores are diverse. Diaspores that produce mucilage in the same way do not necessarily have the same chemical composition. Diaspores of myxospermous plant species might produce mucilage in different ways but this function is restricted to epidermal cells and other external appendages like hairs and wings. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions. This study has only given a broad scale of categories of compound that one could expect when working with mucilaginous diaspores. The chemistry of the mucilage is complex and needs a more detailed study to determine the exact type of polysaccharide forming mucilage in each diaspore.

6.6 Appendix 1

Images of microscope slides showing the reaction of mucilage with different stains

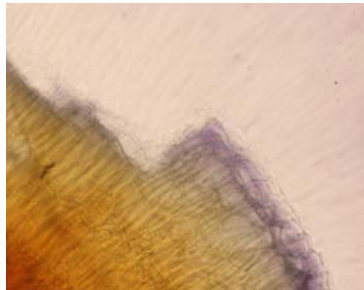
Heliophila thunbergii (Brassicaceae)



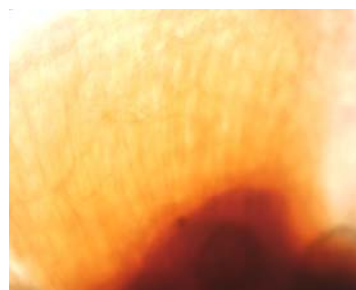
Methylene blue



Ruthenium red



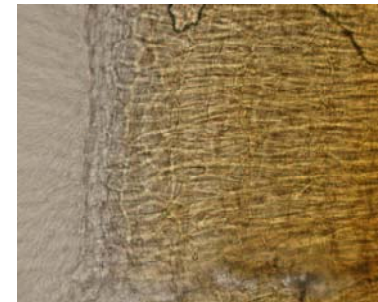
Toluidine blue



Aniline blue



Biuret solution



Phloroglucinol

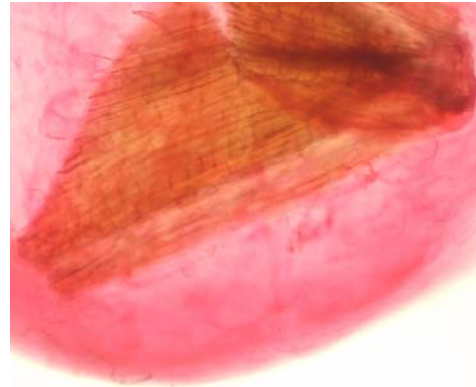


Sudan 4

Cotula barbata (Asteraceae)



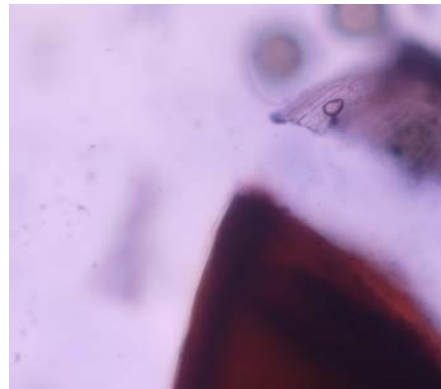
Methylene blue



Ruthenium red

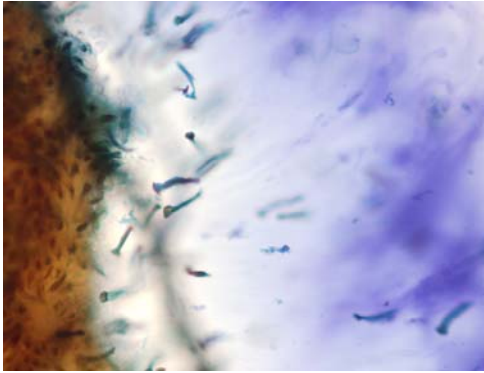


Toluidine blue

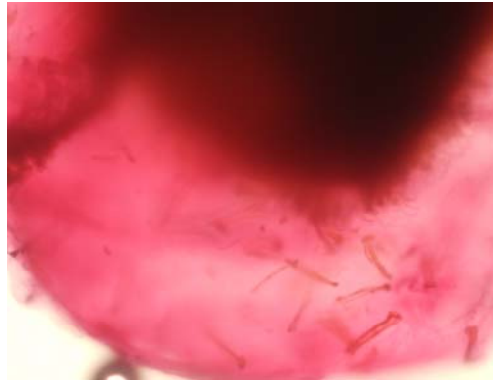


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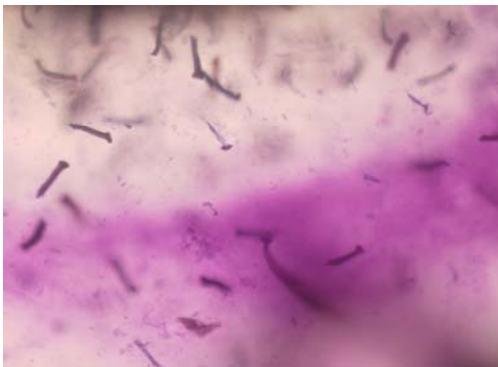
Salvia dentata (Lamiaceae)



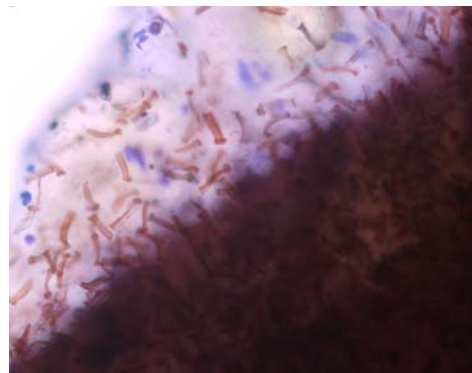
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Ruthenium red



Toluidine blue

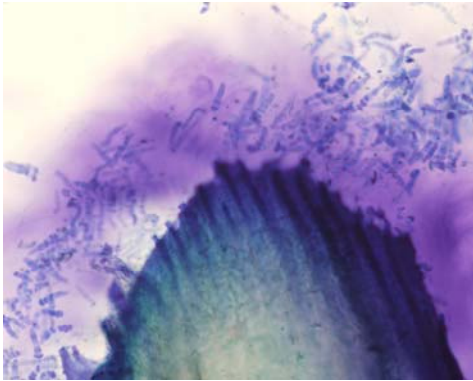


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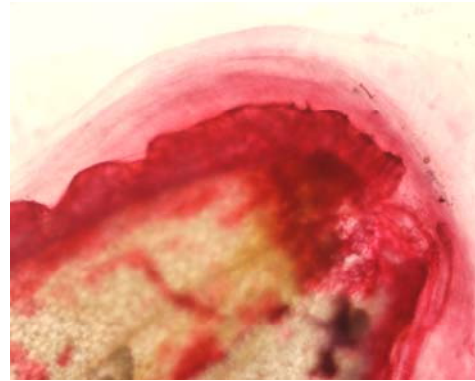


Phloroglucinol

Foveolina dichotoma (Asteraceae)



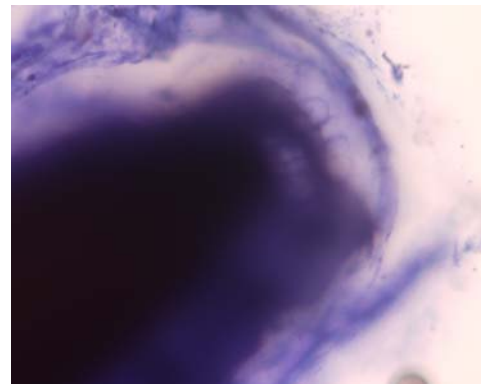
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Ruthenium red



Toluidine blue

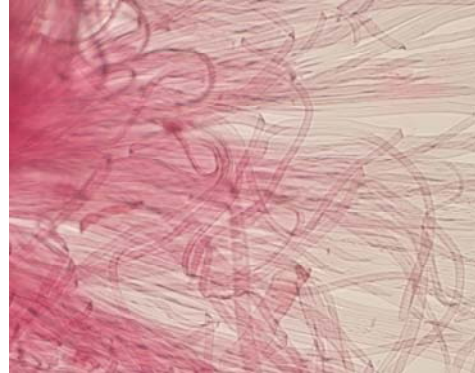


Aniline blue

Ursinia cakilefolia (Asteraceae)



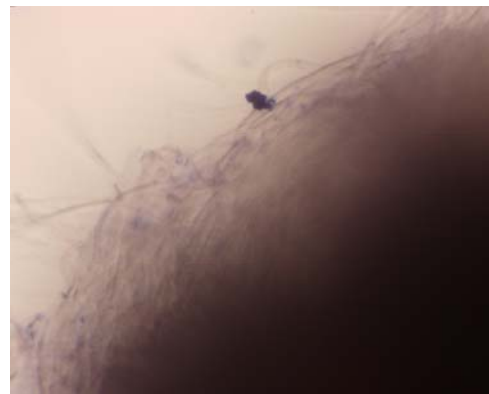
Methylene blue



Ruthenium Red



Toluidine blue



Aniline blue

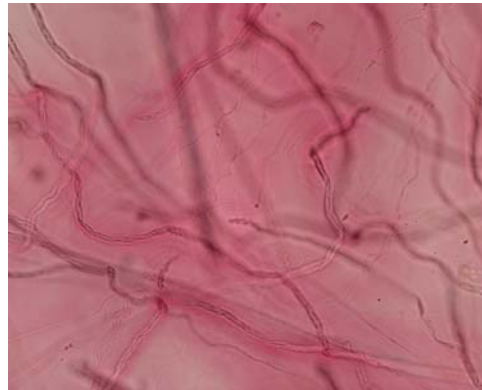


Biuret solution

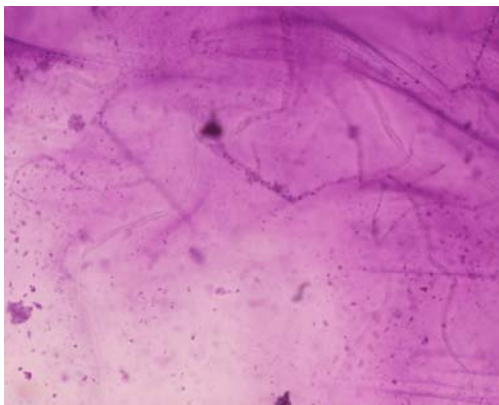
Othonna cylindrica (Asteraceae)



Methylene blue



Ruthenium red

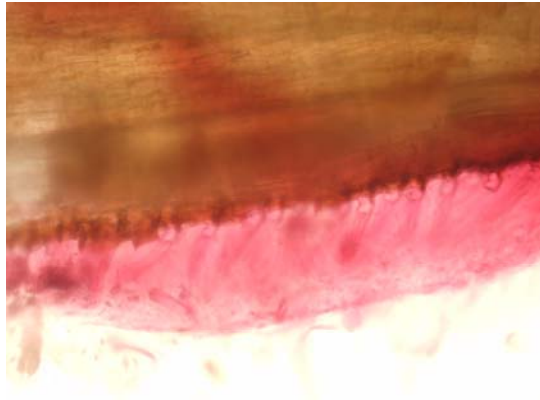


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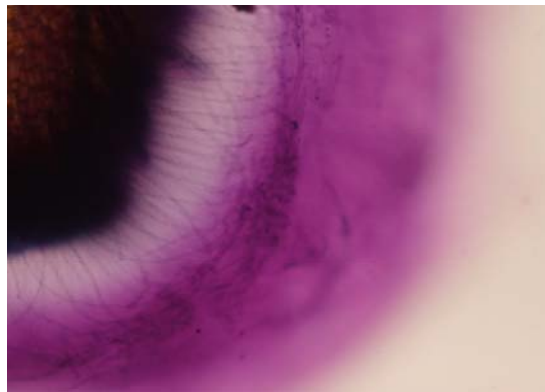


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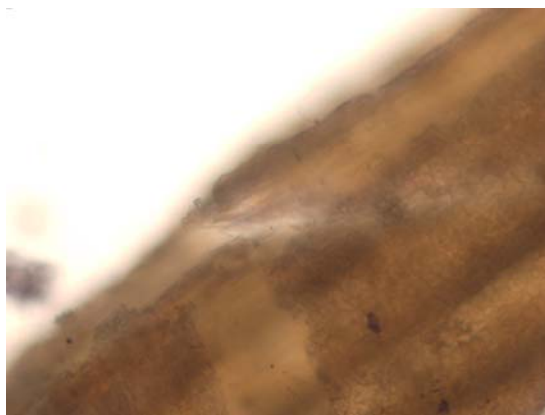
Senecio niveus (Asteraceae)



Ruthenium red

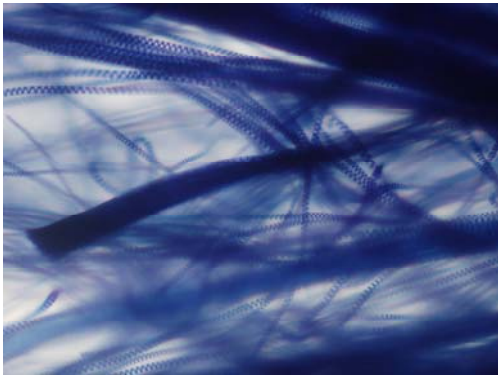


Toluidine blue

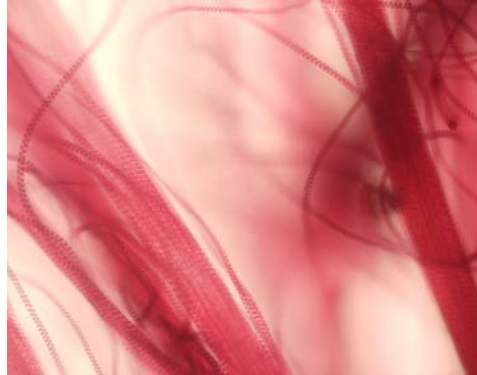


Aniline blue

Acanthopsis horrida (Acanthaceae)



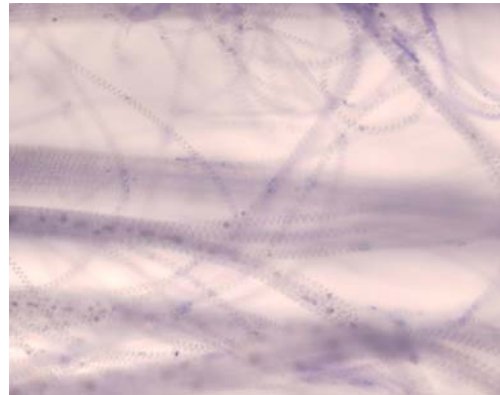
Methylene blue



Ruthenium red



Toluidine blue

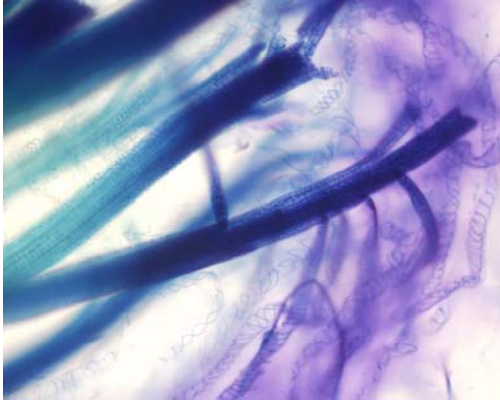


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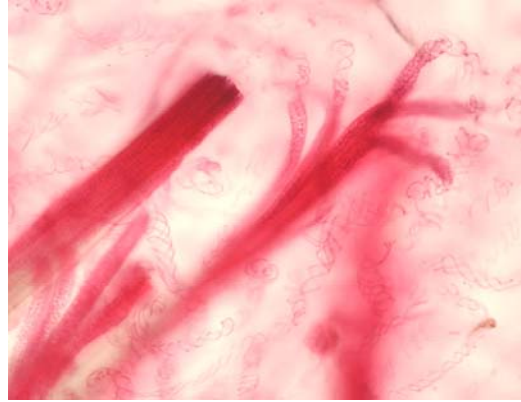


Phloroglucinol

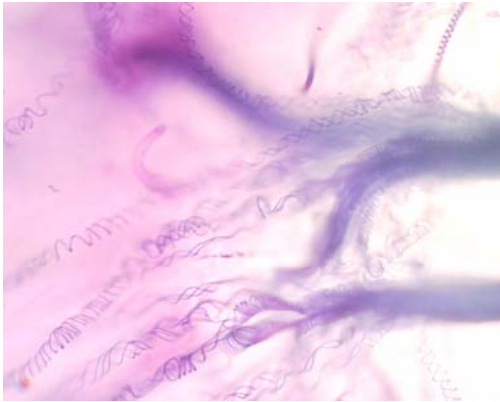
Blepharis furcata (Acanthaceae)



Methylene blue



Ruthenium red



Toluidine blue



Aniline blue



Phloroglucinol

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Chapter 7

General discussion and conclusions

The development of sustainable management systems for dry regions used for stock and crop production need to be underpinned by an understanding of the variety of functional adaptations, which characterize the system. Dispersal and disturbance are significant forces in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Livestock grazing has been identified as a major threat to the biodiversity in the Succulent Karoo Biome.

Based on the concept that vegetation is the most obvious external feature on which to classify ecosystems, a phytosociological classification of the vegetation of the study area was made. The six plant communities found largely reflect differences in land type, although the effect of different grazing intensity on communal and commercial rangeland is not excluded.

The mix of observed dispersal strategies is mirrored in the varied costs and benefits associated with different dispersal modes. In order to compile the dispersal spectra of the study area dispersal types were assigned to each species. The dispersal spectra of the two rangelands and communities were dominated by ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores. Endozoochory was found to be significantly higher in communal land than in commercial land. Ombrohydrochoric, myxospermic, hygrochasic and woolly diaspores were significantly higher in commercial land than in communal land. At community level, endozoochory was significantly higher in the water course community (community 1) than in the plains community (community 3). Autochory and plumed diaspores were significantly lower in the watercourse community than in the sandy valley community (community 2). Ombrohydrochoric, autochoric, hygrochasic and woolly diaspores were significantly higher on the rocky slope community (community 5) and rocky hill community (community 6) than in the water-course community. In general, therefore the water course and sandy valley

communities differed most in their dispersal spectra from the other rockier communities.

Grazing, water, and landscape seem to be the major factors influencing the composition of different dispersal types. Herbivores can be important agents of dispersal for plants, even if they are not primarily seed eaters and their dung provides an ideal environment for germination of seeds and the growth of seedlings. Wind is a regular phenomenon in most desert areas and is minimally modified by vegetation acting as windbreak as is the case with a closed habitat. The lack of significant difference found in most anemochoric dispersal modes between the two rangelands is not surprising as desert plants are characteristically of low stature and allow wind circulation at all height levels. The genus *Eriocephalus* (shrubs) was the most dominant group with woolly diaspores. The low number of individuals with woolly diaspores in communal rangeland can be related to the decrease of *Eriocephalus* plants due to overgrazing by livestock. Furthermore, the movement of diaspores not only depends on the wind velocity but, also on the air humidity which is high in the water course habitat and therefore reduces the efficiency of dispersal. The significantly higher incidence of ombrohydrochory on the commercial land is attributed to the contributions of hygrochasy and trypanospermy. The main advantage of trypanospermy is the enhancement of water uptake due to increased seed-soil contact brought about by the burial of the diaspore. Most hygrochastic species possess a canopy seed bank from which diaspores are slowly released, depending on the amount and frequency of rainfall. This confers an advantage to these species to disperse their seeds at a favourable time for germination. The low number of hygrochasic species in communal land is as a result of indirect and direct effects of overgrazing on plant population dynamics.

Myxospermy was expected to contribute more on communal land than in commercial land given the proposed advantages that mucilage confers to seeds. Mucilage might confers resistance to some types of disturbance it does do not seem to confer resistance to overgrazing. The primary role of mucilage is linked to seed germination and seedling establishment. Although myxospermy acts after rather during the primary dispersal phase. Furthermore, the indirect effect of grazing might also influence the success of myxospermy as changes of the soil microtopography might

influence germination patterns of mucilaginous species. Livestock grazing is commonly considered a disturbance that affects ecological systems, especially if the grazing pressure is high. It may also affect the abiotic environment for example nutrient and water flow and loosening or compaction of the soil. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands. There was not a particular trend for species with telechoric, atelechoric and antitelechoric dispersal groups. Seed germination and seedling establishment are both crucial steps in the life cycle of a plant. The success of a species depends on every step of the life cycle; the interruption of one step might affect the survival negatively.

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid in the management and conservation of arid system. The temperature and light requirements for germination of 23 mucilaginous species of Namaqualand (24 seed types) were investigated. Significantly higher germination percentage in dark treatments were obtained for seven species with the majority being annuals and they all have a low ($\leq 17^{\circ}\text{C}$) optimal germination temperature. Almost half (11 species) of the species investigated required light for optimum germination and all of these species were annuals except the perennial *Tripteris oppositifolia*. The majority of the perennial species investigated and two annuals were not significantly affected by light at various temperatures. Nine species, mostly annuals, obtained significantly shorter mean germination times (days) in light than in the dark. The only perennial species in this group was *Senecio niveus*. Two of the species investigated obtained significantly shorter mean germination times in the dark. Mean germination time was not significantly affected by light in more than 50% of the species. This group included approximately a half of all annuals as well most of the perennial species. The alternating temperature did not show a particular trend in this study. Mucilaginous species have the same germination requirement as most desert species, but their adhesion to the soil (often near the mother plants) provides them with the ability to germinate in a suitable environment. The optimum conditions for germination differed among species, but in general most species obtained their highest germination

percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons. For management purposes keeping livestock on the field during summer months prior to autumn germination could promote the germination of some species because animal movement might bury seeds with negative photoblasty, however, it could also reduce germination of positive photoblastic seed by their burial.

The various ideas that have being suggested about the ecological importance of myxospermy, and its ability to fulfill various functions led to the further investigation of the origin and chemical composition of mucilaginous seeds. The seeds of species of four families were investigated, i.e Acanthaceae, Asteraceae, Brassicaceae and Lamiaceae. Results have suggested three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the cuticle of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs. The chemical composition of the mucilage was found to be very complex and needs a more detailed study to determine the exact type of polysaccharide forming mucilage in each diaspore. However, the mucilage of all these diaspores investigated contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. There was no relationship between family, the origin of the mucilage and its chemical composition. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions.

Understanding the mechanisms of vegetation responses to environmental change is very complex and does not only required a floristic analysis but also the exploration of the multitude of plant functional traits implicated in the internal processes of the community. An in depth knowledge of the standing vegetation, and the various functional traits can aid decision making when considering management practices for conservation or farming.

Chapter 8

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

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12 February 200

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Dispersal strategies in communal versus privately-owned rangeland in Namaqualand, South Africa

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Dispersal and disturbance are significant forces in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale. Livestock is regarded as a disturbance and is major determinant of vegetation dynamics.

The study was carried in Paulshoek, one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape. The site of the present study is a 1 km² section on the southern boundary of the Paulshoek commons and includes another observatory, which extends approximately 1 km from the Paulshoek boundary into one of the adjacent privately owned farms, Remhoogte. Livestock grazing has been identified as a major threat to the biodiversity in the Succulent Karoo Biome. The aim of this study is to compare the dispersal strategies in communal with privately-owned rangeland and further focuses on the importance of myxospermy.

Based on the concept that vegetation is the most obvious external feature on which to classify ecosystems, a phytosociological classification of the vegetation of the study area was made. The six plant communities found largely reflect differences in

land type, although the effect of different grazing intensity on communal and commercial rangeland is not excluded.

The dispersal spectra of the two rangelands and the six communities were dominated by ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores. Grazing, water, and landscape seem to be the major factors influencing the composition of different dispersal types. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands.

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems. The optimum conditions for germination differed among species, but in general most species obtained their highest germination percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons.

The various ideas that have been suggested about the ecological importance of myxospermy, and its ability to fulfill various functions led to the further investigation of the origin and chemical composition of mucilaginous seeds. Results have suggested three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the cuticle of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs. The mucilage of all these diaspores investigated contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions.

Chapter 1

Introduction

The Succulent Karoo hotspot is an extraordinary global biodiversity treasure with over 6 000 plant species of which 40% is found nowhere else on earth. It is the world's most diverse arid environment (Cowling 2003) and occupies 6.5% of South Africa's land surface (Low and Rebelo 1998, Mucina and Rutherford 2006). Climatically the Succulent Karoo separates from the other biomes on the basis of the low annual rainfall, high percentage winter rain, and high absolute and mean minimum temperatures (Desmet and Cowling 1999a).

Despite low population densities in the Succulent Karoo, there are many challenges for conservation in the region. Livestock grazing has been identified as a major threat to the biodiversity in the biome. The livestock industry is based on small stock, especially goats and sheep. The exact mix of goats and sheep in a herd is determined largely by individual farmer preference and suitability of the communal area for different breeds, while on privately owned land, a single landowner usually with one herd of animals manages one or several privately owned farms (Hoffman *et al.* 1999). The mean stocking density for Paulshoek, one of the many communal wards in Namaqualand, over the last 30 years has been approximately 6 ha per small stock unit. This is twice that recommended for the region by the South African Department of Agriculture. In the neighboring commercial rangeland* (Remhoogte) a stocking density of approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999) has been maintained.

Grazing may have a negative impact on plant populations via several mechanisms: by directly increasing mortality, by reducing the competitive ability of grazed plants relative to ungrazed, less palatable plants (Milton *et al.* 1990, Milton 1994), by reducing the reproductive output of grazed individuals or by reducing the success of seedling establishment (Todd 2006, Riginos and Hoffman 2003). The combinations of these effects lead to the loss of palatable species to the benefit of unpalatable species and the replacement of perennial species by annuals and geophytes (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). An increase in species

* The term commercial rangeland as used in this dissertation refers to farming system on privately owned rangeland.

richness as a result of grazing can be interpreted as the outcome of resources becoming available as a result of reduced competition by grazed plants.

The development of sustainable management practices for dry regions used for stock and crop production need to be underpinned by an understanding of the variety of functional adaptations, which characterize the ecosystem. Vegetation is the most obvious external feature on the basis of which ecosystems are defined and classified. Therefore to assess other biological or ecological factors prevailing in an ecosystem, information on vegetation is required.

Dispersal is an important process in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Dispersal is believed to set the template from which community patterns develop (Levine and Murell 2003) and knowledge of seeds dispersal finds applications for purposes of nature conservation and ecological restoration (Strykstra *et al.* 2002). The use of plant functional traits to describe patterns in plant communities provides us with the means to understand the mechanisms of vegetation responses to environmental change which a purely floristic approach does not accomplish. Moreover, such features lend themselves to statistical treatment in the form of spectra, which show the variety, the amplitude and the proportion of the different functions involved in the internal mechanics of the community (Dansereau and Lems 1957).

Seed germination and seedling establishment are the most remarkable and critical stages during a plant's life cycle. Germination is a risky transition, especially in arid climates, between the most drought tolerant stage (the seed) and the weakest stage (the seedling) in plant development (Guttermann 1993). Determining what controls the timing of seed germination in the field requires information on the seed, environmental conditions in the habitat, and how the two interact from the time of seed maturation to germination (Baskin and Baskin 1998). Factors such as temperature, moisture, light, oxygen, nutrients as well as combinations of all play a major part in breaking dormancy and can inhibit, delay, or promote germination. The response to these factors depends on environmental and maternal influences during

seed maturation. This response in turn determines the germination traits of a species (Guterman 1993, Fenner 2000).

The abiotic and biotic environmental factors in arid regions influence the adaptations and survival strategies of plants growing there. Arid areas or habitats are characterized by temperature fluctuations often extending beyond the limiting temperatures for germination, by recurrence of moisture deficiency and sometimes by deficiencies of nutrients in the soil. In addition, rainfall is unpredictable, and precipitation at the beginning of the growing season will not always be followed by enough rainfall for plants to complete their life cycles (El-Sharkawi *et al.* 1989, Philippi 1993). Myxospermy is a trait often associated with arid environments. Mucilaginous diaspores produce copious amounts of mucilage once they come into contact with water. If they dry out, the diaspores adhere to the soil. The origin of the mucilage and factors influencing the germination of mucilaginous seeds are poorly known. Information on the anatomy and the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems.

Aims of this study

Firstly, the study aims to give an overview of the vegetation structure and floristic composition of the communal land Paulshoek and the neighboring commercial farm Remhoogte.

Secondly, it aims to compare dispersal spectra between the communal and commercial land in the study area. Dispersal is one of the crucial steps in a plants life cycle and it is influenced by many environmental factors. A particular type of dispersal might be promoted by the land-use practice in an area.

Thirdly, special attention is given to myxospermy, one of the mechanisms restricting long-range dispersal in plant species. The light and temperature requirements for germination of selected myxospermic plant species of Namaqualand are investigated. Finally, the study also aims to give a detailed anatomical description of mucilaginous diaspores of selected plant species in Namaqualand.

Chapter 2

An overview of the Succulent Karoo Biome

2.1 Location

The Succulent Karoo occupies 6.5% of South Africa's land surface (Low and Rebelo 1998). It extends from the western part of Namibia (26°8'S, 14°56' E) southwards along the western side of the South African escarpment to the eastern border of the Western Cape Province in the Little Karoo (34°S, 23°11'E) (Rutherford 1997, Lombard *et al.* 1999). It forms part of a Greater Cape floristic region rather than part of the Palaeotropical Kingdom, which includes the Nama Karoo Biome (Cowling *et al.* 1999). The Succulent Karoo Biome is one of eight biomes in southern Africa (Mucina *et al.* 2005) and covers approximately 111 000 km² (Mucina and Rutherford 2006).

The altitude of this biome is mostly below 800 m above sea level, but in the east it may reach 1 500 m (Low and Rebelo 1998). The region experiences a low but fairly reliable rainfall (mean 170 mm per annum) with 60% of it received during winter (May to September) (Rutherford and Westfall 1986, Desmet and Cowling 1999a, Milton *et al.* 2003). Some of the eastern areas of the Succulent Karoo Biome may also receive rain at any time of the year (Hilton-Taylor 1996). Summer temperatures are relatively high but winter temperatures are seldom below 0°C (Hoffman 1996, Hilton-Taylor 1996).

The Succulent Karoo Biome is bounded by the Desert, Thicket, Nama Karoo and Fynbos Biomes. In the west it is limited by the cold Atlantic coastline, in the south by the Fynbos Biome and in the east by the Nama Karoo and Thicket Biomes (Palmer and Hoffman, 1997). The Desert Biome forms the northern boundary (Rutherford and Westfall 1986, Milton *et al.* 2003, Mucina and Rutherford 2006).

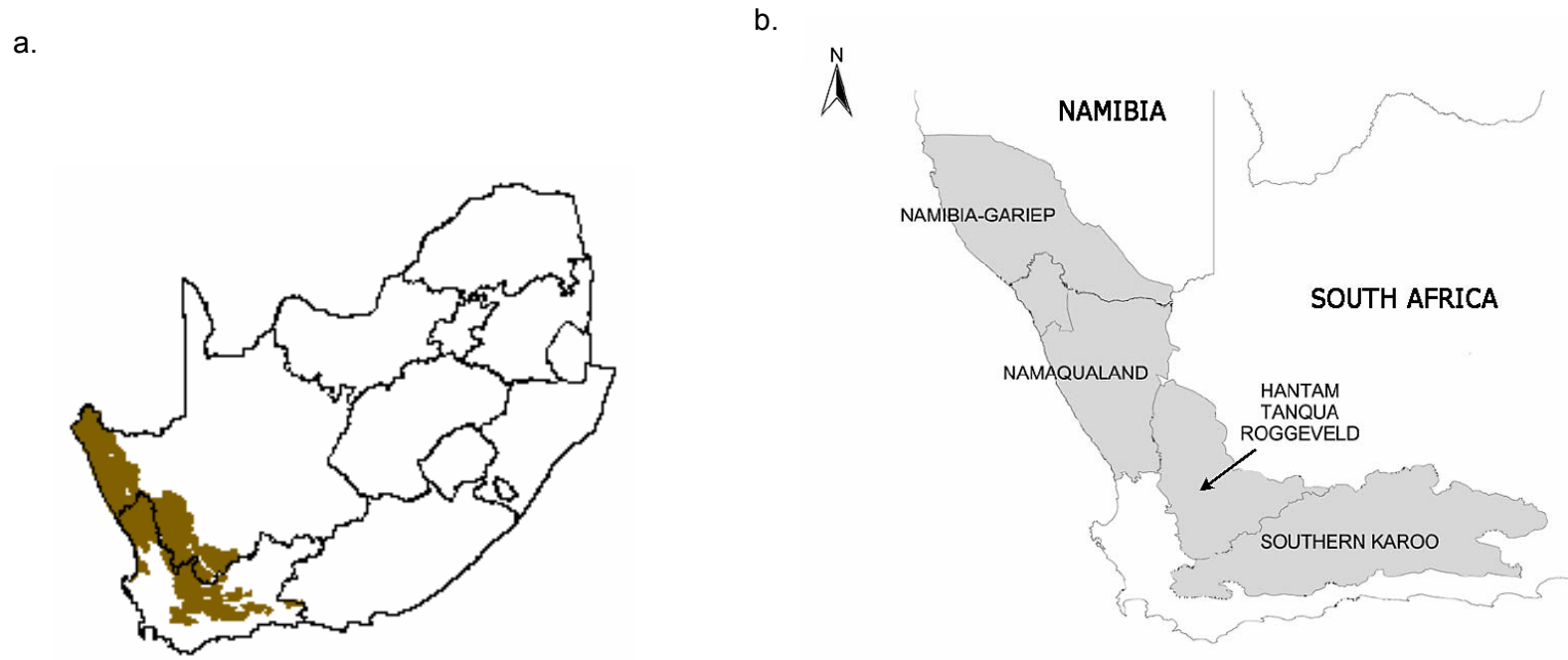


Figure 1.1 The a) location and b) SKEP planning domains of the Succulent Karoo Biome (www.SKEP.org).

Based on the topography, the total amount of rainfall received and the flora, the Succulent Karoo can be divided into 6 bioregions (Mucina and Rutherford 2006). Four of those represent traditional regions of Namaqualand (Richterveld, Namaqualand Harderveld, Namaqualand Sandveld and Knersvlakte), while the other two regions represent a series of units occupying rain shadow, low-altitude valleys and plains (Rainshadow Valley Karoo) and high-altitude semi desert plains, still characterized by prevalent winter-rainfall regime (Trans-Escarpment Succulent Karoo).

The Succulent Karoo Biome has approximately 6 356 plant species (Cowling 2003). Research in the Succulent Karoo Biome has highlighted the unique aspects of this winter rainfall desert compared to other desert with similar climates (Esler *et al.* 1999). For example, the Sonoran Desert has a flora of 2 440 species in an area which is an order of magnitude larger than the Succulent Karoo Biome, while the Sinai Desert has 1 130 species and is 1.2 times the size of the Succulent Karoo Biome (Petersen 2004). In addition to long-lived succulent plant species the Succulent Karoo has a remarkable diversity of short- to medium-lived leaf-succulent shrubs as well as a rich geophyte flora. With more than 40% of its taxa being endemic, and the high local and regional diversity; the Succulent Karoo undoubtedly has the highest level of endemism and diversity for an arid region in the world (Lombard *et al.* 1999, Esler *et al.* 1999).

2.2 Climate

Fine weather in the Succulent Karoo is associated with subtropical anticyclones whereas cold fronts are responsible for the rain during winter. Cold fronts are also associated with inversions of cold air from the south and southwest that produce characteristic cold snaps. At the biome scale, the Succulent Karoo sites separate from the other biomes on the basis of the low annual rainfall, high percentage winter rain, and high absolute and mean minimum temperatures (Desmet and Cowling 1999a).

Rainfall

The Succulent Karoo Biome experiences a broad range in rainfall from 50 to 500 mm per annum. There is a general trend for rainfall to decrease uniformly westwards (Desmet and Cowling 1999a). Most of the area, however, receives a winter rainfall of less than 150 mm per annum. The coefficient of variation of annual rainfall is relatively low and therefore; this low rainfall is relatively predictable. The meager rainfall is supplemented by fog from the Atlantic Ocean and as a result of high humidity and low temperatures, copious dewfalls occur during mid winter (www.gouritz.com, 2006).

The Succulent Karoo Biome is predominantly a winter rainfall area with most of the rainfall received from May to September. In the northeastern, eastern and southeastern parts of this biome it grades into summer rainfall. Although most of the rainfall is received in the winter months there can be great variability in monthly rainfall peaks. Even though the mean annual rainfall might be the same in some areas, within the biome, there is a great variation in the temporal distribution of rainfall (Desmet and Cowling 1999a).

Temperature

High temperatures, low relative humidity and little to no cloud cover are characteristic of this biome, which result in large annual and daily ranges of temperature. These are general characteristics of arid climates (Desmet and Cowling 1999a). However, along the west coast where there is an abundance of moisture in the air due to the predominantly onshore breeze, relative humidity is high, and temperature is regulated by the cold Benguela current (Desmet and Cowling 1999a). Mean daily minimum temperatures are highest along the west coast and increase as one moves toward the equator. In winter temperatures are mild, but occasional frosts occur on upland peaks. In summer temperatures in excess of 40°C are common. These temperatures are usually recorded when hot, turbulent air, known as “berg wind”, descends coastward from the high altitude plateau of southern Africa (Low and Rebelo 1998).

Compared to the Nama Karoo Biome, the Succulent Karoo has moderate temperatures which drop no lower than 5°C on typical winter nights and reach 15°C or more on winter days (Desmet and Cowling 1999a).

2.3 Vegetation of the Succulent Karoo

The vegetation is dominated by dwarf, succulent shrubs of which the vygies (Mesembryanthemaceae now included in the Aizoaceae) and stonecrops (Crassulaceae) are particularly prominent. Therophytes and geophytes are also common. The vegetation of the Succulent Karoo can be described as an open to sparse (15 to 50% canopy cover), low to dwarf (usually less than 1 m tall) shrubland (Hilton-Taylor 1994). During spring, especially in disturbed areas there are spectacular masses of flowering annuals (mainly Asteraceae, Brassicaceae and Scrophulariaceae) (Van Rooyen *et al.* 1992). Small trees or large shrubs (less than 3 m tall) (e.g. *Diospyros ramulosa*, *Lebeckia sericea* and *Rhus undulata*), occur on rocky outcrops and along river courses. Grasses seldom dominate in this biome (Hilton-Taylor 1994, Milton and Hoffman 1994). Acocks (1988) maintains that low grass cover is a result of overgrazing and that grasses were important prior to the European settlement.

Diversity and endemism

The Succulent Karoo contains a number of areas with concentrations of endemic species. This region is considered as one of the earth's hotspots; it is one of only two entirely arid hotspots. The flora of the Succulent Karoo Biome is unusual, both in terms of taxonomic composition and growth form mix (Desmet and Cowling 1999b). It includes 730 genera of which 67 are endemic. This is more than three times the number of endemic genera in the Arabian Sahara and North American arid lands which are an order of magnitude larger than the Succulent Karoo (Cowling and Hilton-Taylor 1999).

Not only is the total diversity high, but the Succulent Karoo also supports the richest succulent flora of the earth. Succulents make up to 29% of all plant species in the biome. The world's highest local diversity of succulents was recorded in the

mountainous desert of the Gariep area, with over 330 species in an area of just 1.3 km² (Cowling 2003). This biome has about 40% of the world's approximately 10 000 succulent species (Van Jaarsveld 1987, Smith *et al.* 1993). Succulents are associated with many of the larger families such as Aizoaceae, Asteraceae, Liliaceae, Crassulaceae, Geraniaceae, Euphorbiaceae and Asclepiadaceae.

Another remarkable group of plants in the Succulent Karoo is the geophytes. The remarkable diversity of geophytes can be seen clearly in the flora of the Goegap Nature Reserve near Springbok where they make up to 19% of the flora (Van Rooyen *et al.* 1990). In contrast, the diversity and importance of geophytes in all of the other four Mediterranean regions of the world drop off sharply as one move into winter rainfall desert regions (Rundel 1996). For example, geophytes comprise only about 1% of the floras of the winter rainfall Mojave and Sonoran Deserts in North America, and a similarly small fraction in the winter rainfall regions of the northern Sahara Desert and areas of Western Australia (Rundel 1996).

The Succulent Karoo Biome has very few affinities with other arid land floras of the world (Shmida 1985). There is a general consensus that the Succulent Karoo flora is largely derived from an ancient Cape stock (Acocks 1988, Cowling and Hilton-Taylor 1999) and shares more than half of its taxa and three quarters of the large genera with the Fynbos (Gibbs Russell 1987, Van Wyk and Smith 2001). At community scale species richness of perennial plants is unusually high in the Succulent Karoo compared with the Nama Karoo, or with other parts of the world that have a similar climate (Milton *et al.* 2003). The Succulent Karoo is closely related to the Fynbos Biome. Born *et al.* (2007) argue for the recognition of a Greater Cape Floristic region which includes all the winter rainfall areas, i.e. the Fynbos, Namaqualand region and the Hantam-Tanqua-Roggeveld region.

2.4 Vegetation and phytosociological research in the Succulent Karoo Biome

Many ecological studies have been completed in the Succulent Karoo Biome. One of the earliest attempts to describe the vegetation in a part of the Succulent Karoo was that of Adamson (1938) in the Kamiesberg. The first recognized phytosociological

study in the Succulent Karoo Biome was undertaken almost fifty years after Adamson's first description in 1938 by Le Roux (1984) who worked in the Goegap Nature Reserve. Phytosociological research continued in the Succulent Karoo Biome through the work of Lloyd (1985) in Vaalputs. This site is situated approximately 100 km southeast of Springbok. The study area is located in a transition zone between the Nama Karoo and Succulent Karoo Biome (Petersen 2004).

In 1990 Smitherman and Perry contributed to the ongoing phytosociological research in the Succulent Karoo through the completion of their study in the Karoo National Botanical Gardens. This study site is ± 2 km north of Worcester between the flats of the Breede River Valley and the Hex River Mountains. Milton *et al.* (1992) completed another descriptive vegetation study at Tierberg. The Tierberg Karoo Research Centre is situated on the southern edge of the Great Karoo and is transitional between the Succulent Karoo and the Nama Karoo. In 1996 Desmet completed a phytosociological study on the western arid coastal belt of the Succulent Karoo Biome. The study site is located between Port Nolloth and Alexander Bay and covers a narrow band, approximately 10 km wide along the coast. This study site falls within the southern zone of the Namib Desert and is one of five west coast deserts in the world lying within subtropical latitudes (Petersen 2004). De Villiers *et al.* (1999) studied the vegetation diversity at Brand-se-Baai on the Namaqualand coast, some 350 km north of Cape Town and about 80 km northwest of the nearest town, Vredendal.

The most recent phytosociological study was done by Petersen (2004). Her study area was situated at Paulshoek, one of the nine villages in the Leliefontein Communal Reserve in Namaqualand. Leliefontein is in the Kamiesberg, an escarpment at 900 to 1 500 m above sea level, about 50 km wide between the low-lying Sandveld in the west and the Bushmanland plateau in the east. A section of the Paulshoek commons is also the focus of the present study.

Petersen (2004) stratified the Paulshoek area into three altitude classes: 900 to 1 120 m above sea level corresponding broadly with the lowlands, >1 120 to 1 200 m above sea level constituting mid slopes and 1 200 to 1 400 m above sea level

comprising the upper slopes and crest. Four plant communities were identified and landscapes seemed to be the driving factor (Petersen 2004). The *Galenia africana* community was restricted to the low-lying flats and footslopes and was dominated by *Hermannia cuneifolia*, *Galenia africana*, *Hypertelis salsoloides* and *Drosanthemum floribundum*. The *Ruschia robusta* community was found on the footslopes and mid-slopes of the mountains and was dominated by *Ruschia robusta*, *Hallianthus planus*, *Crassula subaphylla* and *Eriocephalus microphyllus*. The *Pteronia glomerata* community on mid- and upper-slopes with high rock cover, was dominated by *Pteronia glomerata*, *Pteronia laterifolius*, *Eriocephalus microphyllus*, *Pelargonium karooicum*, *Asparagus capensis*, *Leipoldtia schultzei*, *Hallianthus planus*, *Ruschia robusta*, and *Rhus burchelli*. The *Diospyros austro-africana* community was restricted to the upper-slopes and crests which is the area receiving the highest annual rainfall for the entire area. It was dominated by *Diospyros austro-africana*, *Antizoma miersiana*, *Lebeckia multiflora*, *Dicerotheramnus rhinocerotis*, *Osteospermum rigidum*, *Pteronia glomerata*, *Ruschia lerouxii* and *Ruschia viridifolia*.

2.5 Conservation status of the Succulent Karoo Biome

The high species richness and unique global status of the biome require urgent conservation attention (Low and Rebelo 1998, Cowling and Hilton-Taylor 1999, Lombard *et al.* 1999). The conservation status of the biome has increased from 2% (Lombard *et al.* 1999) to 5.8% or 6 500 km² formally protected in statutory and nonstatutory reserves (Mucina and Rutherford 2006). However this area still substantially under-represents the diversity associated with the biome as it does not incorporate key ecological processes and evolutionary biodiversity drivers which include riverine and sand movement corridors, quartz patches, edaphic interfaces, climatic and upland-lowlands gradients (Mucina and Rutherford. 2006).

National parks and large reserves represent only four of the 12 bioregions (Lombard *et al.* 1999). Nationally protected areas are in the Gariep Centre (Richtersveld National Park), the Tanqua Karoo (Tankwa Karoo National Park) and the Namaqua Rocky Hills (Namaqua National Park) (Lombard *et al.* 1999). The Namaqua National park (previously Skilpad Wild Flower Reserve) now covers more than 70 000

hectares of land that was bought under the auspices of the Leslie Hill Succulent Karoo Trust. A number of provincial, local authority and private reserves occur within the Western Mountain Karoo, Bokkeveld/Olifants River/Biedou bioregion, Worcester-Robertson Karoo and Little Karoo.

Most of the region, an estimated 100 000 km², is used as communal or commercial grazing. Although this land-use can be compatible with the maintenance of biodiversity, overgrazing has severely degraded as much as two-thirds of this area (Cowling 2003). Recovery from overgrazing is not possible in a short time frame of a few decades due to the lack of dormant seeds, short dispersal distances, or the exclusion through competition by other perennials that have filled the spaces left by the demise of palatable species (Milton and Hoffman 1994). The recent expansion of the ostrich farming industry has devastated thousands of hectares in the Little Karoo, and is likely to pose a greater threat in the future. Mining and agriculture along river corridors have also had a significant impact on the region and are likely to expand in the future. Succulent species are highly prized by collectors and are threatened by illegal collection and trade (Cowling 2003). Ecotourism has good potential, as an alternative form of income generation in this biome. However, it requires that the area be properly used and managed (Lombard *et al.* 1999).

As a signatory to the Convention on Biological Diversity (United Nations Conference on Environment and Development, Rio de Janeiro, 1992), South Africa is committed to conserve its exceptionally high biodiversity. The Succulent Karoo has been identified as one of the least conserved biomes (Rutherford and Westfall 1986, Low and Rebelo 1998) and requires a large proportion of additional reserves to protect its flora.

The Succulent Karoo Ecosystem Planning Project (SKEP) has provided a 20 year vision to attempt to improve conservation management in the region. They have identified that large, conservation-worthy tracts of land are owned and used by private mining, agricultural and tour companies, as well as by communities and private farmers. There is a need to develop mechanisms to stimulate the participation of these sectors in the development of conservation areas and to

promote and facilitate innovative programs that involve local land owners in the creation of effective conservation areas within the Succulent Karoo (Cowling 2003).

2.6 Land-use practices in the Succulent Karoo Biome

A summary of historical practice and general chronology for the region is provided below, based on Hoffman *et al.* (1999). Hoffman (1997) believes it is important to reflect on these impacts in order to understand the vegetation patterns and trends of the past.

Pre-colonial period

San hunter-gathers have been in the Succulent Karoo for more than 300 000 years. Their main activity involved hunting, gathering and in some cases fishing. Although the Succulent Karoo appears to be a dry and harsh environment today with no underground water being available, in the past it was not a stumbling block to human habitation. People knew where to find water, even if they had to dig in dry riverbeds or for underground water-bearing plants to get it. Only since the end of the nineteenth century have underground aquifers been tapped by wind-driven pumps (Smith 1999). This area is dry and any rainfall event creates a micro-environment for animals. Khoikhoi were pastoralists and engaged in transhumance movement in order to exploit the seasonal differences in the availability of grazing and water resources (Hoffman *et al.* 1999).

Early colonial period

European settlement in the Succulent Karoo began around the middle of the eighteenth century (Van der Merwe 1988), and by the end of the eighteenth century there was a rapid expansion and most of the Cape Colony was occupied by colonial farmers. European colonization and settlement disrupted indigenous social structures and in this process the Khoikhoi pastoralists were forced to slavery or serfdom. By the end of the nineteenth century, private property and commercial

livestock production slowly became dominant and the pastoralist economy of the Khoikhoi became confined to the mission stations (Hoffman *et al.* 1999).

Twentieth century

The confinement to the mission stations and reserves severely constrained the Khoikhoi's ability to move with their herds or to engage in transhumance. To secure an income they started to move to the copper and diamond mines which were opened in the region from the mid-nineteenth century. For many residents, local agricultural production gradually assumed the character of supplementing and remittances (Hoffman *et al.* 1999).

2.7 Current land-use practices

There are two main agricultural production systems in the Succulent Karoo with widely differing histories, forms of land tenure, institutional arrangements, land-use practices and production objectives. The communal property regime allows residents of communal land to obtain rights to the use of natural resources if they are "registered occupiers". In contrast to the privately owned land or commercial land, communal areas have more than one farmer with various herds of different sizes. Each farmer within the communal system has his own management strategy, which he undertakes within a confined area of the commons (Hoffman *et al.* 1999).

The livestock industry on communal land is based in small stock, especially goats and sheep. The exact mix of goats and sheep in a herd is determined largely by individual farmer's preference and suitability of the communal area for different breeds. In the last 26 years stock numbers in Paulshoek have averaged nearly twice the recommended stocking density. Livestock production objectives within the communal farming systems in the Succulent Karoo are numerous, as farmers not only keep animals for consumption and selling, but also as an investment (Hoffman *et al.* 1999).

On privately owned land, a single landowner, with one herd of animals, manages one or several privately owned farms. Here the major objective is maximization of total cash income. Since the late 1960s, when extended droughts together with state intervention schemes such as the Stock Reduction schemes, reduced animal numbers (Hoffman *et al.* 1999) farmers of privately owned land have been stocking at densities recommended by the Department of Agriculture.

Several studies that have compared different biological and physical components in communal (Paulshoek) and the adjacent commercial land have highlighted a decrease of species richness on communal land. Todd and Hoffman (1999), Riginos and Hoffman (2003) and Petersen (2004) have suggested that heavy grazing on the communal land has resulted in a reduction in total vegetation cover and altered the dominance of perennials in favour of annuals and geophytes. However, they did not find any significant difference in the mean number of species per relevé.

Chapter 3

A comparison of the vegetation in communal versus commercial land in Leliefontein, Namaqualand, South Africa

3.1 Introduction

Heavy grazing is considered to be among the main threats to floristic diversity of arid and semi-arid regions world wide (Riginos and Hoffman 2003). However, some studies have shown that grazing does and some that it does not affect plant diversity; these contrasting patterns of response have frequently been attributed to differences in grazing intensity (Osem *et al.* 2002).

Grazing can have a negative impact on plant populations through several mechanisms: by directly increasing mortality, by reducing the competitive ability of grazed plants relative to ungrazed, less palatable plants (Milton *et al.* 1990, Milton 1994), by reducing the reproductive productivity of grazed individuals and the success of seedling establishment (Riginos and Hoffman 2003, Todd 2006). The grouping of these effects leads to the loss of palatable species to the advantage of unpalatable species and the substitution of perennial species by annuals and geophytes (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). A boost in species richness as a result of grazing can be interpreted as the outcome of resources becoming available as a consequence of reduced competition by grazed plants.

The improvement of sustainable management practices for dry regions used for stock and crop production needs to be underpinned by an understanding of the diversity of functional adaptations, which characterize the ecosystem. Vegetation is the most conspicuous external feature on the basis of which ecosystems are defined and classified. Therefore to assess other biological or ecological factors prevailing in an ecosystem, information on vegetation is required.

Since the beginning of the twentieth century, different methods of floristic analysis have been developed. These approaches developed into four major schools; the Zürich-Montpellier school, Uppsala School, the Raunkaier School and the Hybrid

Schools (Kent and Coker 1992). These schools use a subjective classification because the site of the vegetation sampling, the relevé is not chosen randomly, but is carefully selected as a representative area of a particular vegetation type (Kent and Coker 1992). Although the various schools did initially have differences in their approach; most methodology has now converged on the technique of the Zürich-Montpellier school. All these schools of thought are based on the community unit concept, which suggests that vegetation consists of plant communities. The plant community can be defined as the collection of plant species growing together in a particular location that show a definite association or affinity with each other.

The BIOTA* Africa network, uses a joint interdisciplinary and integrative approach to analyse changes in biodiversity and to gain knowledge for decision makers for feasible and sustainable land-use management (www.biota.africa.org). This study forms part of the BIOTA “Subproject S06” of phase II which aims to analyse biodiversity changes caused by human land-use and climate change. For this purpose long-term monitoring vegetation data are collected at selected sites in the Succulent Karoo to compare the effects of land-use practices.

3.2 Study area

3.2.1 Location

The study site is located near Paulshoek (30°20'S, 18°15'E), one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape (Figure 3.1). Paulshoek is a remote village about 50 km east of Garies and is situated in the eastern foothills of the Kamiesberg Mountain Range. The communal land of Paulshoek covers approximately 20 000 ha (Riginos and Hoffman 2003) and lies at an altitude from 980 to 1 400 m above sea level (Todd and Hoffman 1999). The Paulshoek commons is fenced on three sides by commercial farms. The site of the present study is a 1 km² section (called an observatory) on the southern boundary of the Paulshoek commons. The study site includes another observatory (1 km² section), which extends approximately 1 km from the Paulshoek boundary into one of the adjacent privately owned farms, Remhoogte (southeast from Paulshoek village).

*BIOTA = Biodiversity Monitoring Transect Analysis in Africa

a)

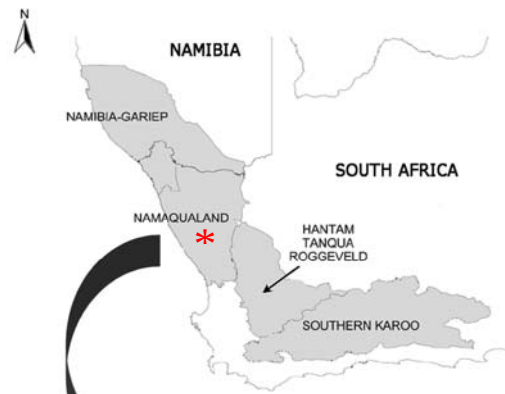


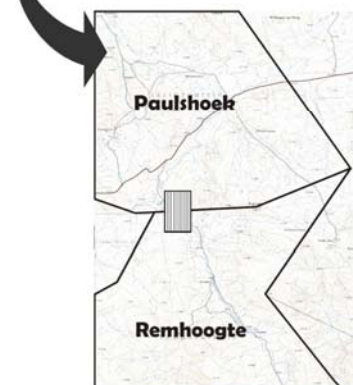
Figure 3.1 a) The Succulent Karoo Biome (shaded area) with location of study area (*).

b) The location of the study area (shaded part in Fig 3.1b).

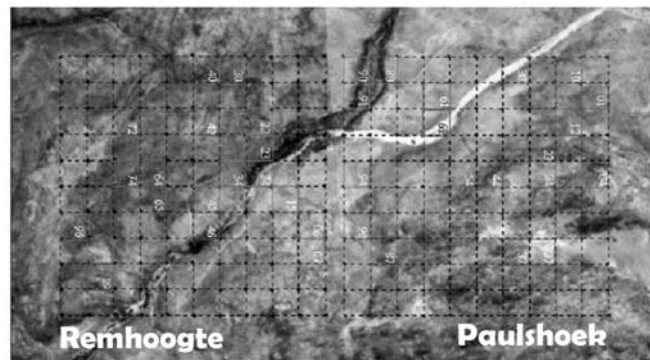
c) An aerial photograph of the two observatories on Paulshoek and Remhoogte.

d) Vegetation on the two observatories

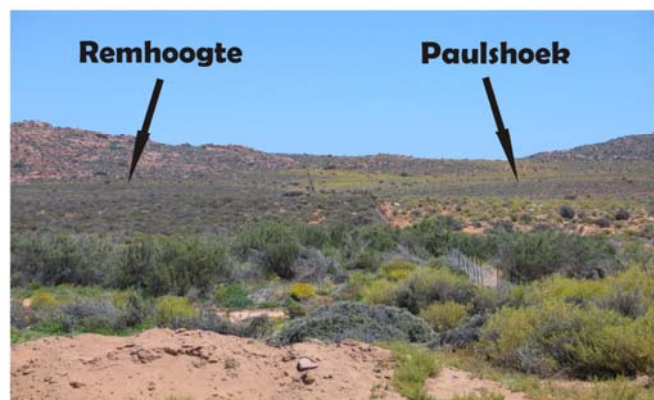
b)



c)



d)



The mean stocking density for Paulshoek over the last 30 years has been approximately 6 ha per small stock unit; which is twice that recommended for the region by the South African Department of Agriculture. Local commercial farmers maintain stocking densities of approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999). The grazing regime on the communal land is characterized by heavy and continuous grazing, whereas the neighboring commercial rangeland is moderately and rotationally grazed (Todd and Hoffman 1999, Petersen 2004).

3.2.2 Topography

The Remhoogte observatory is located predominantly in Land Type Ib132, whereas the western part of the Paulshoek observatory is classified as Land Type Ib132, but the eastern part is classified as Land Type Ib274 (Fitzpatrick *et al.* 1987). Both Land Types are characterized by terrain units 1, 3, 4 and 5. The steep mountain slopes cover around 20% of the study area and are characterized by big gneiss boulders and domes. The midslope is convex with 70% rock cover and occupies 60% of the area. The footslope and the valley are alternate in some area and have a very low rock cover (<20%). The slope shape varies from concave to straight (Fitzpatrick *et al.* 1987).

3.2.3 Geology

The geology of the study site forms part of the Namaqualand Metamorphic Province. It is part of the assemblage represented by medium to high grade infrastructural gneisses and granitoids associated with metamorphosed supracrustal rocks (Saggerson and Turner 1995). The Little Namaqualand Suite comprises a silicious series of augen gneisses (Blignaut 1977). The augen gneisses weather to a pink colour, on fresh surfaces. The principal component of augen gneiss being aggregates of quartz, plagioclase, alkali feldspars and opaque minerals (Jack 1980). Rocks are cross-bedded sandstones with a granular appearance where the feldspar has been altered and weathered out. Superficial deposits of fine-grained quartz conglomerates, shales and sandstones overlie the valley bottoms (Jack 1980).

3.2.4 Soils

The large gneiss domes, characteristic of the Succulent Karoo Biome, break down into gravel and coarse sand, which dominate the Paulshoek area. Burke (2002) suggested that soils derived from granite are generally low in clay and silt. The soils are thus coarse, with a particle size of greater than 0.1 mm, allowing rapid infiltration but with low water holding capacity (Milton and Dean 1996). The soil of Paulshoek is generally infertile. The nitrogen content is around 350 µg/g, total phosphorus of 154 µg/g, soil organic matter is 1.55% and pH ranged from 6.5 to 7.9 (Allsopp 1999). Petersen (2004) reported little evidence of soil erosion on Paulshoek except for shallow run-off gullies along some of the major footpaths and tracks. The soil in this area generally appears stable in relation to wind or water erosion despite the large bare and exposed areas. The soil becomes more vulnerable to erosion when disturbed by ploughing or footpaths. There has been no formal measurement of the extent of soil loss in the area.

3.2.5 Climate

Climate data were collected at the BIOTA weather station at the study site situated between the two 1 km² observatories. The data were collected for the period of April 2001 to February 2006. The monthly mean of various climatic parameters are represented in Table 3.1.

Table 3.1 Climate data recorded by BIOTA South from April 2001 to February 2006 at Paulshoek/Remhoogte (Observatories 24 and 25)*. Data include mean monthly values for air temperature (°C), relative air humidity (%), soil temperature (°C) at 10cm soil depth, wind speed (m/s), Rainfall (mm) and wind direction (0° = N; 90° = E; 180° = S; 270° = W)

Months	Mean monthly air temperature (°C)	Mean monthly minimum air temperature (°C)	Mean monthly maximum air temperature (°C)	Air relative humidity (%)	Soil temperature (°C)	Wind speed (m/s)	Rain (mm)	Wind direction
Jan	21.5	12.0	30.9	52.0	31.2	2.65	18.9	S
Feb	23.0	14.0	33.2	49.2	31.8	2.53	6.6	SW
March	20.1	12.2	30.08	55.8	28.2	2.40	9.6	NW-SW
April	17.5	10.25	26.31	60.2	22.8	2.35	28.0	N
May	13.8	12.2	22.9	62.8	16.3	2.18	7.6	NW
June	10.1	3.5	18.0	68.8	12.7	2.10	11.1	NW
July	10.0	3.3	18.3	62.5	11.3	2.10	19.7	N
Aug	10.2	3.4	19.2	69.3	14.2	2.50	14.1	NW
Sept	14.0	6.3	23.0	57.6	18.3	2.32	7.7	NW
Oct	16.5	7.0	26.3	53.4	22.7	2.40	21.8	N
Nov	18.8	10.2	28.4	51.4	27.7	2.60	17.4	S
Dec	20.3	10.3	30.2	51.0	31.5	2.72	6.8	S
Year	16.3						169.3	

* Data supplied by Ute Schmiedel, Institute of General Botany, University of Hamburg; Klaus Berger, Institute of Soil Science, University of Hamburg.

Rainfall

Rainfall spanning more than 100 years shows that the region is subject to periodic episodes of high rainfall which can be more than 100% above the mean, also to episodic droughts (Desmet and Cowling 1999a). Long-term records show that the majority of rain is received during the winter months (May to September) and occurs as a result of circumpolar frontal westerlies. The mean annual rainfall at

Kamieskroon is 230 mm (Mucina and Rutherford 2006) which is higher than the mean annual rainfall of 169.3 (Table 3.1) recorded by BIOTA in Paulshoek. Because Paulshoek lies on the ecotone between the summer and winter rainfall regions, it occasionally enjoys summer rainfall from thundershowers from the east. Climatic models produced by the Institute for Soil, Climate and Water suggest that the region to the northwest of Paulshoek has significantly higher rainfall (250 mm/per annum) (National Botanic Institute Claremont, South Africa) (www.maposda.net/global'report/pdf/1.satasko.pdf, 2005).

Paulshoek has a high degree of local rainfall variability despite the fact that the Succulent Karoo Biome generally has a low coefficient of variation (Hoffman and Cowling 1987, Desmet and Cowling 1999a). Winter rains are mainly received from the rain bearing winds from the northwest, especially from May to September when large frontal systems sweep past the sub-continent bringing rain to a large part of the region. During autumn and spring monthly rainfall is at its most unpredictable in Paulshoek, and large downpours can result from a single event which is usually associated with southwesterly winds and cut-off lows (Desmet and Cowling 1999a).

Fog can be an important alternative source of moisture for plants along the west coast. Although generally no direct precipitation of water occurs on the soil surface, interception by vegetation may lead to a significant amount of water entering the soil below the plant (Desmet and Cowling 1999a). The occurrence of fog in Paulshoek is relatively insignificant and is generally confined to the high-lying western part of the Kamiesberg and the low-lying valleys to the south of the village (Petersen 2004).

Temperature

Winter months in Paulshoek are surprisingly cold probably because of relatively high altitudes. The mean annual temperature is 16.3°C (Table 3.1). The mean monthly maximum temperature reaches 33.2°C in the summer (February) while the mean minimum temperature falls to 3.3°C in the winter months (July). There is a dramatic fluctuation of daily temperature between September and October (from 8.9 to 36.6°C from BIOTA data) which can be disastrous for livestock owners. These critical extremes in the climate affect livestock and crop production in this area and have

had a significant influence on the way in which people manage their natural resources (Petersen 2004).

3.2.6 Vegetation

The study area is situated within the Succulent Karoo Biome (Rutherford and Westfall 1986). Petersen (2004) described the vegetation of Paulshoek as dominated by two major vegetation types, which are closely associated with the geomorphological features of the area. In the south- to east-facing upper slopes, the large granite domes support tall shrubland dominated by a mixture of non-succulent genera such as *Eriocephalus*, *Euclea*, *Hermannia*, *Lebeckia*, *Pteronia*, *Rhus*, and succulent genera such as *Euphorbia*, *Ruschia*, *Tylecodon*. This vegetation agree with what was described as Mountain Renosterbosveld (VT 43) by Acocks (1953, 1988), and Northwestern Mountain Renosterveld (LR 59) by Low and Rebelo (1998). Mucina *et al.* (2005) describe it as Namaqualand Granite Renosterveld (FRg1). The second major type is found on flat or gently sloping rock sheets and is dominated by dwarf evergreen shrubs such as *Pentzia incana* and the poisonous kraalbos *Galenia africana* or prostrate succulents. It also covers the wide plains and broad valleys with dry water courses This dwarf shrubland contains many succulents such as *Ruschia robusta*, plants with ericoid leaves (e.g. Asteraceae), geophytes and ephemeral herbs and forms part of Acocks's (1953) Namaqualand Broken Veld (VT33), or Upland Succulent Karoo (LR 56) by Low and Rebelo (1998). Mucina *et al.* (2005) recognised three vegetation types in this area: a) the plains and broad valleys with dry water courses is described as Namaqualand Blomveld (SKn3) b) the flat, gently sloping rock sheet is described as Namaqualand Klipkoppe Shrubland (SKn 1) and c) steep slopes of the large granite domes described as Kamiesberg Mountains Shrubland(Skn6)

The area covered by observatories falls entirely within Acocks (1953) classified as Namaqualand Broken Veld and Low and Rebelo (1998) as Upland Succulent Karoo. According to the more detailed classification of Mucina and Rutherford (2006) the Namaqualand Blomveld covers the western part of the observatories, with the Namaqualand Klipkoppe Shrubland in the eastern part. A small section in the

northeastern corner of the Paulshoek observatory falls in the Kamiesberg Mountain Shrubland.

3.3 Methods

An observatory can be defined as a permanent study area of 1 km² which was chosen by the BIOTA task team based on certain ecological and biological characteristics. An observatory is further subdivided into plots and subplots of different sizes and are monitored each year. Vegetation surveys were done by the task team of BIOTA in 2002, 2003, 2004. The layout of each 1 km² observatory is presented in Figure 3.2. The individual hectares in each observatory were ranked according to habitat type and the 20 highest ranking hectares were selected for the vegetation survey. Ranking was done so that a minimum of three plots were selected per habitat type in each observatory. The layout of Whittaker plots in each hectare is also illustrated in Figure 3.2. A species inventory and counting of individuals was made by the the task team in the Whittaker plots. This was repeated annually during the three years. The data used in this study were those of 10m x 10 m plots. Soil data was also provided by a member A. Petersen*.

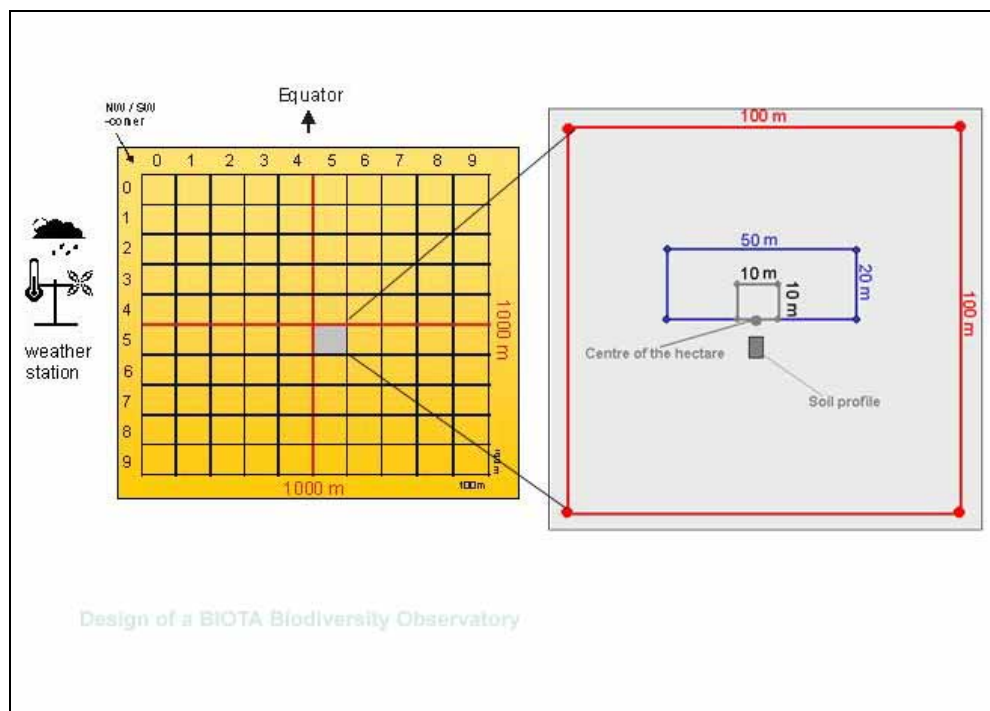


Figure 3.2 The design of the Whittaker plots in the BIOTA biodiversity observatory.

Data analysis

The values used in this study represent the mean number of individuals per species per plot across the three years. Because of the large number of individuals encountered for some species the number of individuals per species was converted to an eight-point scale as set out in Table 3.2.

Table 3.2 Eight-point scale used for the phytosociological classification

Number of individuals per species	Corresponding scaled value
0 -1	1
>1-5	2
>5-10	3
>10-25	4
>25-50	5
>50-100	6
>100-500	7
>500-1500	8

The first classification of the vegetation, based on the total data set, was obtained by the application of the TWINSpan classification algorithm (Hill 1979). Twinspan divides the data set into distinct groups on the basis of differences in floristic composition between samples or groups of samples. Further refinement of the classification was achieved by Braun-Blanquet (Zürich-Montpellier) procedures i.e the successive rearrangement of rows (species) and columns (relevés) in the matrix until a clear pattern of mutually discriminant nodes of species – relevé groups was obtained (Werger 1974, Mueller-Dombois and Ellenberg 1974, Bredenkamp and Bezuidenhout 1995). A phytosociological table including six communities was constructed

A hierarchical clustering analysis based on the incremental sum of square and chord distance in the Syn-Tax 2000 (Podani 2001) was carried out to compare with the results of the original classical table sorting. A principal coordinate analysis (PCoA) based on chord distance in Syn-Tax 2000 was used as the ordination technique to show the relationships between the relevés in multidimensional space. With the aid of an aerial photograph obtained from M. Keil* the final communities obtained were mapped. With the exception of one subcommunity, mapping could not be done at subcommunity level.

3.4 Results

The vegetation of the two observatories as other parts of Namaqualand was species rich and a total of 322 species were recorded in the 40 plots sampled. Paulshoek had a total number of 249 species with a mean of 42 species per plot. Remhoogte had a total number of 207 species with a mean number of 44 species per plot. The vegetation of Paulshoek and Remhoogte can broadly be classified as *Galenia africana*-*Lycium cinereum* shrubland. Plant species with high constancy in all communities were: the shrubs *Galenia africana*, *Lycium cinereum*, the annual herbs *Ursinia nana* and *Leysera tenella* (species group X, Table 3.3). Other plant species that were relatively common were the grass *Schismus barbatus* and the shrub *Ruschia viridifolia* (species group X, Table 3.3). The vegetation was divided into six major communities or associations of which three were further subdivided into subcommunities (Table 3.3 Figure 3.3).

The six communities were classified as follows:

- 1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water course community
 - 1.1 *Carpobrotus edulis*-*Erodium cicutarium* water course subcommunity
 - 1.2 *Oncosiphon suffruticosum*- *Lepidium desertorum* water course subcommunity
- 2 *Crassula vaillantii*-*Galenia africana* sandy valley community
- 3 *Chaetobromus dregeanus*-*Galenia africana* plains community
- 4 *Oxalis foveolata*-*Moraea serpentina* old field community
- 5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community
 - 5.1 *Anthospermum dregei*-*Polymita albiflora* rocky slope subcommunity
 - 5.2 *Pteronia ciliata*-*Eriocephalus microphyllus* rocky slope subcommunity
 - 5.3 *Cheiridopsis denticulata*-*Leipoldtia schultzei* rocky slope subcommunity
 - 5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity
- 6 *Antimima miersiana*-*Chrysocoma ciliata* rocky hills community
 - 6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hills subcommunity
 - 6.2 *Osteospermum rigidum* -*Chrysocoma ciliata* rocky hills subcommunity

The cluster analysis (Figure 3.4) and the ordination (Figure 3.5) showed similar trends on the relationships of plant communities. The position of the communities could be related to the land-use, but mostly to the position on the landscape. Community 1 that occurred in the water course and community 2 occurring in the sandy valley community were closely related. These two communities were very distinct from the other communities and were the most disturbed areas (Figure 3.4). Community 3 and 4 both occurred on the plains but differed in the previous land-use as community 4 was formerly used for agricultural purposes. Community 5 and 6 occurred in the rocky areas and were less disturbed, with community 5 restricted to the privately-owned rangeland and community 6 occurring predominantly on communal rangeland.

Table 3.3 Phytosociological table of the plant communities of Paulshoek (P) and Remhoogte (R)

Community number	1									2									3									4									5									6								
Subcommunity number	1.1			1.2															5.1			5.2			5.3			5.4			6.1			6.2																				
Paulshoek/Remhoogte	P	R	P	P	P	R	P	P	R	P	P	P	P	P	R	R	P	P	R	R	R	R	R	R	R	R	R	R	R	P	P	P	P	P	R																			
Releve number	9	4	6	9	8	2	2	2	2	3	9	1	9	2	8	1	1	6	5	9	7	4	2	7	8	6	6	4	3	4	0	3	0	8	0	0	4	3	1	8														
	0	6	2	1	0	3	7	4	2	0	4	0	6	3	1	5	1	1	4	6	4	2	4	2	7	5	4	5	0	0	6	4	7	7	1	4	4	7	2	8														
Species group A																																																						
Carpobrotus edulis	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.													
Dicrothamnus rhinocerotis	4	.	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Cotula coronopifolia	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Albuca sp. 3	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Arctotheca calendula	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Ballota africana	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Ehrharta calycina	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Berkheya onobromoides	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Species 4	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Juncus sp. 2	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Polygonum kitaibelianum	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Bromus japonicus	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Juncus sp. 1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Species 5	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Species Group B																																																						
Atriplex semibaccata	.	2	2	6	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Lepidium desertorum	.	2	.	6	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Sonchus oleraceus	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Psilocaulon leptarthron	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Amsinckia calycina	.	7	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Species Group C																																																						
Crassula vaillantii	.	.	.	.	2	3	7	7	2	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Arctotis acaulis	.	.	1	.	.	.	1	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Conicosia elongata	.	.	.	.	.	.	1	1	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Pharnaceum croceum	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Species Group D																																																						
Oncosiphon suffruticosum	.	3	1	5	.	7	.	5	4	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.	.	.	.	.	.	.	.	.														
Septulina glauca	.	1	.	1	2	1	.	1	1	.	.	.	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Erodium cicutarium	4	5	2	3	.	.	1	.	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														
Stipagrostis namaquensis	.	.	.	.	.	5	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.														
Oxalis sp. 5	5	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.														

[illegible]

											5.2		5.3		5.4								
Species Group K																							
<i>Pteronia ciliata</i>	2										4	2	4	2	1			1	1				
<i>Othonna protecta</i>								1				1		2				1					
<i>Pteronia glomerata</i>													1	4	1								
<i>Gnidia scabra</i>													1		2								
<i>Hermania cuneifolia</i> var. <i>glabrescens</i>														1	1				2				
<i>Crassula atropurpurea</i>						2						2			2				1				
Species Group L																							
<i>Sarcocaulon salmoniflorum</i>					3					1								2	2				
<i>Larryleachia cactiformis</i>																		1	1				
<i>Geophyte</i> sp. 11																		1	1				
<i>Geophyte</i> sp. 12																			3				
<i>Lotononis</i> sp.																		2					
<i>Pharnaceum dichotomum</i>						1												3					
<i>Senecio muricatus</i>						1												3					
<i>Antimima</i> sp. 4																		1					
<i>Dimorphotheca sinuata</i>																		2					
<i>Tulbaghia dregeana</i>	1																	2	2				
<i>Ornithogalum</i> sp. 4																		2					
<i>Adromischus filicaulis</i> ssp. <i>filicaulis</i>																		3					
<i>Lessertia capitata</i>						1												2					
Species Group M																							
<i>Cheiridopsis denticulata</i>	2							3	5				5		5	3	4	4	1				
<i>Antimima clavipes</i>					2								3		2	3	1	3					
<i>Aridaria noctiflora</i> ssp. <i>noctiflora</i>								1	1				1		2	1			2				
<i>Amellus microglossus</i>															4				3				
<i>Phyllobolus trichotomus</i>						2										1		1					
Poaceae													4					1					
<i>Androcymbium</i> sp. 2														1				1					
<i>Brunsvigia bosmaniae</i>						1							1		1								
<i>Albuca viscosa</i>													1			2			4				
Species Group N																							
<i>Leipoldtia schultzei</i>	2				4				5				4	2	3	6	1	2	7	6	6	4	7
<i>Crassula columnaris</i> ssp. <i>prolifera</i>		4						2	1				1	1	2	1	2		3	2	1		3
<i>Cephalophyllum rigidum</i>													2		2	1	2		2			2	
<i>Tripteris hyoserioides</i>																	2		3		1		
<i>Lotononis oligocephala</i>		1												2				1	3		1		

[illegible]



	6.1																																6.2								
Species Group R																																									
Moraea serpentina	.	.	3	.	.	.	3	.	.	4	5	3	5	3	5	.	6	5	6	.	4	4	4	3	3	.	.	5	5	.	3	4	5	2	4	.	.	.	.	.	
Helichrysum cf leontonyx	.	.	4	2	.	.	7	6	7	3	4	.	5	2	4	.	.	7	3	.	2	4	.	2	.	3	.	2	2	.	.	.	2	.	.	.	.	.	.	.	
Lotononis falcata	.	.	2	.	2	.	3	3	2	2	2	.	2	.	.	1	.	1	2	.	2	.	.	.	.	.	2	2	.	.	2	1	.	2	.	.	.	.	.	.	
Albuca cooperi	.	.	.	.	2	.	2	1	2	4	3	3	2	3	2	3	.	2	.	.	.	3	4	.	.	3	2	2	3	2	2	2	4	.	.	.	.	.	.		
Rhynchosidium pumilum	.	7	.	.	3	.	.	.	1	6	3	1	.	.	.	.	5	.	3	3	4	.	.	.	.	.	4	.	3	.	5	.	3	.	.	.	.	.	.		
Hypertelis salsoloides	.	1	1	.	.	5	1	.	2	.	3	2	1	.	1	.	2	1	.	.	2	.	.	.	.	1	.	.	1	1	.	2	.	.	.	.	.	.	.		
Moraea fugax	.	.	.	.	2	.	.	.	.	2	2	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.		
Galenia sarcophylla	.	.	2	.	.	3	.	.	.	.	3	.	1	1	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.		
Species Group S																																									
Osteospermum rigidum var. rigidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	.	
Rhus undulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.		
Microlooma sagittatum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.		
Hyobanche sanguinea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	8	.	1	.	.	.		
Senecio rowleyanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	.		
Species Group T																																									
Antizoma miersiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	2	1	.	
Arctotis laevis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	4	1	3	.	.	
Crassula hemisphaerica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	3	.	.
Crassula sp. 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	2	.	3	.	3	.	.
Wahlenbergia androsacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	4	.	.	.	.	
Asteraceae sp.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.		
Species Group U																																									
Polymita albiflora	.	.	.	.	3	.	1	.	.	.	.	1	4	.	.	.	.	.	.	5	5	5	.	3	6	2	5	4	4	6	4	6	1	2	2	1	1	5	1	4	
Cotula leptalea	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	4	.	4	.	3	.	.	3	.	7	.	.	.	.	.	2	.	3	5	.	.	
Bulbine praemorsa	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	1	.	1	2	3	.	1	2	2	.	.	.	
Wiborgia monoptera	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	.	.	.	.	.	.	.	.	2	2	2	1	.	.	.	.	.	
Zygophyllum sessilifolium	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	2	.	2	.	.	.	.	.	.	2	.	.	.	2	2	.	.	.	
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Acanthopsis carduiifolia	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	3	.	.	.	2	.	3	.	2	.	2	.	2	.	.	.	.		
Lebeckia multiflora	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	5	2	.	.	3	4	.	4	.	.	.	.	.	.	.	2	.	2	.	.		
Lampranthus godmaniae	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	2	.	.	.	.	.	1	.	1	.	.	.		
Felicia filifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.		
Lachenelia carnososa	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	1	.	.	.	.	2	.	.	



Species Group V

<i>Eriocephalus microphyllus</i> var. <i>pubescens</i>	.	.	.	.	.	.	.	.	.	3	2	4	4	4	2	3	5	2	3	.	.	2	5	4	5	2	4	5	6	4	5	5	6	5	3	.	4	2	4	2
<i>Heliophila variabilis</i>	.	4	.	.	.	3	.	.	.	3	1	3	3	2	4	2	2	2	4	4	5	4	3	4	3	2	4	4	4	5	4	5	3	4	1	.	.	2	5	
<i>Pelargonium carnosum</i>	.	.	.	.	.	.	.	.	.	.	2	.	1	.	2	1	.	1	1	.	.	4	.	1	2	1	.	1	1	4	2	.	2	2	.	1	.	2		
<i>Hermannia cuneifolia</i> var. <i>cuneifolia</i>	.	.	.	.	.	.	.	.	.	1	2	.	.	1	2	.	.	.	2	.	.	2	.	2	2	.	3	2	2	1	2	3	.	2	2	.	1	2	3	
<i>Hirpicium alienatum</i>	.	.	.	.	.	.	.	.	.	2	.	.	2	.	3	.	.	1	2	4	4	4	1	5	3	.	3	4	4	2	3	.	2	3	1	1	.	2	2	.
<i>Chlorophytum undulatum</i>	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	.	.	2	3	3	3	.	3	2	.	.	2	2	3	.	.	1	2	2	.	.	3	1	.	
<i>Pteronia incana</i>	.	.	.	.	.	.	.	.	.	.	1	2	.	1	.	.	1	.	.	1	.	.	.	1	.	.	1	.	.	4	.	1	2	2	5	2	2	.		
<i>Cyphia longiflora</i>	.	.	.	.	.	.	.	.	.	1	2	.	2	.	.	.	.	.	2	1	.	1	2	.	.	1	2	.	1	.	1	.	1	.	1	.	1	.		
<i>Phyllobolus</i> sp. 1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	2	2	.	1	.	.	.	.	.	.	.	.	2	1	.	.	1	.	1	.	
<i>Eriocephalus africanus</i>	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	.	.	.	2	.	.	2	.	.	.	.	.	.	.	1	.	.	3	.	3	4	.	2	.	
<i>Crassula muscosa</i> var. <i>muscosa</i>	.	.	1	.	.	.	.	.	.	.	.	.	2	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	3	.	1	.	1	.	.	1	1	.		
<i>Crassula sericea</i> var. <i>sericea</i>	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	4	2	.	2	.	2	
<i>Tripteris sinuata</i> var. <i>sinuata</i>	.	.	.	.	4	.	.	.	.	.	.	.	2	.	3	2	.	.	4	.	1	1	.	.	3	.	2	2	.	2	2	2	.	1	.	2	1	4		
<i>Zygophyllum retrofractum</i>	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	6	3	.	.	4	2	.	.	.	5	.	5	.	.	.	.	1	.	2	.	.	1	.		
<i>Pentaschistis airoides</i> ssp. <i>airoides</i>	.	.	.	.	.	.	.	.	.	3	2	.	1	.	.	.	.	.	3	.	.	4	.	.	.	.	3	.	.	.	3	.	.	3	.	.	3	.		
<i>Euphorbia mauritanica</i>	.	.	.	.	.	.	.	.	.	4	.	3	.	4	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	3	.	3	.	4	.	.		
<i>Asparagus capensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	1	.	2	1	.	.	.	.	.	.	.	.	1	.	1	.		
<i>Bulbine frutescens</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.		
<i>Fockea comaru</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.			
<i>Lampranthus</i> sp. 1	.	.	1	.	.	.	.	.	.	4	1	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	4	.	.	.	.		
<i>Adromischus filicaulis</i> spp. <i>filicaulis</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	1	.	.	1	.	

Species Group W

<i>Chrysocoma ciliata</i>	.	.	.	.	.	1	1	.	4	5	5	5	4	5	1	.	3	5	.	1	2	2	.	.	1	2	4	1	4	4	2	5	3	1	3	4	3	3
<i>Ehrharta barbinodis</i>	.	.	.	.	.	.	2	.	2	3	.	3	3	2	.	.	.	4	3	3	.	4	3	.	2	.	.	4	2	4	2	4	4	3	2	3	3	3
<i>Euphorbia decussata</i>	.	.	.	.	.	1	3	.	.	.	.	2	3	.	.	.	1	.	2	4	2	4	.	3	.	.	2	1	2	1	3	2	.	2	2	2	1	
<i>Zaluzianskya benthamiana</i>	.	.	.	.	.	.	.	4	4	3	2	2	.	.	2	.	.	2	.	.	1	.	3	.	3	4	.	2	.	.	.	3	.	2	3	.	1	2
<i>Aizoon canariense</i>	.	.	.	.	.	2	.	.	3	5	3	4	2	3	2	.	4	5	.	.	.	.	.	.	.	.	2	.	.	2	.	3	.	.	.	4	2	
<i>Babiana attenuata</i>	.	.	.	.	.	1	.	.	1	.	2	.	2	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	2	.	.	.	.	.	
<i>Sceletium exalatum</i>	.	.	.	.	.	.	2	.	2	2	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.
<i>Galenia meziana</i>	.	.	.	.	.	4	1	.	1	3	3	4	.	1	2	.	2	2	.	.	1	.	.	.	.	1	.	.	.	1	2	.	.	1	.	.	.	
<i>Oxalis obtusa</i>	.	.	.	.	.	.	3	.	5	.	3	2	3	.	2	.	2	.	.	1	.	3	.	.	.	1	.	.	3	2	4	2	.	2	.	.	.	
<i>Dorotheanthus</i> sp.	.	.	.	.	.	2	.	2	.	3	2	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	4	3	.	

Species Group X

<i>Galenia africana</i>	.	2	2	2	4	1	6	6	4	4	5	4	4	3	6	3	2	5	6	.	.	1	.	.	1	4	2	1	1	3	2	2	3	3	.	2	3	2	.
<i>Lycium cinereum</i>	.	2	.	2	4	3	.	1	2	1	2	.	2	1	2	2	3	2	1	.	.	1	3	.	2	1	1	1	.	1	.	2	2	1	.	2	.	1	.
<i>Ursinia nana</i> ssp. <i>nana</i>	.	7	.	.	2	.	3	2	3	5	5	.	4	.	7	.	2	2	4	3	.	5	.	.	3	4	.	4	3	.	3	3	3	.	4	3	.	1	
<i>Trichogyne lerouxiae</i>	.	3	.	.	5	3	4	5	.	8	5	.	.	.	3	2	.	5	.	3	5	.	.	.	.	3	1	2	.	.	4	.	3	.	3	3	.		
<i>Ruschia viridifolia</i>	.	5	.	.	.	.	1	.	.	.	.	.	4	1	.	.	1	.	.	.	.	.	4	.	.	.	3	1	.	.	2	5	3	5	3	5	.		

<i>Tetragonia fruticosa</i>	.	2	.	.	.	2	.	.	.	2	.	2	.	.	.	.	1	2	.	.	.	1	.	2	.	2	.	2	1	2	2	2	3	1	1				
<i>Leysera tenella</i>	.	8	3	7	7	4	5	5	7	4	4	3	4	.	5	2	4	5	6	.	4	2	.	.	.	3	.	.	3	3	.	.	3	.	1	.	.	4	3
<i>Schismus barbatus</i>	6	.	1	.	2	.	4	3	3	3	3	6	5	.	.	.	2	4	.	.	.	.	.	.	5	.	6	1	.	7	.	3	.	4	2	.	.	.	
<i>Atriplex lindleyi</i> ssp. <i>inflata</i>	.	.	.	1	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Adromischus</i> sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Adromischus marianiae</i> var. <i>immaculatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	
<i>Albuca</i> sp. 1	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Albuca longipes</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Albuca</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	
<i>Aloe krapohlana</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
<i>Anacampseros karamontana</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Anacampseros filamentosa</i> ssp. <i>namaquensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
<i>Androcymbium</i> sp. 1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Anisodonteia triloba</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Antimima</i> sp. 3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Aptosimum spinescens</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
<i>Gomphocarpus fruticosus</i>	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Asparagus</i> sp.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Avonia papyracea</i> ssp. <i>namaensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Avonia quinaria</i> sp. <i>quinaria</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	
<i>Bulbine</i> sp. 1	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cephalophyllum</i> sp. 1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cheilanthes capensis</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chenopodium album</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chenopodiaceae</i>	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chrysocoma</i> sp. 1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Conophytum calculus</i> ssp. <i>vanzylia</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cotyledon papillaris</i>	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula cotyledonis</i>	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula pyramidalis</i>	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula</i> sp.1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula umbella</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Crassula</i> sp. 2	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Diascia rudolphii</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Dimorphotheca polyptera</i>	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

[illegible]

[illegible]

[illegible]

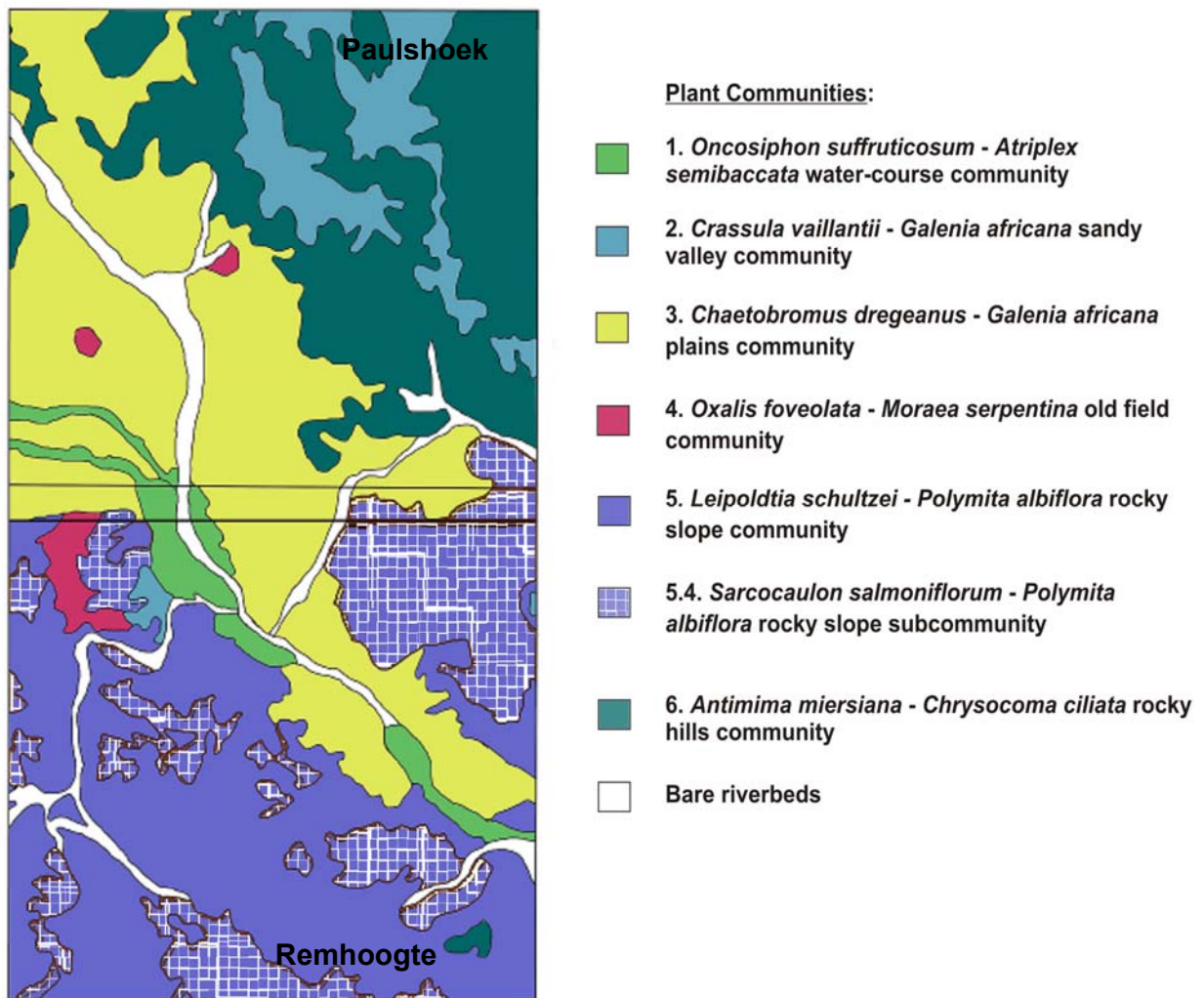


Figure 3.3 Vegetation map of observatories on Paulshoek and Remhoogte in the study area.

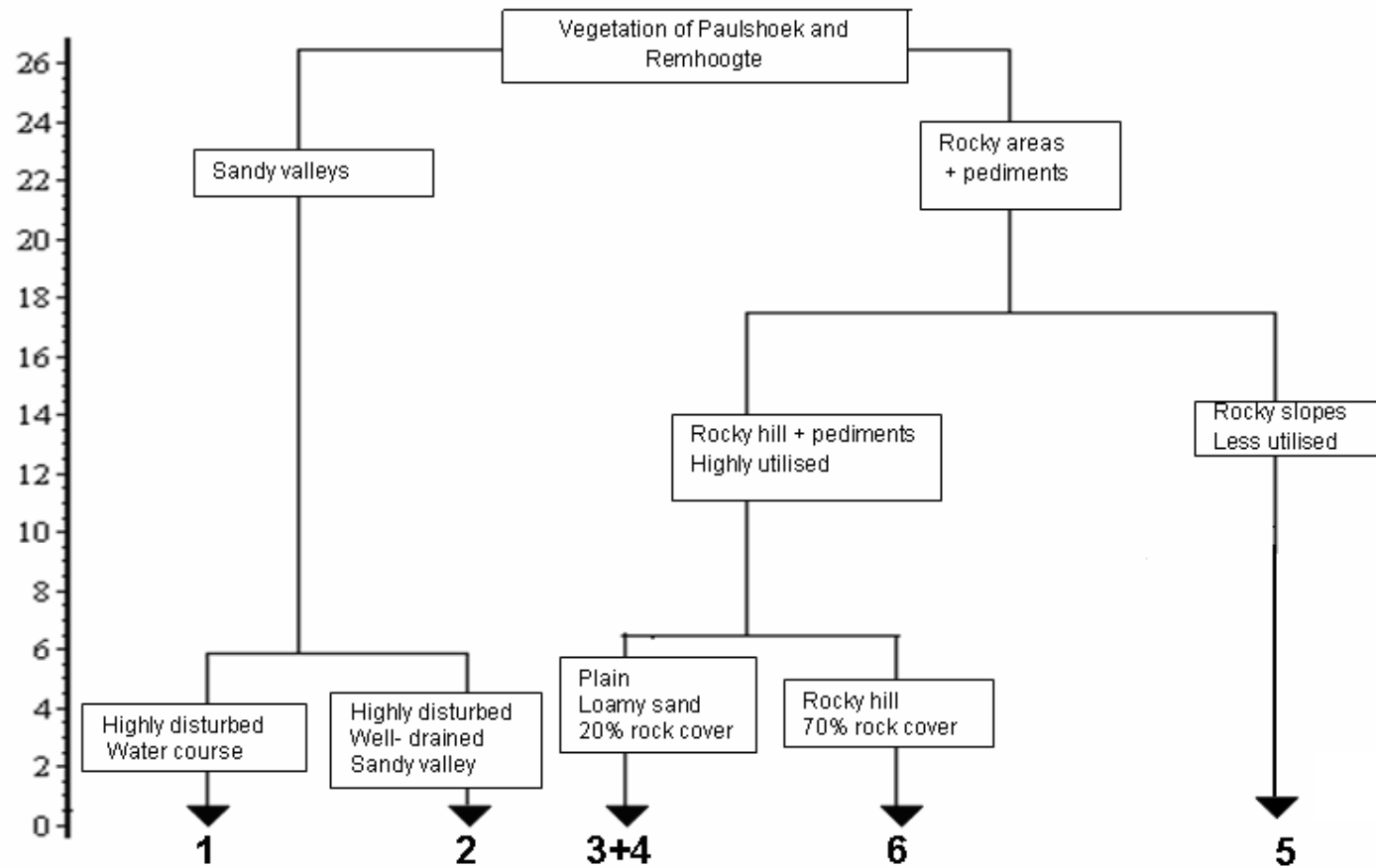


Figure 3.4 The hierarchical cluster analysis with incremental sum of squares using chord distance of the 40 relevés shows the six main plant communities of Paulshoek and Remhoogte. Numbers of plant communities correspond with numbers and descriptions of communities in the text.

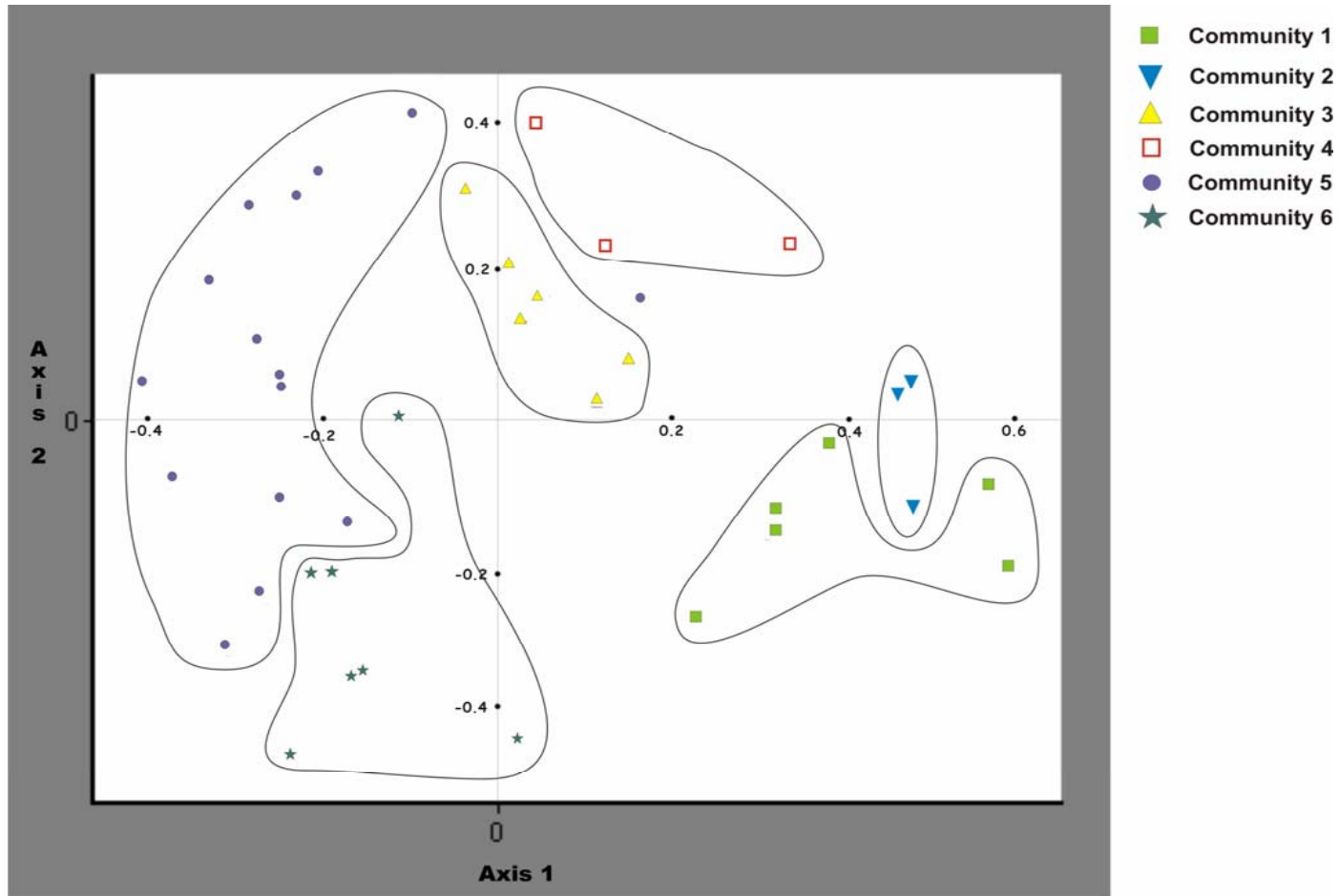


Figure 3.5 The relative positions of plant communities along the first and second axes of an ordination of floristic data by means of a principal coordinate analysis (PCoA).

Description of plant communities

1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water course community

This community is mainly restricted to the riverbed and its banks. It is a highly disturbed area with fine sandy loam soils and a rock cover of 10%. The soil pH_{H2O} ranges from 7.1 to 8.1 and the electric conductivity from 76 to 6380 µS/cm. This community has a mean of 31 species per 100 m² relevé and is linked to community 2 by species group D (Table 3.3, Figure 3.4 and 3.5). It is characterized by species group B (Table 3.3). The annual herb *Atriplex semibaccata* (species group B) and *Oncosiphon suffruticosum* (Species group D, Table 3.3) are the characteristic species of this community. Other prominent species include the annual succulent *Mesembryanthemum guerichianum* (Species group H, Table 3.3), *Leysera tenella* (species group X, Table 3.3), the shrub *Galenia africana* (species group X, Table 3.3) *Lepidium desertorum* (Species group B, Table 3.3) and *Erodium cicutarium* (Species group D, Table 3.3). This community is subdivided into two subcommunities.

1.1 *Carpobrotus edulis*-*Erodium cicutarium* water course subcommunity

This plant subcommunity is found very close to the river stream. It is generally the most disturbed habitat in most parts of Namaqualand. This subcommunity has a mean of 47 species per plot. It is characterized by species group A (species group A, Table 3.3). The perennial succulent creeper *Carpobrotus edulis* is the dominant diagnostic species with the shrub *Dicrothamnus rhinocerotis* and the perennial grass *Ehrharta calycina* found almost exclusively in this community. The dominant annual species in this subcommunity are *Leysera tenella* (species group X, Table 3.3), *Erodium cicutarium*, *Oncosiphon suffruticosum* (species group D, Table 3.3) and *Arctotheca calendula* (species group A, Table 3.3). A common shrub is *Ballota africana* (species group A, Table 3.3).

1.2 *Oncosiphon suffruticosum*- *Lepidium desertorum* water course subcommunity

This subcommunity is also found in the water stream but also includes patches some distance from the stream. In general, these are highly disturbed patches dominated by annual species. This subcommunity has a mean of 30 species per plot. It is characterized by species group B and the absence of species group A. The

dominant characteristic species are the annual herbs *Oncosiphon suffruticosum* (species group D, Table 3.3), *Atriplex semibaccata* and *Lepidium desertorum* (species group B, Table 3.3). Other conspicuous species include the succulent *Mesembryanthemum guerichianum* (species group H, Table 3.3), the annual herb *Oncosiphon grandiflorum* (Species group P, Table 3.3) and the semi-parasite *Septulina glauca* (species group D, Table 3.3).

2 *Crassula vaillantii*--*Galenia africa* sandy valley community

This community is encountered in high-lying well-drained sandy valleys which are heavily grazed by livestock. It is almost restricted to Paulshoek but occurs as a small patch in the vicinity of the water stream in Remhoogte. The soil pH_{H₂O} ranges from 6.3 to 7.7 and electrical conductivity from 15 to 32 µS/cm. It has a mean of 32 species per plot.

This plant community is differentiated by the diagnostic species of species group C such as the succulent herbs *Crassula vaillantii* and *Conicosia elongata*, and the herb *Arctotis acaulis*. The dominant species are the annuals *Lotononis falcata*, *Helichysum* sp. cf. *leontonyx* (species group R, Table 3.3), *Ursinia nana* subsp. *nana*, *Leysera tenella* and the grass *Schismus barbatus* (species group X, Table 3.3) and the unpalatable shrub *Galenia africana* (species group X, Table 3.3).

3 *Chaetobromus dregeanus*-*Galenia africana* plains community

This community is located on the sandy plains and footslopes. It is a well-drained area with a slight to moderate slope and a rock cover of more or less 20%. The soil pH_{H₂O} ranges from 5.7 to 7.7, and the electrical conductivity from 9.6 to 153 µS/cm. A high degree of trampling and erosion are characteristic of this area. This community covers a large area of Paulshoek and extends into Remhoogte on the plains along the water course. A mean of 55 species were recorded per plot. It is related to community 2 by the shared presence of species group F and to community 4 by the shared presence of species group G.

This plant community is characterized by species group E (Table 3.3). The dominant diagnostic species is the perennial grass *Chaetobromus dregeanus*. Prominent species in this community are the geophytes *Moraea serpentina* and *Albuca cooperi*

(species group R, Table 3.3); the annuals *Aizoon canariense* (species group W, Table 3.3), *Gazania lichtensteinii* (species group Q, Table 3.3), *Leysera tenella* (species group X, Table 3.3) and *Heliophila variabilis* (species group V, Table 3.3); the perennial shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3). The shrub *Pentzia incana* (species group Q, Table 3.3), herb *Galenia meziana* (species group W, Table 3.3) and the succulent *Mesembryanthemum guerichianum* (species group H, Table 3.3) are species with high constancy. The annual *Lessertia diffusa* and the geophyte *Ornithogalum secundum* are exclusive to this group.

4 *Oxalis foveolata*-*Moraea serpentina* old fields community

This community is found on abandoned fields on the sandy slopes on both Remhoogte and Paulshoek. The soil pH_{H2O} ranges from 6.3 to 6.8 and the electrical conductivity ranges from 30 to 114 µS/cm. There is not a specific species group distinguishing this community, which consists of relevés 11, 61 and 54. Its floristic composition shows a close affinity to community 3 by the shared species groups G and H. The dominant species in this community are the shrubs *Pentzia incana* (species group Q, Table 3.3), *Galenia Africana* (species group X, Table 3.3) and *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), the annuals *Oxalis foveolata*, *Gazania lichtensteinii* (species group Q, Table 3.3), *Leysera tenella*, and *Ursinia nana* subsp. *nana* (species group X, Table 3.3). It has a mean of 39 species per plot.

5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community

This community covers most part of Remhoogte, on rocky hills and mid-slopes. The pH_{H2O} ranges from 4.9 to 8.7 and the electrical conductivity ranges from 21 to 982 µS/cm. It is characterized by species group N. It has a mean of 67 species per plot, the highest species richness of all communities. This area is less disturbed and the difference between variants can be related to the rock size and possibly the rock cover percentage. It can be subdivided in four weakly defined subcommunities of which one (Subcommunity 5.4) was mapped separately. The dominant species are the annual *Heliophila variabilis* and dwarf shrub *Hirpicium alienatum* (species group V Table 3.3) and the succulent shrubs *Euphorbia decussata* (species group W,

Table 3.3), *Polymita albiflora* (species group U, Table 3.3) and *Leipoldtia schultzei* (species group N, Table 3.3).

5.1 *Anthospermum dregei* subsp *dregei*-*Polymita albiflora* rocky slope subcommunity

This subcommunity is characterised by the diagnostic group I (Table 3.3). The dominant species are the shrub *Pteronia ciliata* (species group K, Table 3.3), *Hirpicium alienatum* (species group V, Table, 3.3), the succulent shrub *Polymita albiflora* (species group U, Table 3.3), the annual *Phyllobolus* sp. (species group V, Table, 3.3), the geophyte *Chlorophytum undulatum* (species group V, Table, 3.3) and the grass *Ehrhata barbinodis* (species group W, Table 3.3).

5.2 *Pteronia ciliata*- *Polymita albiflora* rocky slope subcommunity

This subcommunity is found in the area with high rock cover (80%) and poorly drained soils. It does not have a diagnostic species group. It is characterized by the absence of species groups I, J and L. It consists of relevés 34, 72, 87 of species group K. It is intermediate between subcommunities 1 and 3. The dominant species are the perennial succulent *Cheiridopsis namaquensis* (species group O, Table 3.3), the shrub *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3) the succulent *Cephalophyllum rigidum* (species group N, Table 3.3), annuals *Gazania lichtensteinii* (species group Q, Table 3.3) and *Heliophila variabilis* (species group V, Table 3.3) and the geophyte *Oxalis* sp. (species group Q, Table 3.3).

5.3 *Cheiridopsis denticulata*- *Polymita albiflora* rocky slope subcommunity

This subcommunity is also found on the rocky slopes of Remhoogte and has a mean of 27 species per plot.

This subcommunity does not have a distinctive species group. It is composed of the five relevés 65, 64, 45, 30 and 40. It is characterized by the absence of species group I, K and L (Table 3.3). In addition to common species other dominant species include the perennials *Hermannia cuneifolia* var. *cuneifolia* (species group V, Table 3.3), and the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Hirpicium alienatum*, *Eriocephalus microphyllus* var. *pubescens* (species group V, Table, 3.3), the succulent shrubs *Polymita albiflora* (species group U, Table 3.3), *Leipoldtia*

schultzei (species group N, Table 3.3), the geophyte *Chlorophytum undulatum* (species group V, Table, 3.3). These species are not particularly good choices of high constancy. They were not encountered in all the relevés, whereas there are many species that were.

5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity

This subcommunity is found on plains and is characterized by species group L. It is strongly related to the previous subcommunity but has some exclusive species. The dominant species are the perennials *Leipoldtia schultzei* (species group N, Table 3.3), *Wiborgia monoptera* (species group U, Table 3.3), *Polymita albiflora* (species group U, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table, 3.3), *Chrysocoma ciliata* (species group W, Table 3.3), the succulent shrubs *Euphorbia decussata* (species group W, Table 3.3), the grass *Ehrharta barbinodis* (species group W, Table 3.3) and the annual *Heliophila variabilis* (species group V, Table 3.3).

6 *Actotis laevis*-*Tetragonia fruticosa* rocky hills community

This community is restricted to the uplands with boulders and highly rocky areas of Paulshoek. The soil pH_{H₂O} ranges from 5.3 to 7.8 and the electrical conductivity from 77 to 285 µS/cm. It has a mean of 41 species per plot. This community is characterized by the presence of species group T and to a lesser extent species group S. The dominant species of this community include the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Arctotis laevis* (species group T, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), *Pteronia incana* (species group V, Table 3.3), *Ruschia viridifolia* (species group X, Table 3.3), *Polymita albiflora* (species group U, Table 3.3), the grass *Ehrharta barbinodis* (species group W, Table 3.3). It can be subdivided into two subcommunities.

6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hill subcommunity

This subcommunity does not have a specific species group. It is characterized by the absence of species group S and differs from subcommunity 6.2 by the presence of species group R. The dominant species of this variant are the geophytes *Albuca cooperi* (species group R, Table 3.3) and *Chlorophytum undulatum* and the perennial shrub *Hirpicium alienatum* (Species group V, Table 3.3).

6.2. *Osteospermum rigidum* var. *rigidum*-*Pteronia incana* rocky hills subcommunity

This subcommunity is characterized by species group S and the absence of species group R. The dominant species include the succulents *Euphorbia decussata*, (species group W, Table 3.3) and *Polymita albiflora* (species group U, Table 3.3), the shrubs *Chrysocoma ciliata* (species group W, Table 3.3), *Eriocephalus microphyllus* var. *pubescens* (species group V, Table 3.3), *Pteronia incana* (species group V, Table 3.3), the annuals *Zaluzianskya benthamiana* (species group W, Table 3.3) and *Cotula leptalea* (species group U, Table 3.3).

3.5 Discussion and conclusions

There appears to be some clear differences in plant communities between the communal and commercial land. The communal land contains communities 2 and 6 which are poorly represented on the commercial land, while the commercial land is dominated by community 5 which does not occur on the communal land. The two land-uses share the same communities along the river courses and on the abandoned cropland (communities 1 & 4 respectively) which are the most disturbed sites of the study area. Another community shared by the two land-uses is community 3 which occurs on the undulating plains.

An important consideration to bear in mind when comparing the vegetation on the two observatories is that land type differences do occur. Communities 2 and 6 on Paulshoek occur predominantly in the area covered by land type Ib274 which would probably classify as Kamiesberg Mountain Shrubland (Mucina and Rutherford 2006) such an underlying difference cautions against making sweeping statements on the effect of land-use.

The total number of species recorded was higher in the communal land than in the privately owned land. This agrees with many findings (Landsberg *et al.* 2002, Todd 2006) that suggest that grazing increases species richness at a local scale by providing opportunities for more species to establish. However, on a plot basis,

species richness was almost the same in both rangelands and varied with the landscape.

The sampling method used in this study could influence the final results. Plots were not chosen according to the plant community concept where the plot has to be representative of the community sampled, but they were situated north of the centre of the hectare which does not necessarily represent the floristics of the hectare or the community. Although the method used was not ideal for a phytosociological study, the data could be successfully used to classify the vegetation into distinct communities.

3.6 Appendix

List of unidentified species and their description by BIOTA task team.

- Adromischus* Flachblatt - *Adromischus* sp. 1
Androcymbium behaart - *Androcymbium* sp. 1
Androcymbium Schmalblatt - *Androcymbium* sp. 2
Albuca 5blatt = *Albuca* sp. 1
Albuca Vielblatt gestreift = *Albuca* sp. 2
Albuca Zurückgeschlagene tepalen = *Albuca* sp. 3
Antimima cf Klein - *Antimima* sp.1
Antimima Kurz Spitzblatt = *Ru robusta*? - *Antimima* sp. 2
Antimima Polster Paulshoek - *Antimima* sp. 4
Antimima *Ruschia robusta* ähnlich - *Antimima* sp. 3
Asparagus kurze Blätter - *Asparagus* sp.
Asteraceae gewelltes Pfeilblatt, rotes Köpfchen, verholzt – Asteraceae sp.
Asparagus kurze Blätter – *Asparagus* sp.
Bulbine breite Blätter, behaarter Rand - *Bulbine* sp. 3
Bulbine frutescens drüsig - *Bulbine* sp. 1
Bulbine klein bläulich – *Bulbine* sp. 2
Cephalophyllum Spitzblatt – *Cephalophyllum* sp.
Chenopodiaceae – Chenopodiaceae sp.
Chrysocoma große Blüten – *Chrysocoma* sp. 1
Crassula mini-Blätter verholzt – *Crassula* sp. 2
Crassula strauichig aufrecht - *Crassula* sp. 3
Crassula verh., rote Blätter – *Crassula* sp. 1
Drosanthemum abstehend verzweigt, schuppig – *Drosanthemum* sp. 2
Drosanthemum behaart weiss – *Drosanthemum* sp. 4
Drosanthemum fein, bläulich – *Drosanthemum* sp. 3
Drosanthemum klein weiß – *Drosanthemum* sp. 1
Fabaceae kl. 3-Blätter, Blasenfrüchte – Fabaceae sp.
Geophyt großes Blatt mit hellem Rand –Geophyte sp. 11
Geophyt heller Rand – Geophyte sp. 3
Geophyt Korkenzieher glatt - Geophyte sp. 4
Geophyt Lockenwickler – Geophyte sp. 1
Geophyt Lockenwickler gekerbt – Geophyte sp. 7
Geophyt Lockenwickler glatt – Geophyt sp. 5
Geophyt Lockenwickler hairy- Geophyte sp. 6
Geophyt Lockenwickler sukkulent – Geophyte sp. 8
Geophyt Riemenblatt – Geophyte sp.12
Geophyt Spirale sukkulent – Geophyt sp. 2

Geophyt stachlig – Geophyt sp. 9
 Geophyt welliger Rand – sp. 10
 Gras breite Blätter, behaart – Poaceae sp. 1
 Gras Langblatt – Poaceae sp. 2
Helichrysum cf. Blüten in Blattachse (, od. *Crassula*?) - *Helichrysum* sp.
Hirpicium gestreckte Achse – *Hirpicium* sp. 1
Jamesbrittenia Rundblatt – *Jamesbrittenia* sp.
Juncus klein – *Juncus* sp. 1
Juncus sp – *Juncus* sp. 2
 Keimlinge – Species 5
Lachenalia sp- *Lachenalia* sp. 4
Lachenalia Herzblatt – *Lachenalia* sp. 1
Lachenalia Zebrafuß – *Lachenalia* sp. 2
Lampranthus unordentlich/*Scopelogenia* – *Lampranthus* sp. 3
Lycium große Früchte – *Lycium* sp.
Ornithogalum 3Blatt – *Ornithogalum* sp. 3
Ornithogalum große Knolle – *Ornithogalum* sp. 1
Ornithogalum mini behaart – *Ornithogalum* sp. 2
Oxalis am Wasser – *Oxalis* sp. 2
Oxalis Fabaceae – *Oxalis* sp. 3
Oxalis Herzblatt mini – *Oxalis* sp. 1
Oxalis zusammengefaetete miniblatte – *Oxalis* sp. 4
Oxalis mini – *Oxalis* sp. 5
Pelargonium weich – *Pelargonium* sp.
Pharnaceum Basis verholzt locker – *Pharnaceum* sp.
Phyllobolus flach – *Phyllobolus* sp.
 Roggen/Hafer – species 4
Ruschia rotes Polster – *Ruschia* sp. 1
Salicornia niederliegend – *Salicornia* sp. 1
 Strauch längliche Blätter – species 1
 Strauch schmale Blätter – species 2
 Strauch spatelblättrig – species 3
Tylecodon 3 Blatt – *Tylecodon* sp. 1
Tylecodon hellgrün glatt – *Tylecodon* sp. 2

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Chapter 4

Dispersal spectra of communal versus commercial rangeland in Namaqualand, South Africa

4.1 Introduction

Dispersal is a key process in the ecological and evolutionary dynamics of a population. Dispersal plays an important role not only in range expansion of a species but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Although ecologists have long appreciated the importance of dispersal for spread and persistence of populations, the last decade has witnessed a surge of interest in how this phase of the life cycle influences community structure (Nathan and Muller-Landau 2000, Cain *et al.* 2000). Dispersal is believed to set the template from which community patterns develop (Levine and Murrell, 2003) and knowledge of seed dispersal finds applications in nature conservation and ecological restoration (Strykstra *et al.* 2002).

The persistence and distribution of any plant species is affected by many factors and the mode of dispersal of any plant species must reflect many different pressures and constraints of the environment. Every individual plant struggles to ensure that its own offspring make up as big a fraction as possible of the next generation, and for each individual plant there is an evolutionary gain to leave more surviving seedlings than its neighbour (Crawley 1993). Because natural selection must work with existing variation, and many plants have very long generation times, there are phylogenetic constraints (Willson and Traveset 2000).

In general, about 75% of the seeds produced by plants are consumed before and after dispersal. The notion of a safe site was proposed by Harper *et al.* (1965) to describe those specific conditions which permit a seed to escape all hazards of the pre-germination phase, to overcome dormancy and to establish successfully. To start a next generation in a safe site, an individual has to reach the next safe site in time as well as space through dispersal (Strykstra *et al.* 2002). An unequal distribution in habitat quality with a constant rate of dispersal results in source-sink

processes, with a net flow of individuals from rich habitats into the poor ones (Kisdi 2002, Levin *et al.* 2003).

The term dispersal is defined as the unidirectional movement of an organism away from its place of birth (Levin *et al.* 2003) and includes horizontal and vertical movement (Campos and Ojeda 1997). When studying dispersal mechanisms several criteria can be used to classify the dispersal mode. Dansereau and Lems (1957) suggested four alternative criteria: the morphological nature of the diaspore, the genetic composition of the diaspore, the presumed or observed agent of dispersal and conditions for establishment. Any one of these classification systems cannot be wholly satisfactory, since a certain structure may be adapted for dispersal in different and sometimes even antagonistic ways.

Most studies in plant community ecology in South Africa have focused on the floristic analysis of the vegetation and vegetation attributes have seldom been applied. The use of plant functional traits to describe patterns in plant communities provides us with the means to understand the mechanisms of vegetation responses to environmental change which a purely floristic approach does not accomplish. Moreover, such features lend themselves to statistical treatment in the form of spectra, which show the variety, the amplitude and the proportion of the function involved in the internal mechanics of the community (Dansereau and Lems, 1957).

Some relationships between particular dispersal methods and environmental conditions have been proposed. Stocking pressure imposes a rigorous but complex selection process on the flora by the direct grazing by herbivores, the associated trampling effects and the redistribution of nutrients through urine and faeces (Navie and Rogers 1997). Many authors (Collins and Uno 1985, Milton *et al.* 1990, Willson *et al.* 1990, Nakanishi 2000b) have suggested that epizoochores are more common in disturbed than in undisturbed habitats and that they are often also common in grazed vegetation types due to the availability of the dispersal agent (herbivorous mammals). Plant species possessing more than one type of seed differing in their dispersal mode and germination requirement (heterodiaspory) are likely to resist in unpredictable environments such as disturbed habitats given their ability to adapt to different environments (Harper 1977, Van Mölken *et al.* 2005). It could therefore be

speculated that more heterodiasporic species should be found vegetation that is heavily grazed.

Many studies (Gutterman *et al.* 1973, Johri 1984; Gutterman 1996, Gutterman & Shem-Tov 1997, Gutterman 2002) have speculated on the ecological importance of the mucilage produced by the seeds of certain desert plants upon moistening (myxospermy). The most prominent being that the mucilage: a) adheres the seed to the soil to prevent further movement, b) adheres to passing animals for long distance dispersal, c) provides a good contact between the seed and the soil surface, d) lubricates the area surrounding the seed making it easier for the root to penetrate the soil, and e) the water held by the mucilage could serve as water reservoir for germination. Ellner and Shmida (1981) characterize myxospermy as an anchorage mechanism against surface runoff and the retention of the mother site as a side effect.

The objectives of this study were to analyze and compare the dispersal spectra in a communal and commercial rangeland, and those of the different plant communities found in the study area, to improve our understanding of plant community patterns and processes.

4.2 Study area

The study site is located near Paulshoek (30°20'S, 18°15'E), one of nine villages in the Leliefontein Communal Reserve in Namaqualand, Northern Cape (Figure 2.1). Paulshoek is a remote village about 50 km east of Garies and lies on the eastern foothills of the Kamiesberg Mountain Range at an altitude of between 980 and 1 400m above sea level (Todd and Hoffman 1999). The Paulshoek commons is fenced on three sides by commercial farms. The site of the current study is a 1 km² section on the southern border of the Paulshoek commons. The study site includes another 1 km² section which extends approximately 1 km from the Paulshoek boundary into one of the neighbouring privately owned farms, Remhoogte (Southeast from Paulshoek village).

Over the last 30 years, the mean stocking density for Paulshoek has been roughly 6 ha per small stock unit, which is double the rate recommended for the region by the

South African Department of Agriculture. The stocking density on the local commercial farms remains at approximately 12 ha per small stock unit or lower (Todd and Hoffman 1999). The grazing regime on the communal land has been characterized by heavy and continuous grazing whereas the neighboring commercial rangeland is moderately and rotationally grazed (Todd and Hoffman 1999, Petersen 2004).

Rainfall data of more than 100 years shows that the region is subject to periodic episodes of high rainfall as well as episodic droughts (Desmet and Cowling 1999a). The majority of the annual rainfall is received during the winter months (May-September). Rain occurs as a result of circumpolar frontal westerlies. The mean annual rainfall is 169.3 mm at Paulshoek (data to 2001 to 2006 for an on-site, BIOTA weather station*). The occurrence of fog in Paulshoek is relatively insignificant and is usually restricted to the high-lying western part of Kamiesberg and the low-lying valleys to the south of the village (Petersen 2004).

Winter months in Paulshoek are unpredictably cold probably because of relatively high altitudes. The mean annual temperature is 16°C (Table 3.1). The mean monthly maximum temperature reaches 30°C in the summer (February) while the mean minimum temperature falls to 3.1°C in the winter months (July) (BIOTA data).

Paulshoek is situated within the Succulent Karoo Biome (Rutherford and Westfall 1986). The study area form part of the vegetation type found in flat or gently sloping rock sheets supporting dwarf evergreen shrubs such as *Pentzia incana* and the poisonous kraalbos *Galenia Africana*. It also covers the wide plains and broad valleys with water courses. This sparse dwarf shrubland contains many succulents such as *Ruschia robusta* plants with ericoid leaves (e.g. Asteraceae), geophyte and ephemeral herbs and forms part of Acocks (1953, 1988) Namaqualand Broken Veld (VT33), or Upland Succulent Karoo (LR 56) by Low and Rebelo (1998). Mucina *et al.* (2005) recognised three vegetation types in these areas: a) the plains and broad valleys with dry water courses are described as Namaqualand Blomveld (SKn 3), b) the flat, gently sloping rock sheet is described as Namaqualand Klipkoppe Shrubland (SKn 1) and c) steep slopes of the large granite domes described as Kamiesberg Mountains Shrubland (SKn 6).

A vegetation survey of the study area revealed six plant communities (Figure 4.1). These six plant communities have been classified as follows:

- 1 *Oncosiphon suffruticosum*-*Atriplex semibaccata* water-course community
 - 1.1 *Carpobrotus edulis*-*Erodium cicutarium* water-course subcommunity
 - 1.2. *Oncosiphon suffruticosum*- *Lepidium desertorum* watercourse subcommunity
- 2 *Crassula vaillantii*-*Galenia africana* sandy valley community
- 3 *Chaetobromus dregeanus*-*Galenia africana* plains community
- 4 *Oxalis foveolata*-*Moraea serpentina* old field community
- 5 *Leipoldtia schultzei*-*Polymita albiflora* rocky slope community
 - 5.1 *Anthospermum dregei* -*Polymita albiflora* rocky slope subcommunity
 - 5.2 *Pteronia ciliata*–*Eriocephalus microphyllus* rocky slope subcommunity
 - 5.3 *Cheiridopsis denticulata*-*Leipoldtia schultzei* rocky slope subcommunity
 - 5.4 *Sarcocaulon salmoniflorum*-*Polymita albiflora* rocky slope subcommunity
6. *Antimima miersiana*-*Chrysocoma ciliata* rocky hills community
 - 6.1 *Moraea serpentina*-*Chrysocoma ciliata* rocky hills subcommunity
 - 6.2 *Osteospermum rigidum* -*Chrysocoma ciliata* rocky hills Subcommunity.

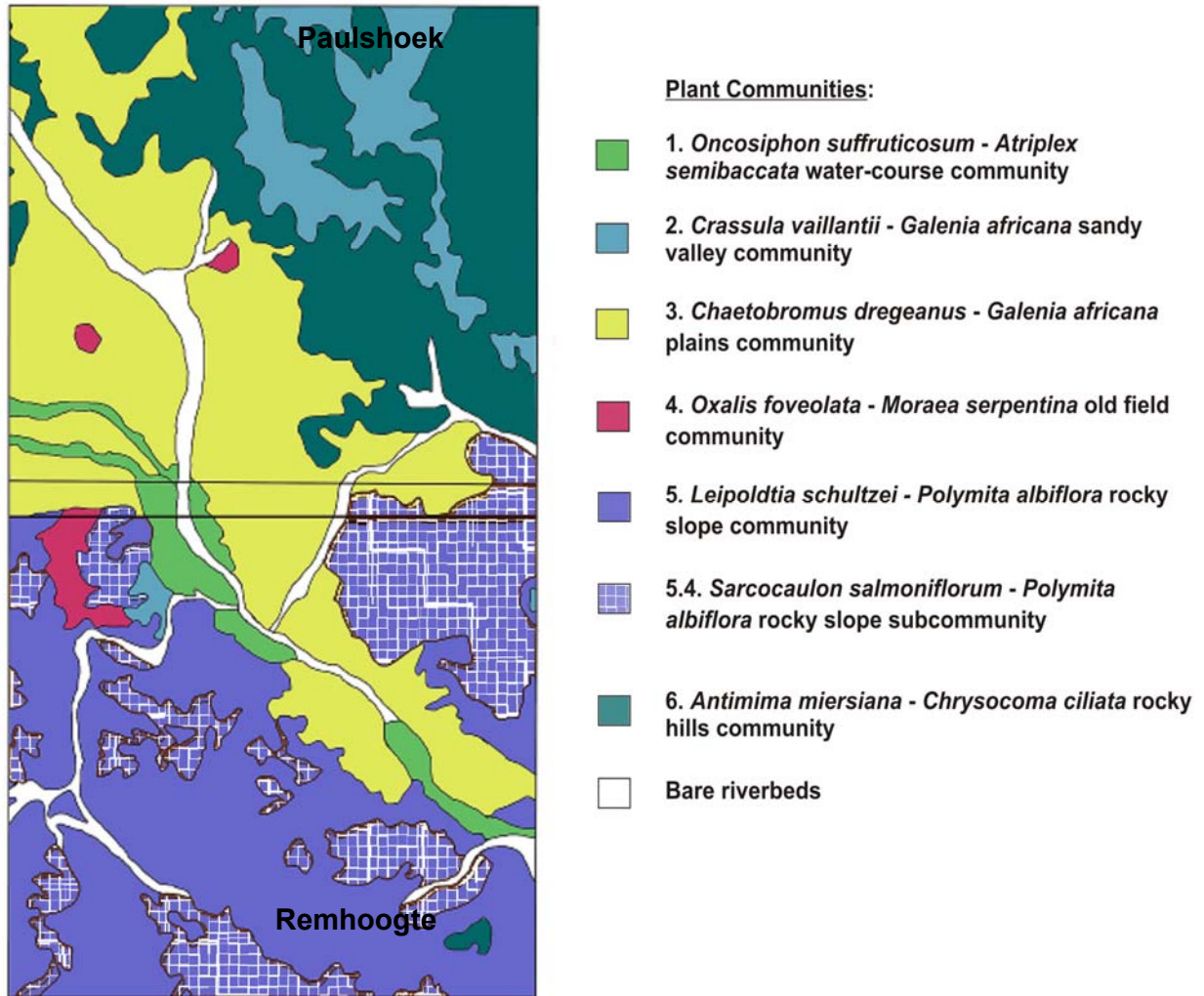


Figure 4.1 Vegetation map of the study area.

4.3 Materials and methods

Dispersal types have been assigned to each plant species recorded in the study area on the basis of apparent morphological adaptations because it requires considerable study to quantify actual dispersal vectors by field observations. There is a general consensus that the character syndromes associated with particular kinds of dispersal vectors can be identified quite reliably in the majority of species (Willson *et al.* 1990). Thus the spectra reported describe the incidence of apparent morphological traits in plants. To attribute a dispersal morphology to the species, a combination of inspection of the diaspores in the herbarium, published data concerning dispersal morphology, and field observations were used. Seventeen categories of dispersal morphology were distinguished based on the following criteria (Van Rheede van Oudshoorn and Van Rooyen 1999):

Autochory (Aut): A diaspore that is propelled explosively, e.g. a fruit that opens suddenly or by a trip-lever, this also includes hygrochasic and trypanospermic diaspores.

Balloon diaspores (Bal): Balloon diaspores contain air that increases the volume and decreases the density of the diaspore.

Dust diaspores (Dus): Small diaspores without special devices for buoyancy.

Endozoochory (End): The diaspore has a fleshy pulp or aril of a type that is associated with consumption by vertebrate frugivores to eject and disperse the seed.

Epizoochory (Epi): The diaspore has hooks, burrs, sticky hairs or other devices such that it adheres to the fur or feathers of vertebrates. Diaspores that adhere to the animals after wetting were excluded.

Heterodiaspory (Het): The production of two or more morphologically distinct types of diaspores by an individual plant.

Hygrochasy (Hyg): The diaspore is contained in a fruit that opens when wet and closes when dry.

Nautohydrochory (Nah): The diaspores are directly dispersed by water currents.

Ombrohydrochory (Omh): The direct or indirect dispersal of diaspores by rain and /or dew. In this study hygrochasic and trypanospermic diaspores are classified as ombrohydrochoric. The term indirect hydrochory has also been used to refer to this term

Myxospermy (Myx): Diaspores that produce mucilage upon wetting.

Atelochory (Ate): The diaspore has no evident morphological specialization associated with dispersal.

Plumed diaspores (Plu): The diaspore is partially covered with appendages acting like a parachute.

Synaptospermy (Syn): Two or more seeds are joined together to form a compound diaspore.

Trypanospermy (Try). The form and /or appendages of the diaspore favour burial in the soil e.g. by drilling or wedging into cracks.

Tumbleweeds (Tum): Spherical structures that consist of the entire inflorescences or even the whole plant are blown along the ground by the wind, while releasing seeds as they move.

Winged diaspores (win): The diaspore has wings that slow the rate of fall.

Woolly (Woo): The diaspore is fully covered with hair that increases air resistance.

Many species have seeds that are dispersed by more than one agent and this makes the classification of many plants species into single categories impossible (Wilson *et al.* 1990, Van Rheede van Oudtshoorn and Van Rooyen 1999). Such species contributed one case to each dispersal syndrome but only once to the total on which percentages were based.

Data analysis

The data analysis was done on a qualitative and a quantitative level. For the qualitative analysis the dispersal spectrum of each rangeland was calculated by expressing the number of species with each type of dispersal as a percentage of the total number of species present in the rangeland. For the quantitative analysis the number of individuals per species (abundance) found in the study area was taken into account to calculate the percentage. For communities the dispersal spectrum of each community was calculated by expressing the number of species/individuals with each type of dispersal as a percentage of the total number of species/individuals present in the community.

The dispersal spectra of the two rangelands, both the quantitative and qualitative analyses were further compiled in two ways. Firstly, a collective species list was compiled for each rangeland. A species was only considered as present or absent for the qualitative analysis and for the quantitative analysis the value represented the total number of individuals found in the rangeland. Secondly, the data of each relevé was considered as a repetition of the rangeland, in this case values are the mean number of species or individuals found in the 20 relevés. These two approaches will be referred as Design 1 and Design 2 respectively in the rest of the text. Design 1 only allows for the comparison of the entire spectra, whereas individual dispersal types can also be compared with Design 2. Design 1 comparisons were done by means of the T-test for independent variables and chi square test; while an One Way ANOVA was used for Design 2 comparisons. All statistical analyses were done with Statistica 7 (Statsoft Inc., Tulsa, Oklahoma).

For dispersal types within communities a One Way ANOVA and a Fisher LSD *post hoc* test were used to determine the significant difference between dispersal types in a community. The criterion for statistical significance was set at $P < 0.05$.

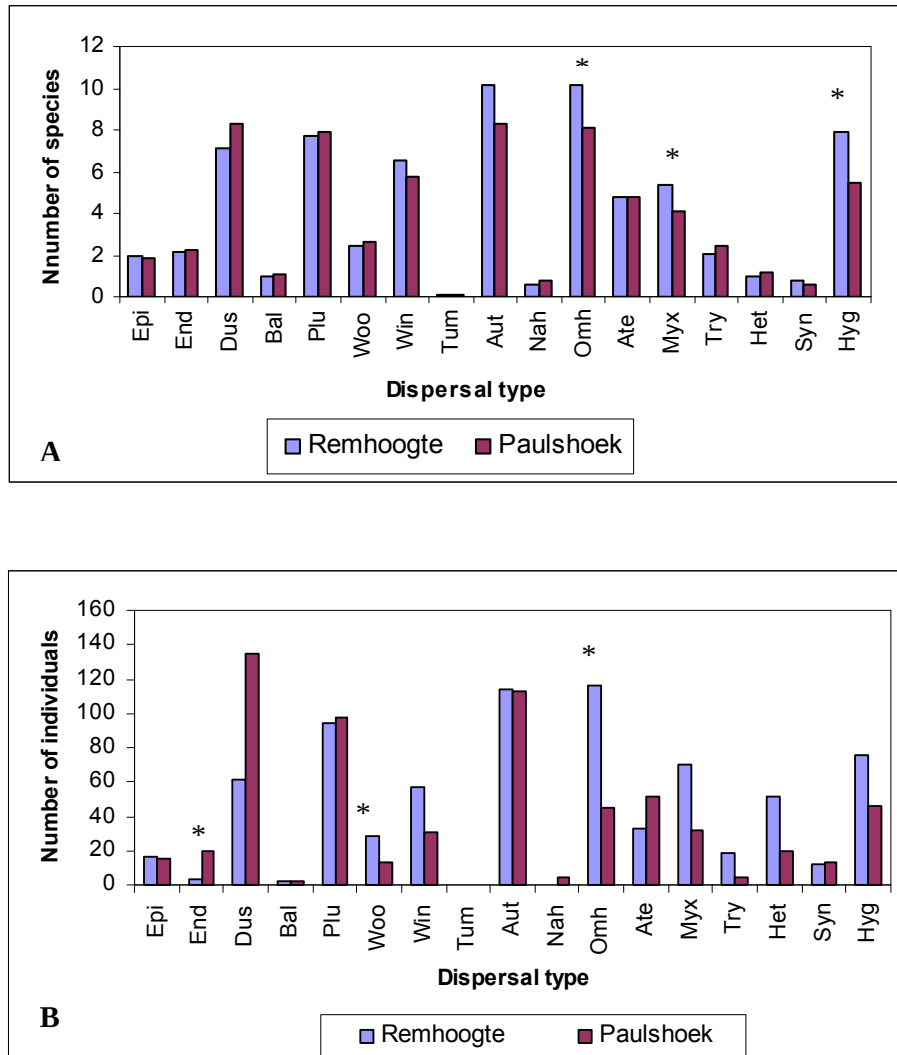
4.4 Results

The dispersal types consistently common in both rangelands and all communities were: ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores (Figure 4.2).

Communal versus commercial rangelands

Design 1, which compared the entire spectra found no significant difference for either the quantitative or qualitative dispersal spectra between the two rangelands (Figure 4.2A & B).

An analysis of the quantitative Design 2 revealed that endozoochory is higher on communal land than in commercial land and individuals with woolly diaspores and ombrohydrochoric diaspores were found to be significantly higher on the commercial land than in the communal land (Figure 4.3B). The qualitative Design 2 analysis



Qualitative

Quantitative

Figure 4.3 (A) Qualitative and (B) quantitative dispersal spectra of Paulshoek and Remhoogte observatories derived by evaluating the means of 20 plots surveyed in each rangeland (Design 2). Explanations of abbreviations can be found on pp. 59-60.

Between communities

In general the dispersal spectra did not differ much between communities even though some dispersal types seemed to be more prominent in one community than others on a qualitative or quantitative basis. The comparison of dispersal types among communities is summarised in Tables 4.1 and 4.2. For qualitative data endozoochory, autochory and woolly diaspores show significant variation between

communities. Endozoochory was found to be significantly higher in the water course community (community 1) than in the plains community (community 3) and in the rocky slopes community (community 5). Woolly diaspores were found to be significantly lower in the water course community (community 1) than in the rocky hill community (community 6) (Table 4.1, Figure 4.3) and autochoric species were significantly more in the sandy valley (community 2) than in water course community.

Table 4.1 Qualitative comparisons of dispersal spectra of six plant communities of Paulshoek and Remhoogte.

Dispersal type	Community						P
	1	2	3	4	5	6	<0.05
A. Telechory							
Zoochory							
Epizoochory	3.86	4.51	3.14	2.18	4.05	6.81	0.17 ^{ns}
Endozoochory	10.81 ^b	6.46 ^{ab}	3.15 ^a	5.07 ^{ab}	3.36 ^a	5.88 ^{ab}	0.00 [*]
Anemochory							
Dust diaspores	12.89	23.57	17.86	15.53	15.40	16.94	0.07 ^{ns}
Balloon diaspores	3.07	3.50	2.40	2.44	2.36	0.25	0.13 ^{ns}
Plumed diaspores	17.47	17.03	16.69	17.05	15.49	18.74	0.91 ^{ns}
Woolly diaspores	2.45 ^a	4.24 ^{ab}	5.39 ^{ab}	6.36 ^{ab}	5.14 ^{ab}	7.64 ^b	0.00 [*]
Winged diaspores	9.12	18.24	11.68	9.93	13.86	15.75	0.06
Tumbleweeds	0.45	0.00	0.21	0.00	0.12	0.00	0.75 ^{ns}
Autochory	10.90 ^a	26.73 ^b	18.43 ^{ab}	17.00 ^{ab}	21.59 ^{ab}	19.57 ^{ab}	0.02 [*]
Hydrochory							
Nautohydrochory	0.00	0.00	0.00	0.00	0.00	0.00	1
Ombrohydrochory	13.32	25.25	20.95	19.47	20.39	17.48	0.11 ^{ns}
B. Atelechory	9.56	12.52	10.35	10.44	9.60	9.30	0.87 ^{ns}
C. Additional features (Antitelechory)							
Anchorage mechanisms							
Myxospermy	11.00	7.27	9.20	14.51	10.87	10.07	0.74 ^{ns}
Trypanospermy	2.96	2.76	5.84	3.70	4.25	4.93	0.08 ^{ns}
Reduction in dispersal potential							
Synaptospermy	2.07	1.48	1.62	0.00	1.28	2.23	0.93 ^{ns}
Heterodiaspory	4.1	3.03	2.51	2.67	1.82	1.74	0.57 ^{ns}
Restriction of dispersal in time							
Hygrochasy	13.27	16.30	15.89	11.43	14.59	11.37	0.74 ^{ns}

For quantitative data significant differences were found in the contributions of plumed, woolly, autochoric, ombrohydrochoric, and hygrochasic diaspores. The number of individuals with plumed diaspores was significantly higher in the sandy valley (community 2) than in water course community (community 1) old field community (community 4) and rocky hill community (community 6), the number of individuals with woolly diaspores were significantly lower in water course community (community1) than in rocky hill community (community 6) and the number of ombrohydrochoric individuals was found to be significantly higher in the rocky slopes community (community 5) than in the water course community (community 1). Autochory and hygrochasy was significantly higher in the rocky slopes (community 5) than in the water-course community (community 1) (Table 4.2, Figure 4.4).

Within communities

Some dispersal types show the same trend in all the communities (Table 4.3 A&B), Figure 4.4 & 4.5). Indirect hydrochory, dust diaspores and plumed diaspores are the dominant types in most communities. Epizoochory, endozoochory, balloon diaspores tumbleweeds, synaptospermy and heterodiaspory are represented in low numbers in all communities. Qualitative analysis showed less differences than quantitative analysis.

Table 4.2 Quantitative comparisons of dispersal spectra of six plant communities of Paulshoek and Remhoogte.

Dispersal type	Community						P
	1	2	3	4	5	6	<0.05
A. Telechory							
Zoochory							
Epizoochory	2.27	0.43	5.14	0.24	2.25	2.76	0.62 ^{ns}
Endozoochory	4.52	1.40	3.54	1.09	0.51	2.01	0.09 ^{ns}
Anemochory							
Dust diaspores	7.97	41.60	21.79	17.24	15.16	24.90	0.09 ^{ns}
Balloon diaspores	0.13	0.83	0.32	0.30	0.76	0.22	0.15 ^{ns}
Plumed diaspores	14.62 ^a	43.16 ^b	24.00 ^{ab}	11.38 ^a	16.07 ^{ab}	14.82 ^a	0.02*
Woolly diaspores	0.65 ^a	0.36 ^a	4.85 ^{ab}	5.41 ^{ab}	8.10 ^b	7.15 ^b	0.02*
Winged diaspores	3.65	3.82	9.41	8.09	12.61	10.90	0.26 ^{ns}
Tumbleweeds	0.00	0.00	0.05	0.00	0.01	0.00	0.55 ^{ns}
Autochory	4.54 ^a	12.95 ^{ab}	22.58 ^{ab}	14.59 ^{ab}	32.29 ^b	22.60 ^{ab}	0.00*
Hydrochory							
Nautohydrochory	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Ombrohydrochory	3.80 ^a	5.18 ^{ab}	17.85 ^{ab}	7.50 ^{ab}	33.40 ^b	17.62 ^{ab}	0.00*
B. Atelechory	10.82	4.50	11.80	20.11	7.52	3.51	0.30 ^{ns}
C. Additional features (Antitelechory)							
Anchorage mechanisms							
Myxospermy	14.10	4.92	17.34	12.20	13.41	7.59	0.59 ^{ns}
Trypanospermy	0.67	0.45	1.10	0.25	5.40	1.44	0.44 ^{ns}
Reduction in dispersal potential							
Synaptospermy	0.48	0.98	4.95	0.00	2.95	0.93	0.82 ^{ns}
Heterodiaspory	13.22	3.2	2.94	2.63	4.40	2.50	0.24 ^{ns}
Restriction of dispersal in time							
Hygrochasy	2.68 ^a	3.19 ^{ab}	13.39 ^{ab}	10.76 ^{ab}	20.45 ^b	20.69 ^b	0.00*

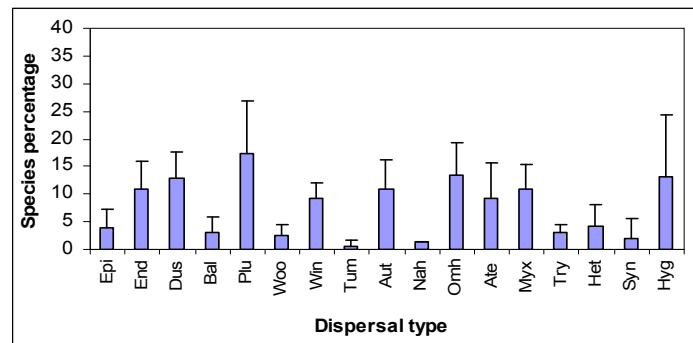
Table 4.3 Qualitative Comparisons of dispersal types within communities Within a column values with the same superscript do not differ significantly at $p < 0.05$

Dispersal type	Community					
	1	2	3	4	5	6
A Telechory						
Zoochory						
Epizoochory	3.86 ^{ab}	4.51 ^{abcd}	3.13 ^{abc}	2.18 ^{ab}	4.05 ^{abc}	6.81 ^{abcd}
Endozoochory	10.82 ^{ab}	6.49 ^{abcd}	3.15 ^{abc}	5.07 ^{abc}	3.67 ^{abc}	5.88 ^{abc}
Anemochory						
Dust diaspores	12.89 ^{ab}	23.57 ^{bcd}	17.86 ^{cd}	15.54 ^{bc}	15.40 ^{de}	16.93 ^{de}
Balloon diaspores	3.06 ^{ab}	3.50 ^{abc}	2.40 ^a	2.44 ^{ab}	2.36 ^{ab}	0.24 ^a
Plumed diaspores	17.47 ^b	17.03 ^{abcd}	16.6 ^{cd}	17.05 ^{bc}	15.49 ^{de}	18.74 ^e
Woolly diaspores	2.45 ^{ab}	4.24 ^{abcd}	5.39 ^{abcd}	6.35 ^{abc}	5.14 ^{abc}	7.65 ^{abcd}
Winged diaspores	9.10 ^{ab}	18.24 ^{abcd}	11.68 ^{abcd}	9.93 ^{bc}	13.86 ^{de}	15.75 ^{cde}
Tumbleweeds	0.45 ^a	0.00 ^a	0.21 ^a	0.00 ^a	0.12 ^a	0.00 ^a
Autochory	10.92 ^{ab}	26.73 ^d	18.43 ^{de}	17.00 ^{bc}	21.59 ^f	19.57 ^e
Hydrochory						
Nautohydrochory	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a
Ombrohydrochory	13.30 ^{ab}	25.25 ^{cd}	20.95 ^e	19.47 ^c	20.39 ^{ef}	17.48 ^{de}
B. Atelechory	9.30 ^{ab}	12.52 ^{abcd}	10.35 ^{abcd}	10.44 ^{abc}	9.59 ^{bcd}	9.29 ^{abcde}
C. Additional features (Antitelechory)						
Anchorage mechanisms						
Myxospermy	4.10 ^{ab}	7.27 ^{abcd}	9.20 ^{abcd}	14.51 ^{abc}	10.87 ^{cd}	10.07 ^{abcde}
Trypanospermy	11.00 ^{ab}	2.76 ^{abc}	5.84 ^{abcd}	3.70 ^{ab}	4.25 ^{abc}	4.93 ^{ab}
Reduction in dispersal potential						
Synaptospermy	2.96 ^{ab}	3.03 ^{abc}	2.51 ^{ab}	2.67 ^{ab}	1.82 ^a	1.74 ^{ab}
Heterodiaspores	2.07 ^{ab}	1.48 ^{ab}	1.62 ^a	0.00 ^a	1.28 ^a	2.23 ^{ab}
Restriction of dispersal in time						
Hygrochasy	13.26 ^{ab}	16.29 ^{abcd}	15.89 ^{bcd}	11.43 ^{abc}	14.59 ^{de}	11.36 ^{bcde}

Table 4.4 Quantitative comparisons of dispersal types within communities. Within a column values with the same superscript do not differ significantly at $p < 0.05$

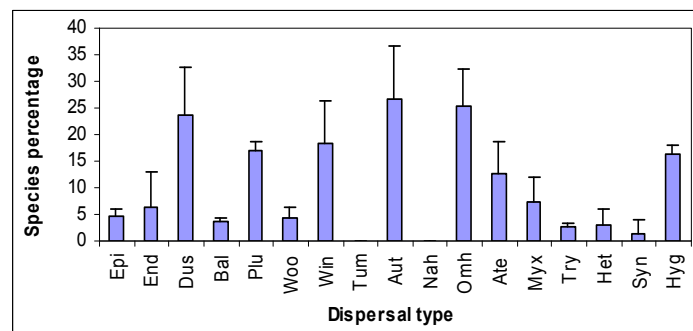
Dispersal type	Community					
	1	2	3	4	5	6
A. Telechory						
Zoochory						
Epizoochory	2.27 ^a	0.43 ^a	5.14 ^a	0.24 ^a	2.25 ^{ab}	2.76 ^{abc}
Endozoochory	4.52 ^a	1.19 ^a	3.54 ^a	1.09 ^a	0.51 ^a	2.01 ^{abc}
Anemochory						
Dust diaspores	7.97 ^{ab}	41.60 ^b	21.79 ^b	17.24 ^{ab}	15.16 ^{abc}	24.90 ^c
Balloon diaspores	0.12 ^a	0.83 ^a	0.32 ^a	0.30 ^a	0.76 ^a	0.22 ^{ab}
Plumed diaspores	14.62 ^b	43.16 ^b	24.04 ^b	11.37 ^{ab}	16.06 ^{abc}	14.81 ^{abc}
Woolly diaspores	1.09 ^a	0.36 ^a	4.85 ^a	5.41 ^a	8.10 ^{ab}	7.15 ^{abc}
Winged diaspores	3.35 ^a	3.82 ^a	9.41 ^{ab}	8.09 ^a	12.61 ^{ab}	10.90 ^{abc}
Tumbleweeds	0.09 ^a	0.00 ^a	0.05 ^a	0.00 ^a	0.01 ^a	0.00 ^a
Autochory	4.54 ^a	12.95 ^a	22.58 ^b	14.59 ^{ab}	32.29 ^c	22.60 ^{bc}
Hydrochory						
Nautohydrochory	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a	0.00 ^a
Ombrohydrochory	3.80 ^a	5.18 ^a	17.85 ^{ab}	7.49 ^a	33.39 ^c	17.62 ^{abc}
B. Atelechory	10.5 ^{ab}	4.51 ^a	11.80 ^{ab}	20.11 ^b	7.52 ^{ab}	3.51 ^{abc}
C. Additional features (Antitelechory)						
Anchorage mechanisms						
Myxospermy	10.82 ^{ab}	4.92 ^a	17.33 ^{ab}	12.20 ^{ab}	13.40 ^{ab}	7.59 ^{abc}
Trypanospermy	14.10 ^b	0.44 ^a	1.10 ^a	0.25 ^a	5.40 ^{ab}	1.44 ^{ab}
Reduction in dispersal potential						
Synaptospermy	0.67 ^a	3.20 ^a	2.63 ^a	2.63 ^a	4.40 ^{ab}	2.49 ^{abc}
Heterodiaspory	0.47 ^a	0.38 ^a	4.95 ^a	0.00 ^a	2.95 ^{ab}	0.94 ^{ab}
Restriction of dispersal in time						
Hygrochasy	2.69 ^a	3.19 ^a	13.39 ^{ab}	10.76 ^{ab}	20.45 ^{bc}	20.69 ^{abc}

a)



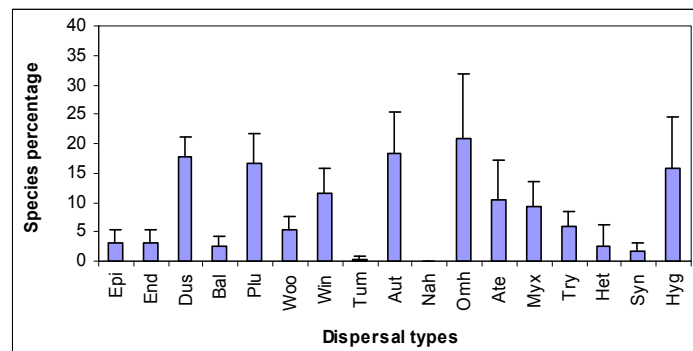
Water course community

b)



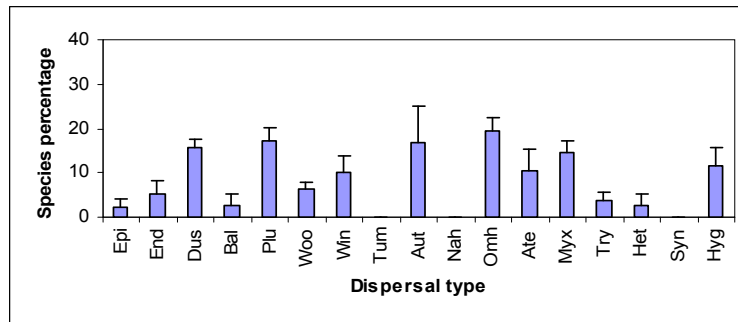
Sandy valley community

c)



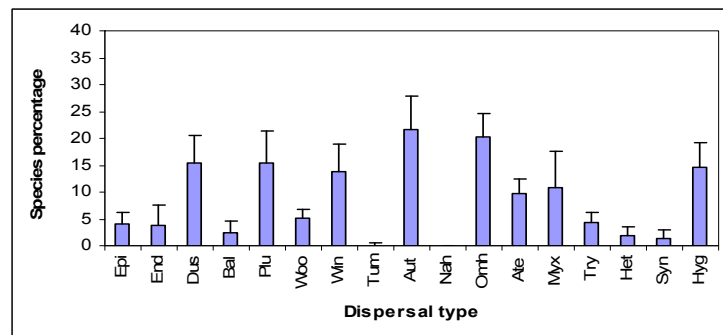
Plains community

d)



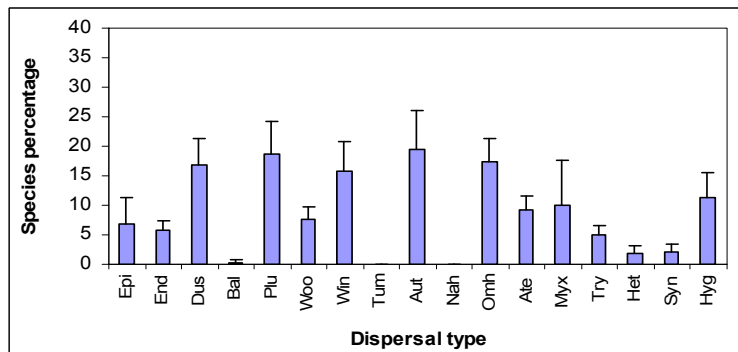
Old field community

e)



Rocky slope community

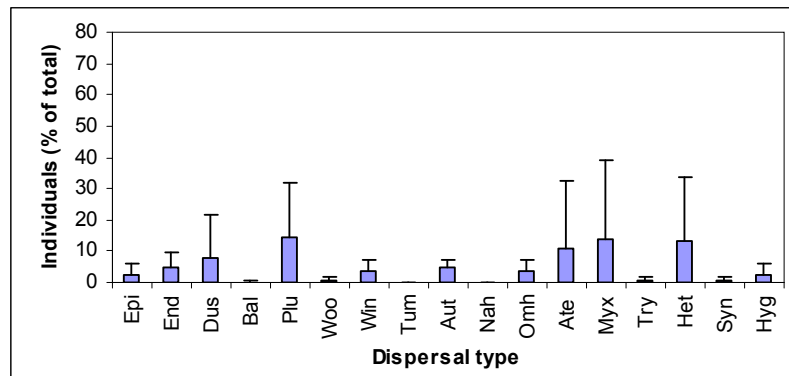
f)



Rocky hill community

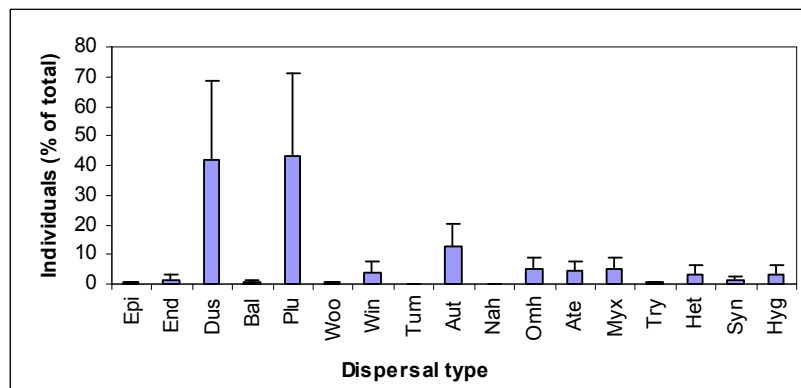
Figure 4.4 Qualitative dispersal spectra of plant communities of Paulshoek and Remhoogte. a) Water course community, b) sandy valley community, c) plains community, d) old field community, e) rocky slope community, f) rocky hill community. Abbreviations of dispersal types as defined in the text.

a)



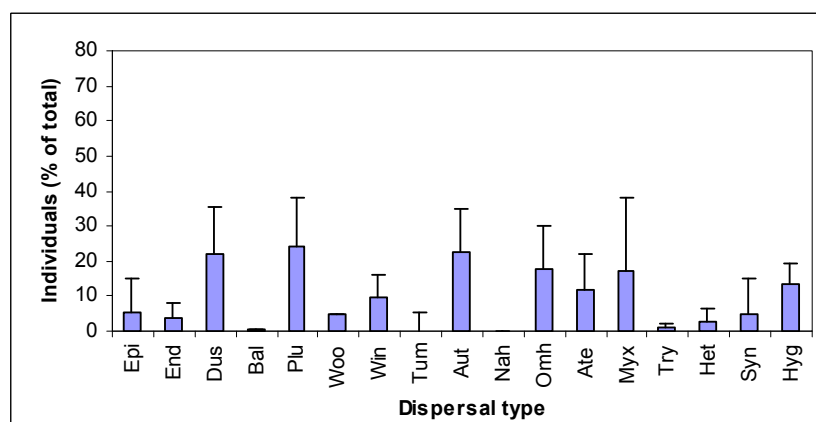
Water course community

b)



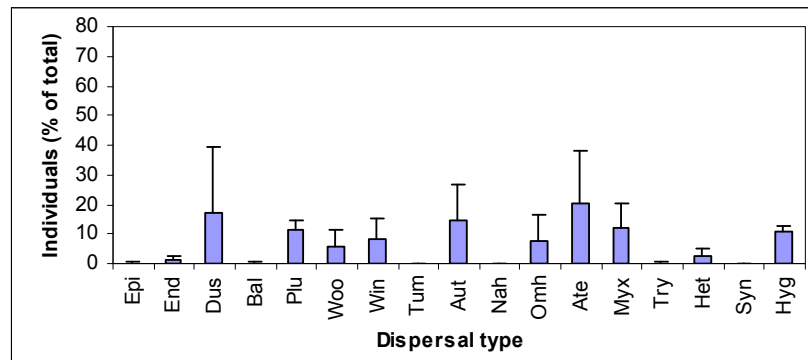
Sandy valley community

c)



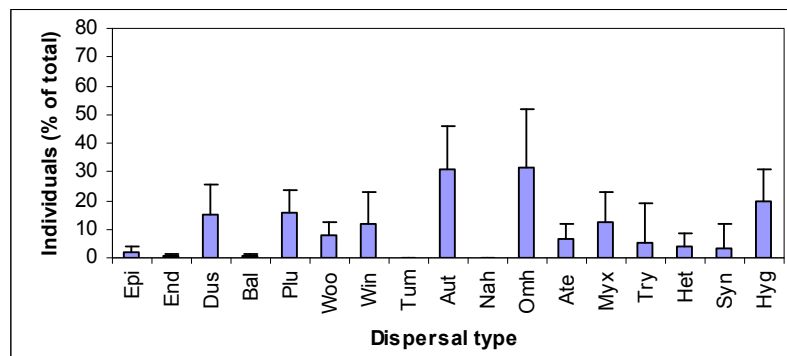
Plains community

d)



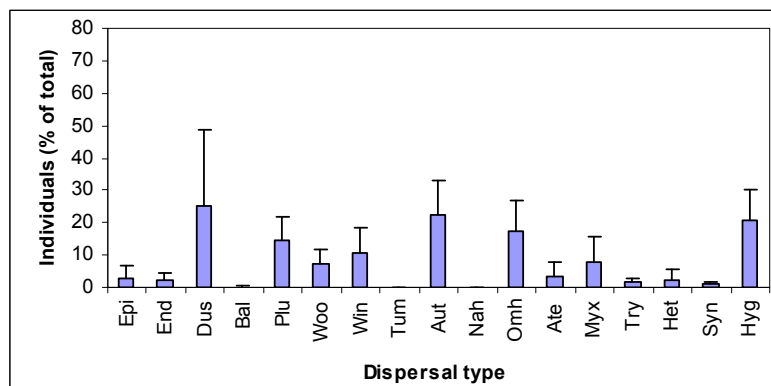
Old field community

e)



Rocky slope community

f)



Rocky hill community

Figure 4.5 Quantitative dispersal spectra of plant communities of Paulshoek and Remooghte. a) Water course community, b) sandy valley community, c) plains community, d) old field community, e) rocky slope community, f) rocky hill community. Abbreviations of dispersal types as defined in text.

4.5 Discussion

The results show clear differences between rangelands and communities for certain types of dispersal while others remain indifferent to management practices.

Retention times of seeds in the fur and in the tract of herbivores allow dispersal over long distances by zoochory (Couvreur *et al.* 2005). Zoochory in general, is a type of dispersal commonly found in forests or humid habitats (van Rooyen *et al.* 1990) and was not common in the present study. Epizoochorous plant species tend to be taxonomically diverse and rare. These plant species do not provide any means of attraction for their disseminators (Nakanishi 2000b), and have evolved in productive habitats, which support a large diversity and biomass of herbivorous mammals. This study did not support the hypothesis of many authors that epizoochory should be more prevalent in the overstocked rangeland (Collins and Uno 1985, Milton *et al.* 1990, Willson *et al.* 1990, Nakanishi 2000b), as no difference was found between the communal and commercial land.

A closer look at the dispersal spectra of the communities revealed the opposite trend with the less disturbed rocky slopes and hills (communities 5 and 6) showing high frequencies of epizoochorous species. In very arid areas epizoochoric species are generally limited to mesic sites in water courses and among rocks on ridges (Milton *et al.* 1990). This study only partially supports these findings because the riverbed and associated vegetation (community 1) did not have a large contribution by epizoochores. However the differences between the communities were not significant (Table 4.3A).

On the other hand the number of endozoochooric individuals was found to be significantly higher in communal land than in commercial land (Figure 4.3B). Herbivores can be important agents of dispersal for plants, even if they are not primarily seed eaters. Animal dung provides an ideal environment for germination of seeds and the growth of seedlings. The fibrous nature of undigested plant material means that it has good moisture retention qualities (Wilson *et al.* 1990). It is rich in nitrogen as well as organic matter which is easily broken down to inorganic nutrients by microorganisms (Dean and Yeaton 1992). Many endozoochorous seeds

germinate after a hard protective layer has been partly digested away (Stiles 1993) and these seeds are usually dispersed in large quantities increasing the probability of at least one seedling establishing. These advantages could explain the significantly higher number of endozoochorous species in the water course community (community 1) (Figure 4.4; Table 4.1) as it is one of the most grazed parts of the study area.

Dust, balloon, woolly and plumed diaspores as well as tumbleweeds, are all anemochoric mechanisms. Anemochory, although extensive, is not an essential mechanism of dispersal among seed plants, but is especially prominent among plant species of open habitats (Bansal and Sen 1981, Willson *et al.* 1990, Chambers and MacMahon 1994, Van Rheede van Oudtshoorn and Van Rooyen 1999). Van Rooyen *et al.* (1990) reported that 66.3% of the species of Namaqualand can be dispersed by wind.

Seed settling velocities vary between species, and low velocities can be very effective to promote long distance dispersal, but they are only reliable if the propagules become entrained by turbulence in convective updrafts above the vegetation canopy (Ozinga *et al.* 2004). Andersen (1992) and Redbo-Torstenson and Telenius (1995) suggested that variation in seed settling velocity may reflect difference in relative importance of dispersal life history and could be influenced by the timing of seed release relative to the seasonal periodicity of winds. Although small seeds such as dust diaspores are dispersed over long distances, larger seeds are only effectively dispersed by wind if their shape reduces the terminal velocity. Low terminal velocities have been measured for several plumed and woolly diaspores from Namaqualand (Van Rheede van Oudtshoorn and Van Rooyen 1999). However, wind dispersal along the soil surface can increase initial dispersal distances by several meters (Bakker *et al.* 1996).

According to Maddox (1985) and Bansal and Sen (1981) anemochory is regarded as a dispersal mode that developed under conditions of both climatic and biotic poverty. It is therefore not surprising that anemochory dominated the dispersal spectra of both these arid rangelands. Wind is a regular phenomenon in most desert areas and is minimally modified by vegetation acting as windbreak as is the case with a closed

habitat. The lack of significant difference found in most anemochoric dispersal modes (except woolly diaspores) between the two rangelands (Figure 4.3 A & B) is not surprising because even though the vegetation cover might be higher on the commercial land than on the communal land, the difference would not affect the wind action as desert plants are characteristically of low stature and allow wind circulation at all height levels (Arbelaez and Parrado-Rossellu 2005).

Woolly diaspores were generally not abundant in the study area. The genus *Eriocephalus* (shrubs) was the most dominant group with woolly diaspores especially the species *Eriocephalus microphyllus* var. *pubescens* (Appendix 2). High intensity grazing is said to reduce the perennial species in favor of annuals (Milton 1995, Todd and Hoffmann 1999, Hendricks *et al.* 2005). The number of species with woolly diaspores on the two rangelands is more or less the same. Significantly lower number of individuals with woolly diaspores in communal rangeland can be related to the decrease of *Eriocephalus* spp. plants due to overgrazing by livestock. According to Van Rheede van Oudtshoorn and Van Rooyen (1999) diaspores entirely covered by hairs are not so well adapted to anemochory and their movement not only depends on the wind velocity but, also on the air humidity. The lowest percentage of species with woolly diaspores was found in the water course community (community 1) which occurs in the riverbed and on its banks (Figure 4.2). This relatively moist habitat could reduce the dispersal ability of woolly diaspores.

One of the simplest means of gaining access to the wind is by being extremely small with a large surface to mass ratio. These dust diaspores are usually produced in enormous numbers at the cost of fewer, larger sized seeds. Dust diaspores are characteristic of lower taxa such as fungi and mosses, but they are also found in families of higher plants such as Crassulaceae, Campanulaceae and Poaceae (Van Rheede van Oudtshoorn and Van Rooyen 1999). Gutterman (1993) suggested that the production of numerous dust-like seeds by desert plants serves as an escape strategy to prevent mass consumption of seeds. This could be one of the reasons why the number of individuals with dust diaspores was found to be higher (although not statistically significantly) in communal land than in commercial land (Figure 4.3B).

Furthermore, in this study the most dominant life forms with dust diaspores are geophytes or annuals and the unpalatable shrub *Galenia africana* (Appendix 2). Many studies (Illius and O'Connor 1999, Fynn and O'Connor 2000) have highlighted increases of annual grasses under an intensive stocking density and the stability of perennials under a low stocking density. Therefore, the higher incidence of dust diaspores on communal land could be because of the high number of annuals as they are known to be opportunistic colonizers and the dominance of the unpalatable shrub *Galenia africana* on the communal land. The rarity of tumbleweeds in the study area is supported by Ellner and Schimida (1981) who suggested that tumbleweeds are generally rare in the semi-desert and almost absent in the desert region.

The significantly higher incidence of ombrohydrochory (Figure 4.2 and 4.3) on the commercial land is attributed to the contributions of hygrochasy and trypanospermy, which are both examples of indirect hydrochory.

Trypanospermy is an anchorage mechanism caused by the presence of a long appendage on the upperside of the diaspore which is composed of two parts, a basal part which is capable of spiral twisting by a hygroscopic mechanism, and an upper part which is always straight and at right angles to the basal part. The main advantage of trypanospermy is the enhancement of water uptake due to increased seed-soil contact brought about by the burial of the diaspore. It also affords anchorage against surface runoff, while the risk of predation is decreased as soon as the diaspores are buried. It is an adaptive convergence within two distinct families, the Poaceae and the Geraniaceae. These families were poorly represented in the study area explaining the low percentage of trypanospermic species, but in general trypanospermic species are few (7%) in Namaqualand (van Rooyen *et al.* 1990). No significant differences were found in the number of trypanospermic species/individuals between the two rangelands although the Design 2 analysis seems to indicate a larger contribution by trypanospermic individuals in the commercial land (Figure 4.3).

Hygrochasy may be due to a cohesion mechanism or an imbibition mechanism or a combination of both. Cohesion mechanisms are based mainly on the water content

of the cell lumen as opposed to imbibition mechanisms that are based on the water content of cell walls. The hygrochasic mechanisms of many desert plants families have been studied in detail (Van Rheede van Oudtshoorn and Van Rooyen 1999). Hygrochasy conveys many advantages to the species. Most hygrochasic species possess a canopy seed bank from which diaspores are slowly released, depending on the amount and frequency of rainfall. This is often referred to as dispersal in time and as a result the timing of germination is also delayed and spread (Van Rheede van Oudtshoorn and Van Rooyen 1999, Nakanishi 2000a). In absolute terms the dispersal distances covered by hygrochastic diaspores are limited (Ellner and Shmida 1981, Van Rheede van Oudtshoorn and Van Rooyen 1999, Parolin 2006).

In Namaqualand the Mesembryanthemaceae (currently often included in the Aizoaceae) is the dominant family that possesses hygrochasic capsules. Some members of this family are palatable but most are not. The significantly lower number of hygrochasic species in the communal land is therefore surprising (Figure 4.3 A & B). However, if overgrazing continues long enough and no more palatable species are left, livestock have to feed on less palatable species. The reduction of these individuals could be explained by the indirect and direct effects of overgrazing on plant population dynamics. Livestock might not feed on the leaves but could consume flowers when other palatable species become rare. Overgrazing could also alter habitat conditions. If these species restrict the dispersal of their seeds in space, most seedlings might fail to establish because the environment previously favourable for the mother plant has lost some of its characteristics and is no longer favourable for the next generation. Ihlenfeldt (1983) suggested that members of this family have very narrow ecological niches because of their unique dissemination system which makes it difficult to colonize more distant suitable sites. This could also explain the significantly lower number of hygrochasic and ombrohydrochoric individuals in the severely disturbed water course (community1) (Table 4.3, Figure 4.4 & 4.5) and the significantly higher number in the less disturbed rocky slope community (community 5) which occurs on commercial land. However, Ellner and Shmida (1981) argue that persistence is not merely a matter of the re-establishment in the mother plant's site and that other nearby sites suitable for establishment can be reached without special mechanisms for long-distance dispersal, and that the superior sites are reachable

only by dispersal in time. As a result of overgrazing these superior sites might have been lost altogether.

Myxospermy, in contrast to hygrochasy, is undoubtedly classified as a mode of restriction of dispersal in space. Given the advantages conferred to the seed by the mucilage it was expected that under the adverse conditions in the communal land myxospermic species would contribute a larger percentage to the total dispersal spectrum than in the commercial land. The results showed an opposite trend (Figure 4.2 & 4.3) as the number of species was significantly higher on commercial land than in communal land. Although mucilage might therefore confer resistance to some types of disturbance it does not seem to confer resistance to overgrazing. The primary role of mucilage is linked to seed germination and seedling establishment. Myxospermy acts after rather than during the primary dispersal phase (Ellner and Schmidha 1981). It therefore has little effect on the dispersal distances achieved by primary dispersal, although it does prevent secondary dispersal.

Soil surface conditions may determine the success or failure of establishment of plants and the type of contact made by the seed with the substrate could be critical in determining whether a seed germinates or not. Seeds may interact with variations in soil microtopography or soil crust to determine the abundance and proportion of different species becoming established (Harper *et al.* 1965, Harper and Benton. 1966, Zaady *et al.* 1997). In grazed areas, trampling may cause physical destruction or soil crumbling and loosening of the soil surface (Chambers and MacMahon 1994, Zaady *et al.* 2001). These changes of the soil microtopography might influence germination patterns of mucilaginous species.

Autochorous species are well represented in all communities except in community 1 (Figure 4.4 & 4.5). One ecological constraint for autochorous species is the seed size and the plant height, because neither very heavy nor very light seeds can be projected effectively. Hygroscopic movement occurs over a range of relative humidities and increase with time (Lacey 1980). The higher number of autochorous species in commercial rangelands and lower number in the water course community (community 1) largely reflect the contribution of hygrochasy as this mechanism is considered to be autochorous. Autochorous species do not disperse their seed over

a long distance and consequently there is a possibility of competition among siblings when the natural resources available are limited.

Flowing water as an agent of dispersal is primarily important for plants in or close to water. In deserts and arid shrublands nautohydrochory is accidental (Van Rheede van Oudtshoorn and Van Rooyen 1999). No nautohydrochorous species were found in this study area. Furthermore, to be a successful hydrochore it is not necessary for a species to have well-developed morphological adaptations for water dispersal. This emphasizes that classifying dispersal mechanisms strictly according to morphology can lead to false predictions on the dispersal capacity of a species (Johansson *et al.* 1996). The lack of nautohydrochory can be related to the landscape, for species inhabiting the rocky hills and slopes there would be no advantage if their seeds were to be carried by water currents from the hills to end up in the flat areas.

Heterodiaspory in plants is often linked with physiological polymorphism in some germination requirements. It typically occurs in annual, weedy species of variable, unpredictable environments such as frequently disturbed habitats in arid and semi-arid environments. Heterocarpy enhances the ability of a species to survive in a highly variable environment (Harper 1977, Venable and Levin 1985). This could explain the higher (although not significant) number of heterocarpic individuals in the communal land (Figure 4.2 & 4.3). When unsuitable environmental conditions arise, species with more than one type of dispersal are more likely to survive because different seed morphs usually differ in their dispersal mode and germination requirement, dormancy and competitive performance (Venable and Levin 1985, Beneke *et al.* 1992, Zhang 1994, Van Mølken *et al.* 2005). Plants grown from dispersed diaspores are usually more vigorous and produce more seeds than plants grown from non-dispersed diaspores, when conditions are favourable. Plants grown from the non-dispersed seeds, however are more stress tolerant and can produce some seeds in extreme conditions when others cannot (Beneke *et al.* 1992, Van Mølken *et al.* 2005).

Seed germination and seedling establishment are both crucial steps in the life cycle of a plant. The success of a species depends on every step of the life cycle; the interruption of one step might affect the survival negatively (Levine and Murell 2003).

Livestock grazing may affect the plant biomass and the reproductive capacity of plants and long-term grazing may affect the seed bank (Zaady *et al.* 2001). Most herbivores do not consume seeds, however, they feed on flowers, thus reducing seed production. Furthermore, Schupp and Fuentes (1995) argue that the best site for seed survival may not be best for germination; the best for germination may not be best for seedling growth or best for juvenile growth and survival. It is to be noted that the unequal number of relevés in each community could possibly influence the dispersal spectra, but we do believe that the difference could be minor as the percentage of dispersal types found on each community could be related to the level of disturbance and the position on the landscape.

4.6 Conclusions

Livestock grazing is commonly considered a disturbance that affects ecological systems, especially if the grazing pressure is high. It may also affect the abiotic environment for example nutrient and water flow and loosening or compaction of the soil. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands.

The high percentage of dust diaspores and heterocarpic species in the communal land is proof of the effect of grazing on the dispersal types and community structure. Dust diaspores can be easily dispersed by wind on soil that is compact or bare as a result of trampling and heterocarpic species can persist in spite of disturbance because of the different strategies displayed by the different seeds types on the same plant. A higher percentage contribution by epizoochorous species was expected in the communal land given the large number of livestock but no significant difference was found between the two land-uses. The lower number of hydrochastic species in the communal land could be the result of indirect effects of grazing on plant fitness and maybe on the soil microtopography. Many myxospermic species are highly palatable and their low number could be a direct result of grazing.

Plumed diaspores and ombrohydrochory are the dominant dispersal types in the study area. The most open community (community 2), was dominated by species with dust diaspores emphasizing the high activity of wind in this area. Water

definitely influences the spread of woolly species as they cannot be easily blown by wind when wet.

4.7 Appendix

Dispersal mode (or plant traits) of plants species found in the study area. Values in the last two columns indicate the total of individuals per species in the different land-uses

	Zoochory		Anemochory					Atelechory	Hydrochory	Autochory	Atelechoty		Total number of individuals					
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Acanthopsis carduifolia</i>											x		x		x		20.33	10.67
<i>Adromischus alstonii</i>			x														2.00	0.00
<i>Adromischus filicaulis</i> ssp. <i>filicaulis</i>			x														7.67	9.67
<i>Adromischus</i> sp.			x														1.67	0.00
<i>Adromischus marianiae</i> var. <i>immaculatus</i>			x														0.33	1.67
<i>Aizoon canariense</i>										x						x	11.22	133.33
<i>Albuca</i> sp. 1								x									0.00	8.33
<i>Albuca cooperi</i>								x									40.52	62.00
<i>Albuca longipes</i>								x									0.33	0.00
<i>Albuca</i> sp. 2								x									0.00	3.33
<i>Albuca viscosa</i>								x									3.00	13.33
<i>Albuca</i> sp. 3								x									0.33	2.00
<i>Aloe krapohlana</i>								x									1.00	0.00
<i>Amellus microglossus</i>					x												16.00	0.00
<i>Amsinckia calycina</i>									x								175.00	0.00
<i>Anacampseros karamontana</i>								x									0.67	0.00
<i>Anacampseros filamentosa</i> ssp. <i>namaquensis</i>								x									345.67	5.00
<i>Androcymbium</i> sp. 2									x								0.00	0.67
<i>Androcymbium</i> sp. 3									x								1.00	0.00
<i>Androcymbium</i> sp. 1									x								2.67	10.33
<i>Anisodonteia triloba</i>									x								0.67	0.00
<i>Anthospermum dregei</i> ssp. <i>dregei</i>				x													6.67	0.00
<i>Antimima</i> sp. 1										x	x				x		21.33	0.00
<i>Antimima</i> sp. 2										x	x				x		0.00	1.00
<i>Antimima</i> sp. 4										x	x				x		0.00	0.67
<i>Antimima</i> sp. 3										x	x				x		2.00	3.67
<i>Antimima clavipes</i>										x	x				x		5.33	0.00
<i>Antizoma miersiana</i>		x															0.67	0.00
<i>Aptosimum indivisum</i>										x					x		2.00	88.67
<i>Aptosimum spinescens</i>										x					x		0.00	0.67
<i>Arctotheca calendula</i>							x										2.00	4.33
<i>Arctotis acaulis</i>							x										5.00	0.33
<i>Arctotis laevis</i>							x	x									0.00	22.33
<i>Aridaria noctiflora</i> ssp. <i>noctiflora</i>										x					x		5.67	0.67
<i>Asclepias</i> sp.				x													0.00	0.33
<i>Asparagus capensis</i>		x															4.92	4.67
<i>Asparagus</i> sp.1		x															0.33	0.00
<i>Atriplex semibaccata</i>		x															2.67	89.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty					Total number of individuals		
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Atriplex lindleyi</i> ssp. <i>inflata</i>		x	x															2.00	0.33
<i>Avonia papyracea</i> ssp. <i>namaensis</i>								x										12.00	0.00
<i>Avonia quinaria</i> ssp. <i>quinaria</i>								x										0.33	0.00
<i>Babiana attenuata</i>																		0.83	15.33
<i>Ballota africana</i>									x									1.67	3.33
<i>Berkheya onobromoides</i>	x			x														0.67	4.00
<i>Bromus japonicus</i>	x																	167.00	0.00
<i>Brunsvigia boesmaniae</i>						x												1.00	1.33
<i>Bulbine</i> sp. 3								x										10.01	1.67
<i>Bulbine frutescens</i>								x										0.00	5.33
<i>Bulbine</i> sp.1								x										3.33	26.00
<i>Bulbine</i> sp. 2								x										15.67	9.00
<i>Bulbine praemorsa</i>								x										2.67	0.00
<i>Carpobrotus edulis</i>		x																2.67	15.33
<i>Cephalophyllum rigidum</i>										x							x	14.00	0.00
<i>Cephalophyllum</i> sp										x	x						x	0.00	3.33
<i>Chaetobromus dregeanus</i>	x			x						x	x			x	x			22.00	22.67
<i>Cheilanthes capensis</i>			x															15.00	0.00
<i>Cheiridopsis denticulata</i>										x	x						x	113.44	0.00
<i>Cheiridopsis imitans</i>										x	x						x	54.67	60.67
<i>Cheiridopsis namaquensis</i>										x	x						x	139.89	6.67
<i>Chenopodiaceae</i> sp			x															0.00	3.33
<i>Chenopodium album</i>			x															0.00	1.67
<i>Chlorophytum undulatum</i>								x										41.33	26.00
<i>Chrysocoma ciliata</i>					x													108.56	194.67
<i>Chrysocoma</i> sp. 1					x													0.00	0.00
<i>Conicosia elongata</i>								x	x									2.44	1.67
<i>Conophytum calculus</i> ssp. <i>vanzeylii</i>										x	x						x	0.00	1.00
<i>Cotula barbata</i>			x											x				45.00	0.00
<i>Cotula coronopifolia</i>			x											x				0.00	1.33
<i>Cotula leptalea</i>			x											x				220.33	43.33
<i>Cotyledon papillaris</i>			x															0.00	3.00
<i>Crassula atropurpurea</i>			x															5.33	2.33
<i>Crassula cotyledonis</i>			x															0.33	40.67
<i>Crassula deceptor</i>			x															0.00	3.00
<i>Crassula hemisphaerica</i>			x															3.67	1.67
<i>Crassula pyramidalis</i>			x															0.00	1.00
<i>Crassula umbellata</i>			x															0.00	1.00
<i>Crassula vaillantii</i>			x															4.67	355.33

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty					Total number of individuals		
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Crassula columnaris</i> ssp. <i>prolifera</i>			x															23.67	3.67
<i>Crassula</i> sp. 2			x															1.33	0.00
<i>Crassula muscosa</i> var. <i>muscosa</i>			x															8.67	4.33
<i>Crassula muscosa</i> var. <i>obtusifolia</i>			x															69.33	16.33
<i>Crassula sericea</i> var. <i>sericea</i>			x															6.67	66.00
<i>Crassula</i> sp. 3			x															0.00	16.67
<i>Crassula subaphylla</i> var. <i>subaphylla</i>			x															0.00	14.67
<i>Crassula subaphylla</i> var. <i>virgata</i>			x															22.11	6.67
<i>Cyphia longiflora</i>								x										9.00	5.67
<i>Diascia batteniana</i>			x															0.17	0.00
<i>Diascia rudolphii</i>			x															0.44	3.33
<i>Dicerotheramnus rhinocerotis</i>					x													0.00	12.67
<i>Dimorphotheca polyptera</i>								x					x					0.00	1.00
<i>Dimorphotheca sinuata</i>								x					x					1.33	0.00
<i>Dorotheanthus</i> sp. 5										x	x					x		11.67	34.67
<i>Drosanthemum</i> sp. 1										x	x					x		0.00	1.33
<i>Drosanthemum globosum</i>										x	x					x		0.67	1.33
<i>Drosanthemum hispidum</i>										x	x					x		0.00	10.00
<i>Drosanthemum</i> sp. 2										x	x					x		0.00	0.33
<i>Drosanthemum</i> sp. 4										x	x					x		5.50	11.00
<i>Drosanthemum</i> sp. 3										x	x					x		0.00	1.33
<i>Drosanthemum</i> sp.5										x	x					x		11.00	0.00
<i>Duvalia caespitosa</i>								x										7.67	4.00
<i>Ehrharta barbinodis</i>					x													102.00	92.33
<i>Ehrharta calycina</i>					x													6.67	9.33
<i>Eriocephalus africanus</i>								x										7.67	38.33
<i>Eriocephalus microphyllus</i> var. <i>pubescens</i>								x										413.17	156.00
<i>Eriospermum alicorne</i>								x										0.33	2.00
<i>Eriospermum paradoxum</i>								x										0.00	0.33
<i>Eriospermum</i> sp.								x										24.11	1.33
<i>Erodium cicutarium</i>					x					x					x			36.67	34.67
<i>Euphorbia decussata</i>													x					58.33	33.33
<i>Euphorbia mauritanica</i>													x					1.33	64.67
<i>Euphorbia muricata</i>													x					0.33	0.00
<i>Euryops dregeanus</i>								x										0.00	1.33
<i>Euryops multifidus</i>								x										2.00	0.00
<i>Felicia brevifolia</i>					x													1.00	9.33
<i>Felicia filifolia</i>					x													3.67	0.67
<i>Felicia merxmuelleri</i>					x													43.33	2.00
<i>Fockea comaru</i>								x										0.67	2.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty		Total number of individuals					
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxospermy	Trypanospermy	Synaptospermy	Hygrochasy	Remhoogte	Paulshoek
<i>Galenia africana</i>			x															58.89	504.33
<i>Galenia fruticosa</i>		x	x															1.00	0.33
<i>Galenia meziana</i>			x															2.75	58.00
<i>Galenia sarcophylla</i>			x															1.00	23.00
<i>Galium spurium-aparine</i>	x																	0.00	1.33
<i>Gazania lichtensteinii</i>					x								x					137.97	119.00
<i>Gazania othonnites</i>					x								x					2.00	2.00
<i>Gazania tenuifolia</i>					x								x					20.56	26.67
<i>Gethyllis sp.</i>		x																1.67	0.00
<i>Gnidia scabra</i>									x									3.33	0.00
<i>Gomphocarpus fruticosus ssp. fruticosus</i>					x													0.00	9.67
<i>Grielum humifusum</i>	x							x							x			3.67	0.00
<i>Hallianthus planus</i>										x						x		7.67	0.00
<i>Hermannia amoena</i>									x									1.00	7.00
<i>Helichrysum sp</i>					x													3.33	0.00
<i>Helichrysum cylindriflorum</i>					x													0.33	0.33
<i>Helichrysum leontonyx</i>					x													246.67	529.67
<i>Heliophila variabilis</i>													x					258.44	77.33
<i>Hermannia meyeriana</i>									x									13.33	0.00
<i>Hermannia cuneifolia var. cuneifolia</i>									x									32.67	23.67
<i>Hermannia cuneifolia var. glabrescens</i>									x									1.00	1.33
<i>Hirpicium alienatum</i>					x													107.33	30.67
<i>Hirpicium sp1</i>					x													0.33	0.00
<i>Hyobanche sanguinea</i>			x															1.67	668.67
<i>Hypertelis salsoloides</i>			x															3.83	65.67
<i>Jamesbrittenia sp</i>									x									0.00	2.33
<i>Juncus acutus</i>									x				x					0.00	3.33
<i>Juncus sp. 1</i>									x				x					0.00	333.33
<i>Juncus sp. 2</i>									x				x					0.00	6.67
<i>Lachenalia carnosia</i>									x									1.33	5.33
<i>Lachenalia sp. 1</i>									x									0.00	1.67
<i>Lachenalia mutabilis</i>									x									0.00	3.00
<i>Lachenalia sp. 3</i>									x									1.67	3.00
<i>Lachenalia sp. 2</i>									x									0.00	1.00
<i>Lampranthus godmaniae</i>										x					x			5.33	2.00
<i>Lampranthus meyeriana</i>										x					x			2.00	0.00
<i>Lampranthus sp.</i>										x					x			0.00	45.67
<i>Larryleachia cactiformis</i>							x											1.33	0.00
<i>Lasiospermum brachyglossum</i>							x											24.33	12.00
<i>Lebeckia multiflora</i>												x						67.67	9.00
<i>Leipoldtia schultzei</i>										x						x		322.59	0.00

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals						
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Lepidium desertorum</i>													x					183.33	58.33
<i>Lessertia capitata</i>				x														3.67	0.67
<i>Lessertia diffusa</i>				x														0.00	5.33
<i>Leysera tenella</i>					x								x					657.94	409.67
<i>Limeum africanum</i>								x										0.00	0.33
<i>Limonium dregeanum</i>								x										0.00	6.67
<i>Limonium sp.</i>								x										0.00	12.00
<i>Lotononis falcata</i>				x														13.83	37.33
<i>Lotononis oligocephala</i>				x														12.67	0.33
<i>Lotononis sp.</i>				x														3.33	0.00
<i>Lycium sp.</i>	x																	0.00	2.00
<i>Lycium cinereum</i>	x																	37.94	44.00
<i>Manochlamys albicans</i>	x																	6.22	0.00
<i>Manulea cheiranthus</i>			x															12.00	3.67
<i>Massonia depressa</i>								x										2.67	8.33
<i>Melolobium adenodes</i>															x			2.00	0.00
<i>Melolobium candicans</i>															x			0.33	0.00
<i>Mentha longifolia ssp. capensis</i>								x										0.00	8.67
<i>Mesembryanthemum guerichianum</i>										x							x	8.78	78.00
<i>Microloma sagittatum</i>						x												0.33	1.67
<i>Moraea bifida</i>								x										3.56	15.00
<i>Moraea fugax</i>								x										4.33	3.33
<i>Moraea serpentina</i>								x										167.28	116.00
<i>Oedera sedifolia</i>							x											0.00	4.00
<i>Oncosiphon grandiflorum</i>							x						x					45.67	32.67
<i>Oncosiphon suffruticosum</i>							x						x					194.33	7.00
<i>Orbea namaquensis/Quaqua mammilaris</i>						x												3.56	1.00
<i>Ornithogalum sp. 3</i>							x											3.33	0.00
<i>Ornithogalum maculatum</i>							x											5.00	0.00
<i>Ornithogalum sp. 1</i>							x											0.33	0.00
<i>Ornithogalum sp. 2</i>							x											0.00	1.00
<i>Ornithogalum pruinosum</i>							x											1.67	0.00
<i>Ornithogalum secundum</i>							x											0.00	13.00
<i>Ornithogalum unifolium</i>							x											0.00	2.00
<i>Ornithoglossum viride</i>								x										8.89	3.00
<i>Osteospermum pinnatum</i>	x								x									13.33	0.33
<i>Osteospermum rigidum var. rigidum</i>	x								x									0.33	5.67
<i>Othonna arbuscula</i>				x										x				5.00	0.00
<i>Othonna hederifolia</i>				x										x				4.00	0.33
<i>Othonna protecta</i>				x										x				2.22	0.33
<i>Othonna retrosa</i>				x										x				2.00	1.67

	Zoochory		Anemochory					Atelechory	Hydrochory	Autochory	Atelechoty		Total number of individuals					
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged	Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Oxalis</i> sp. 3											x						46.00	24.67
<i>Oxalis foveolata</i>											x						108.72	46.00
<i>Oxalis</i> sp. 1											x						0.00	58.67
<i>Oxalis</i> sp. 5											x						0.00	5.00
<i>Oxalis</i> sp. 4											x						0.00	6.67
<i>Oxalis obtusa</i>											x						11.78	102.67
<i>Oxalis</i> sp. 2											x						0.00	1.00
<i>Pelargonium carnosum</i>	x			x						x			x				37.17	12.67
<i>Pelargonium</i> sp. 2	x			x						x			x				4.00	4.33
<i>Pelargonium praemorsum</i>	x			x						x			x				0.00	0.33
<i>Pelargonium</i> sp.	x			x						x			x				0.50	0.00
<i>Pelargonium triste</i>	x			x						x			x				0.67	0.00
<i>Pelargonium</i> sp. 1	x			x						x			x				0.33	2.00
<i>Peliostomum virgatum</i>								x									2.33	8.33
<i>Pentzia incana</i>								x		x			x				57.89	56.67
<i>Pentaschistis airoides</i> ssp. <i>airoides</i>										x				x			24.33	16.67
<i>Polygonum aviculare</i>								x									0.00	1.00
<i>Polygonum kitaibelianum</i>								x									0.00	41.67
<i>Psilocaulon leptarhron</i>										x						x	0.67	0.33
<i>Pteronia ciliata</i>					x												25.33	0.00
<i>Pteronia divaricata</i>					x												1.17	0.00
<i>Pteronia glomerata</i>					x												2.00	3.67
<i>Pteronia incana</i>					x												17.33	39.00
<i>Pteronia mucronata</i>					x												0.00	0.33
<i>Pteronia camphorata</i> var. <i>camphorata</i>					x												0.00	2.67
<i>Pharnaceum exiguum</i>			x														0.00	166.70
<i>Rhus undulata</i>		x															0.00	2.33
<i>Rhynchosidium pumilum</i>					x												56.67	120.00
<i>Ruschia aggregata</i>										x						x	43.61	0.00
<i>Pharnaceum</i> sp.			x					x									7.33	0.33
<i>Pharnaceum croceum</i>			x					x									0.00	25.67
<i>Pharnaceum dichotomum</i>			x					x									6.67	1.33
<i>Phyllobolus congestus</i>										x	x				x		0.00	3.00
<i>Phyllobolus</i> sp. 2										x	x				x		9.00	3.33
<i>Phyllobolus</i> sp. 1										x	x				x		0.00	4.00
<i>Phyllobolus spinuliferus</i>										x	x				x		0.33	0.00
<i>Phyllobolus trichotomus</i>										x	x				x		1.00	3.33
<i>Polymita albiflora</i>										x	x				x		457.33	65.00
<i>Ruschia centrocapsula</i>										x	x				x		0.00	0.67

	Zoochory		Anemochory						Atelechory	Hydrochory	Autochory	Atelechoty			Total number of individuals				
	Epizoochory	Endozoochory	Dust	Balloon	Plumed/Hairs	Tumbleweed	Woolly	Winged		Nautohydrochory	Ombrohydrochory		Heterodiaspory	Myxosperry	Trypanosperry	Synaptosperry	Hygrochasy	Remhoogte	Paulshoek
<i>Ruschia goodiae</i>											x	x				x		72.00	3.67
<i>Ruschia grisea</i>											x	x				x		35.78	0.00
<i>Ruschia robusta</i>											x	x				x		78.56	0.67
<i>Ruschia sp. 1</i>											x	x				x		11.33	0.00
<i>Ruschia viridifolia</i>											x	x				x		72.00	119.67
<i>Salicornia sp.1</i>									x									0.00	22.00
<i>Sarcocaulon crassicaule</i>					x						x				x			4.78	0.00
<i>Sarcocaulon salmoniflorum</i>					x						x				x			10.33	0.33
<i>Sceletium exalatum</i>											x	x				x		0.00	18.00
<i>Schismus barbatus</i>			x															269.67	139.00
<i>Selago namaquensis</i>			x						x									6.67	3.00
<i>Selago divaricata</i>			x						x									0.33	1.00
<i>Senecio abruptus</i>					x									x				0.00	3.33
<i>Senecio arenarius</i>					x									x				1.67	0.00
<i>Senecio bulbinifolius</i>					x									x				0.33	0.00
<i>Senecio cinerascens</i>					x									x				0.33	0.00
<i>Senecio muricatus</i>					x									x				5.67	1.00
<i>Senecio niveus</i>					x									x				0.00	5.33
<i>Senecio radicans</i>					x									x				0.33	0.00
<i>Senecio rowleyanus</i>					x									x				1.00	1.33
<i>Senecio sisymbriifolius</i>					x									x				0.00	0.33
<i>Septulina glauca</i>		x																11.78	3.67
<i>Sonchus oleraceus</i>					x													0.00	1.33
<i>Spergularia media</i>								x										0.00	1.33
<i>Stachys rugosa</i>									x									0.00	1.00
<i>Stipagrostis brevifolia</i>	x				x						x	x			x			6.67	0.00
<i>Stipagrostis dregeana</i>	x				x						x	x			x			23.33	219.00
<i>Stipagrostis namaquensis</i>					x						x	x			x			27.33	2.33
<i>Sutherlandia frutescens</i>				x												x		0.33	0.00
<i>Tetragonia fruticosa</i>								x								x		20.33	19.00
<i>Thesium lineatum</i>		x																3.00	1.67
<i>Trachyandra falcata</i>									x									0.67	0.33
<i>Trachyandra tortilis</i>									x									32.67	13.67
<i>Tribolium utriculosum</i>	x								x									0.00	3.33
<i>Trichogyne lerouxiae</i>			x															50.33	842.00
<i>Trichogyne polycnemoides</i>			x															46.11	55.33
<i>Tripteris aghillana</i>								x						x				0.00	0.33
<i>Tripteris amplexens</i>								x						x				0.67	0.00
<i>Tripteris hyoseroides</i>								x						x				12.33	0.00

	Zoochory	Anemochory	Atelechory	Hydrochory	Autochory	Atelechoty	Total number of individuals
	Epizoochory Endozoochory	Dust Balloon Plumed/Hairs Tumbleweed Woolly Winged		Nautohydrochory Ombrohydrochory		Heterodiaspory Myxospermy Trypanospermy Synaptospermy Hygrochasy	Remhoogte Paulshoek
<i>Tripteris sinuata</i> var. <i>sinuata</i>			x			x	71.22 11.33
<i>Tulbaghia dregeana</i>			x				4.33 1.67
<i>Tylecodon</i> sp. 1		x					1.33 0.00
<i>Tylecodon</i> sp. 2		x					0.00 0.33
<i>Tylecodon reticulatus</i>		x					3.67 4.00
<i>Tylecodon wallichii</i>		x					0.00 0.33
<i>Ursinia nana</i> ssp. <i>nana</i>			x			x x	93.56 144.00
<i>Urtica</i> sp				x			0.00 5.00
<i>Wahlenbergia androsacea</i>		x					0.00 12.00
<i>Wahlenbergia divergens</i>		x					3.33 40.00
<i>Wahlenbergia oxyphylla</i>		x					12.00 0.67
<i>Wiborgia monoptera</i>			x			x	11.33 2.67
<i>Zaluzianskia benthamiana</i>		x					57.33 56.00
<i>Zygophyllum foetidum</i>				x			0.00 3.00
<i>Zygophyllum retrofractum</i>				x			212.44 2.33
<i>Zygophyllum sessilifolium</i>				x			9.00 8.67
<i>Zygophyllum spinosum</i>				x			1.67 0.33

4.8 References

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Chapter 5

Germination strategies of some mucilaginous seeds from Namaqualand:

Temperature and light requirements

5.1 Introduction

Seed germination and seedling establishment are the most remarkable and critical stages during a plant's life cycle. Germination is a risky transition, especially under arid climates, between the most drought tolerant stage and the weakest point in plant development (Guttermann 1993). It marks the end of a period of relative safety rendered by dormancy mechanisms, hard seed testas and the protection by soil. Germination is considered as a major environmental sieve controlling the population dynamics of a species (Harper 1977). Therefore, selection favours environmental cueing mechanisms that decrease the probability of encountering unacceptable growth conditions following germination.

Determining what controls the timing of seed germination in the field requires information on the seed, environmental conditions in the habitat, and how the two interact from the time of seed maturation to germination (Baskin and Baskin 1998). Factors such as temperature, moisture, light, oxygen, nutrients as well as combinations of all, play a major part in breaking dormancy and can inhibit, delay, or promote germination. The response to these factors depends on environmental and maternal influences during seed maturation. This response in turn determines the germination traits of a species (Guttermann 1993, Fenner 2000). The knowledge of these traits and understanding of the underlying processes controlling germination are of vital importance in understanding life history patterns among different plant species in a community.

The abiotic and biotic environmental factors of arid regions influence the adaptations and survival strategies of plants growing there. Arid areas or habitats are characterized by temperature fluctuations often extending beyond the limiting temperatures for germination, by recurrence of moisture deficiency and sometimes by deficiencies of nutrients in the soil. In addition, rainfall is unpredictable, and

precipitation at the beginning of the growing season will not always be followed by enough rainfall for plants to complete their life cycles (El-Sharkawi *et al.* 1989, Philippi 1993).

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Factors influencing the germination of these seeds are poorly known. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid the management and conservation of arid systems.

5.2 Materials and methods

Diaspores (referred to as seeds henceforth) of 23 mucilaginous species (24 seed types) were collected in spring or early summer from natural populations in the Namaqualand Klipkoppe Shrubland and Namaqualand Blomveld which form part of the Namaqualand Hardeveld Bioregion (Mucina and Rutherford 2006). Seeds were stored in brown paper bags at room temperature for a period of six months at the University of Pretoria, before commencing with germination trials.

Species used in this investigation included the following annuals: *Cotula barbata* DC., *Cotula thunbergii* Harv., *Foveolina dichotoma* (DC.), *Gazania lichtensteinii* Less Källersjö, *Heliophila lactea* Schltr., *Heliophila seselifolia* Burch. ex DC., *Heliophila thunbergii* (Eckl. & Zeyh) Steud var. *thunbergii*, *Heliophila variabilis* Burch. ex DC., *Heliophila* sp.1, *Heliophila* sp.2, *Oncosiphon grandiflorum* (Thunb.) Källersjö, *Senecio arenarius* Thunb., *Senecio cardaminifolius* DC., *Tripteris amplexans* Harv., *Tripteris hyoseroides* DC., *Ursinia calenduliflora* (DC.) N.E.Br. and *Ursinia cakilefolia* D.C. (dark and white achenes).

The following perennial species were investigated: *Gazania leiopoda* (DC.) Roessler, *Pentzia incana* (Thunb.) Kuntze, *Salvia dentata* Aiton, *Senecio niveus* (Thunb.) Willd. *Tripteris oppositifolia* (Aiton) B.Nord. and *Tripteris sinuata* DC.

Seeds were germinated in either 50 mm or 90 mm Petri dishes containing two layers of filter paper to which approximately 4 cm³ or 6 cm³ distilled water was added respectively. Germination tests were conducted in incubators and each treatment consisted of four replicates of 50 seeds for each species. To determine the effect of light and different temperature regimes on germination, tests were conducted in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 mol. m⁻² s⁻¹) and dark at six constant temperatures (7°C, 12°C, 17°C, 22°C, 27°C, 32°C) and one alternate temperature regime (12°C/22°C; 12h/12h). Petri dishes of the dark treatment were placed in cardboard boxes and sealed with aluminum foil to prevent light from penetrating. Germination of dark replicates was counted under a green safety light.

Trials continued over a 30 day period. Petri dishes were examined every day during the first seven days of germination and every two days the following weeks. Germination was considered to have occurred when the radicle protruded.

The optimal temperature for germination (T_o) of a specific species was calculated as:

$$T_o = \sum tp / \sum p,$$

where p is the percentage germination at temperature t (Kochankov *et al.* 1998, De Villiers 2000).

The mean germination time (MGT) of each treatment and species was calculated using the equation:

$$MGT = \sum Dn / \sum n$$

where n is the number of seeds which germinate on day D and D is the number of days counted from the beginning of the test (De Villiers 2000).

All data were analyzed using an analysis of variance (ANOVA) of the STATISTICA 7 computer program (Statsoft, Tulsa). The least significant difference (LSD) *post hoc* test was used to determine significant differences ($P \leq 0.05$) in germination percentages and mean germination time between different treatments within a species. The LSD multifactor ANOVA was used to determine significant differences between light and dark and temperature treatment at a $P \leq 0.05$ level.

A principal coordinates analysis (PCoA) in the computer program Syn-Tax 2000 (Podani 2001) was used on mean germination percentages at different temperatures to find patterns in the germination behaviour among species.

5.3 Results

The temperature and light requirements for germination of the 23 mucilaginous species of Namaqualand (24 seed types) investigated, are presented in Tables 5.1, 5.2, and 5.3. Species and seed types were grouped according to their optimum temperature, mean germination time as well as to their responses to light conditions

Significantly higher germination percentages in dark treatments were obtained for seven species (30% of species investigated) (Table 5.1). The majority of these species are annuals except the perennial *Salvia dentata*, and they all have a low ($\leq 17^{\circ}\text{C}$) optimal germination temperature. In general, their germination percentages are higher than 50% in the temperature range from 12-17°C in the dark (Table 5.1).

Almost half (11 species) of the species investigated required light for optimum germination and all of these species were annuals except the perennial *Tripteris oppositifolia*, (Table 5.1). They can be classified into three groups according to their optimum germination temperature: species with optimum temperature (T_{opt}) in the light $\leq 17^{\circ}\text{C}$, those with T_{opt} in light $> 17-20^{\circ}\text{C}$ and finally species with $T_{\text{opt}} > 20^{\circ}\text{C}$.

The majority of the perennial species (four species) investigated and two annuals were not significantly affected by light (26% of the total number of species). As light requiring species, they could also be divided into three groups according to their optimum germination temperature.

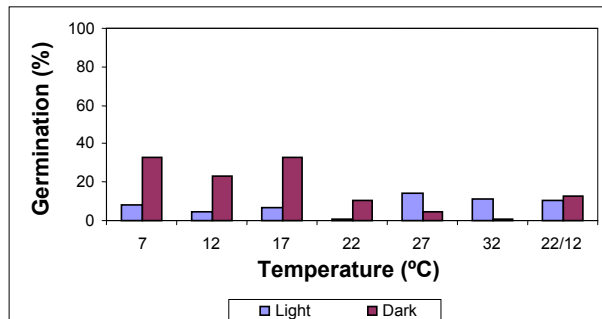
Table 5.1 Mean germination percentage of 23 myxospermic plant species of Namaqualand, at different temperature treatment under light and dark conditions. Within each species values followed by the same letter are not significantly different at $p \leq 0.05$

	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	P-value
Species where mean germination percentages were significantly higher in the dark than in the light															
Species with low optimum temperature in dark $T_{opt} \leq 17^\circ\text{C}$															
<i>Heliophila lacteal</i> (A)	8.0 ^{bc}	4.5 ^b	6.5 ^{bc}	1.0 ^a	14.5 ^{cd}	11.5 ^c	10.5 ^c	32.5 ^d	23.5 ^f	33.0 ^g	10.5 ^c	4.5 ^b	1.0 ^a	13.0 ^{cd}	0,001
<i>Ursinia cakilefolia</i> (dark) (A)	36.0 ^e	6.5 ^{abccc}	44.0 ^g	12.0 ^d	5.0 ^{abcc}	4.5 ^{abcc}	4.0 ^{ab}	53.5 ^f	11.0 ^d	56.0 ^h	9.5 ^{abccc}	7.0 ^{abccc}	2.0 ^a	26.5 ^e	0,000
<i>Heliophila</i> sp. 1 (A)	79.5 ^{ef}	74.0 ^{ef}	41.2 ^{cd}	34.5 ^{bc}	24.5 ^b	1.0 ^a	32.0 ^{bc}	88.0 ^j	79.5 ^{ef}	67.5 ^e	32.5 ^{bc}	21.0 ^d	2.0 ^a	70.5 ^e	0,000
<i>Heliophila</i> sp. 2 (A)	34.0 ^{cd}	61.0 ^{ef}	61.5 ^{ef}	65.0 ^f	30.0 ^{bc}	5.0 ^a	33.0 ^c	58.0 ^{def}	67.5 ^f	61.0 ^{ef}	71.0 ^f	39.0 ^{cde}	6.0 ^{ab}	62.0 ^{ef}	0,000
<i>Heliophila variabilis</i> (A)	72.0 ^g	72.0 ^g	62.0 ^{ef}	44.0 ^c	52.0 ^{cde}	14.0 ^a	53.0 ^{cde}	82.0 ^g	80.0 ^g	72.0 ^g	51.0 ^{cd}	56.0 ^{de}	26.0 ^b	71.0 ^g	0,000
<i>Heliophila thunbergii</i> var. <i>thunbergii</i> (A)	11.0 ^{def}	6.5 ^{bcd}	6.6 ^{bcd}	1.0 ^a	1.0 ^a	0.0 ^a	4.0 ^{abc}	12.5 ^{ef}	12.5 ^{ef}	12.0 ^{def}	8.4 ^{cde}	3.0 ^{ab}	0.0 ^a	16.0 ^f	0,000
<i>Salvia dentate</i> (P)	45.0 ^{bc}	66.5 ^{cde}	61.5 ^{cde}	42.0 ^b	42.6 ^b	10.0 ^a	8.0 ^a	67.0 ^{de}	89.5 ^a	54.7 ^{bcd}	40.7 ^d	42.7 ^{bc}	6.7 ^a	49.6 ^{cd}	0,000
Species where mean germination percentages were significantly higher in the light than in the dark															
Species with low optimum germination temperature in light ($T_{opt} \leq 17^\circ\text{C}$)															
<i>Tripteris oppositifolia</i> (P)	34.0 ^{cd}	50.5 ^e	43.3 ^{de}	30.8 ^c	16.0 ^b	1.5 ^a	20.0 ^b	18.5 ^b	35.5 ^{cd}	33.3 ^{cd}	16.0 ^b	10.5 ^{ab}	0.5 ^a	9.5 ^{ab}	0,000
<i>Senecio cardaminifolius</i> (A)	36 ^f	31.0 ^f	36.0 ^f	23.5 ^e	16.5 ^d	4.5 ^{abc}	22.0 ^e	19.5 ^{ad}	7.0 ^{bc}	8.5 ^c	2.0 ^{ab}	2.5 ^{ab}	0.0 ^a	2.0 ^{ab}	0,000
<i>Cotula barbata</i> (A)	100.0 ^f	100.0 ^f	91.5 ^{ef}	98.0 ^{ef}	84.0 ^{de}	59.5 ^c	100.0 ^f	100.0 ^f	72.0 ^{cd}	75.5 ^d	22.5 ^b	6.5 ^a	12.5 ^{ab}	16.5 ^{ab}	0,000
<i>Ursinia cakilefolia</i> (white) (A)	54.0 ^f	26.0 ^f	51.5 ^{gh}	28.0 ^f	19.5 ^{cdef}	2.0 ^a	20.5 ^{def}	43 ^f	16.5 ^{bcd}	54.0 ^h	25.5 ^{ef}	15.5 ^{bcd}	9.0 ^{ab}	11.0 ^{ab}	0,000
Species with intermediate optimum germination temperature in light ($17 < T_{opt} \leq 20^\circ\text{C}$)															
<i>Cotula thunbergii</i> (A)	94.0 ^{ef}	87.5 ^{de}	93.5 ^{ef}	92.5 ^{ef}	97.5 ^f	81.5 ^d	93.5 ^{ef}	64.0 ^c	67.0 ^c	29.5 ^b	9.0 ^a	9.5 ^a	5.0 ^a	6.0 ^a	0,000
<i>Foveolina dichotoma</i> (A)	29.5 ^d	30.0 ^d	23.5 ^g	17.0 ^{de}	10.5 ^{bcde}	19.5 ^{ef}	16.0 ^{de}	28.0 ^d	10.0 ^{bcde}	12.0 ^{cd}	3.5 ^{ab}	2.5 ^a	1.5 ^a	5.5 ^{abc}	0,000
<i>Heliophila seselifolia</i> (A)	50.0 ^f	32.5 ^{de}	46.5 ^f	33.0 ^e	30.5 ^{de}	21.5 ^c	45.0 ^f	64.5 ^d	25.5 ^{cde}	24.0 ^{cd}	12.0 ^b	3.5 ^a	0.0 ^a	17.5 ^{bc}	0,000
<i>Oncosiphon grandiflorum</i> (A)	19.0 ^{cde}	23.5 ^{def}	37.0 ^g	17.5 ^{bcde}	28.0 ^f	12.0 ^b	25.5 ^{ef}	16.0 ^{bc}	5.0 ^a	3.0 ^a	2.5 ^a	0.0 ^a	1.5 ^a	0.5 ^a	0,000
<i>Ursinia calenduliflora</i> (A)	44.5 ^{ef}	51.0 ^{gh}	66.0 ^g	47.5 ^{ef}	31.0 ^d	16.0 ^b	41.0 ^e	21.0 ^{bc}	32.5 ^d	29.5 ^{cd}	21.0 ^{bc}	15.5 ^d	1.0 ^a	23.5 ^{bcd}	0,000
Species with high optimum germination temperature in light ($T_{opt} \geq 20^\circ\text{C}$)															
<i>Senecio arenarius</i> (A)	30.5 ^{cd}	11.5 ^{ab}	22.5 ^{bc}	41.0 ^{de}	67.0 ^f	46.5 ^e	33.5 ^{cd}	25.5 ^c	3.0 ^a	6.6 ^a	2.0 ^a	3.0 ^a	1.5 ^a	3.0 ^a	0,000
<i>Tripteris amplexens</i> (A)	2.0 ^a	13.0 ^{cd}	26.0 ^e	63.0 ^g	40.0 ^f	21.0 ^{de}	37.0 ^f	2.5 ^{ab}	12.0 ^{bcd}	8.0 ^{abc}	10.0 ^{abc}	8.5 ^{abc}	4.0 ^{abc}	4.0 ^{abc}	0,000
Species where mean germination percentages were not significantly different between light and dark															
Species with low optimum germination temperature ($T_{opt} \leq 17^\circ\text{C}$)															
<i>Senecio niveus</i> (P)	79.0 ^{bcd}	83.0 ^{bcd}	82.0 ^{bcd}	90.0 ^{cde}	86.0 ^{bcd}	70.5 ^{abc}	91.5 ^{de}	100.0 ^e	84.5 ^{bcd}	59.0 ^a	83.0 ^{bcd}	75.5 ^{abcd}	80.5 ^{bcd}	69.5 ^{abc}	0,140
Species with intermediate optimum germination temperature in light ($17 < T_{opt} \leq 20^\circ\text{C}$)															
<i>Gazania leiopoda</i> (P)	70.0 ^{ef}	65.0 ^{cdef}	62.0 ^{cdef}	48.5 ^a	51.0 ^{ab}	48.5 ^a	57.5 ^{abc}	61.5 ^{cde}	72.0 ^f	72.5 ^f	59.5 ^{bcd}	47.0 ^a	47.0 ^a	67.5 ^e	0,0000
<i>Gazania lichtensteini</i> (A)	25.5 ^{cdef}	27.5 ^{cde}	19.5 ^{bcde}	19.0 ^{bcd}	25.0 ^{cdef}	14.0 ^{ab}	19.5 ^{bcde}	26.0 ^{ef}	35.0 ^d	17.5 ^b	16.5 ^b	18.5 ^{bc}	9.5 ^a	13.0 ^{ab}	0,0000
<i>Tripteris sinuata</i> (P)	59.0 ^d	59.0 ^d	59.0 ^{cd}	55.0 ^{cd}	38.0 ^b	18.0 ^a	56.0 ^d	47.5 ^d	60.0 ^d	47.5 ^d	45.2 ^{cd}	50.0 ^c	19.5 ^a	5.07 ^d	0,000
Species with high optimum germination temperature in light ($T_{opt} > 20^\circ\text{C}$)															
<i>Pentzia incana</i> (P)	0.0 ^a	0.5 ^{ab}	4.0 ^{abc}	2.0 ^{ab}	9.0 ^c	1.0 ^{ab}	3.0 ^{ab}	0.0 ^a	2.5 ^{ab}	3.0 ^{ab}	5.5 ^{bc}	2.8 ^{ab}	2.0 ^{ab}	1.5 ^{ab}	0,040
<i>Tripteris hyoseroides</i> (A)	0.0 ^a	0.0 ^a	7.0 ^{bcd}	7.5 ^{cd}	10.0 ^d	2.5 ^b	4.5 ^{abc}	1.5 ^a	1.0 ^a	6.5 ^{bcd}	6.5 ^{bcd}	2.5 ^{ab}	1.0 ^a	3.0 ^{abc}	0,000

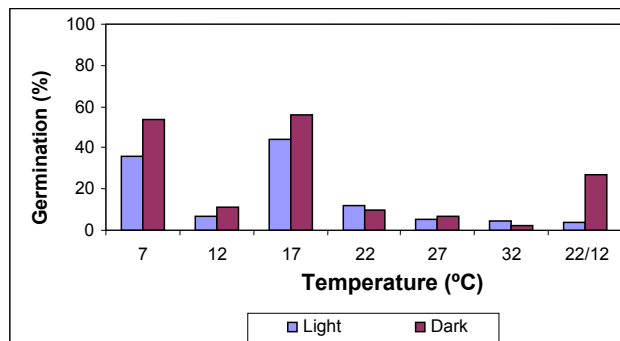
A-Annual

-Treatment not used for this species/seed type

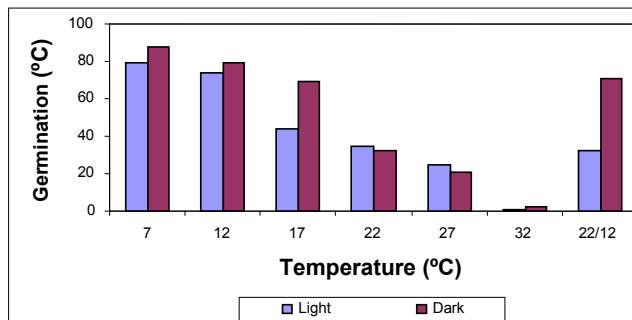
P-Perennial



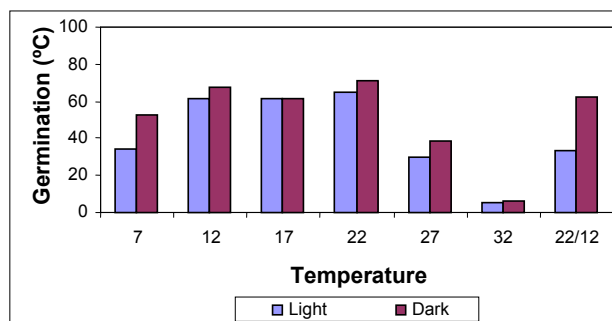
Heliophila lactea



Ursinia cakilefolia (black achenes)

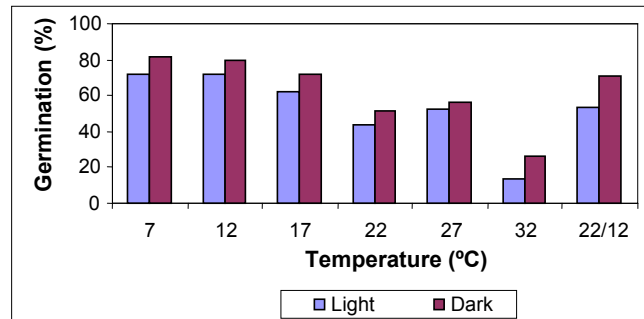


Heliophila sp. 1

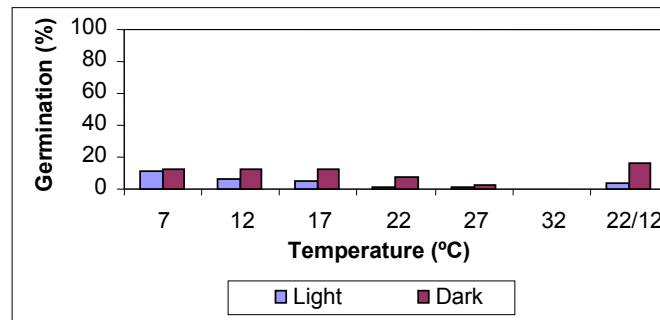


Heliophila sp. 2

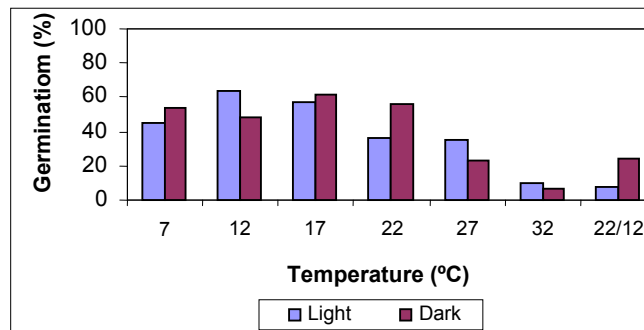
Figure 5.1 Germination percentages of 23 myxospermic species in light and dark at different temperatures. Order follows that in Table 5.1.



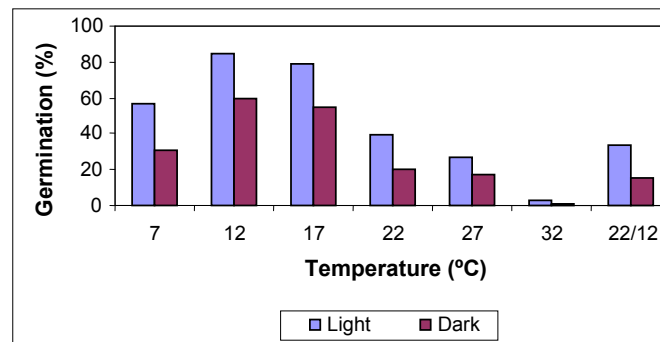
Heliophila variabilis



Heliophila thunbergii var. *thunbergii*

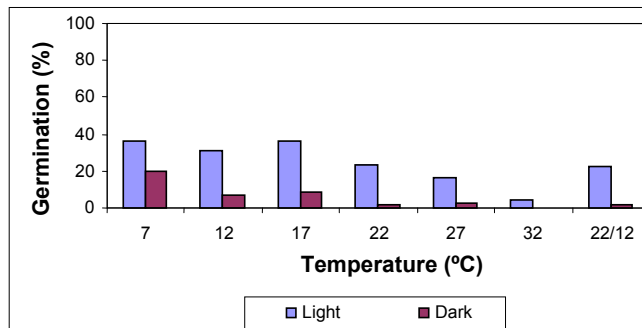


Salvia dentata

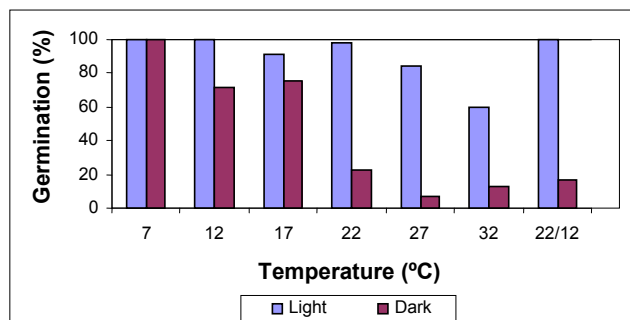


Tripteris oppositifolia

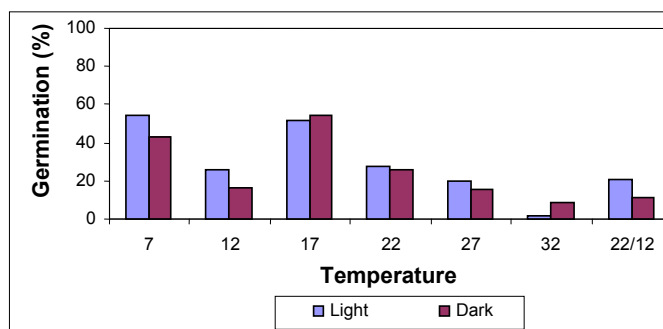
Figure 5.1 (Continued)



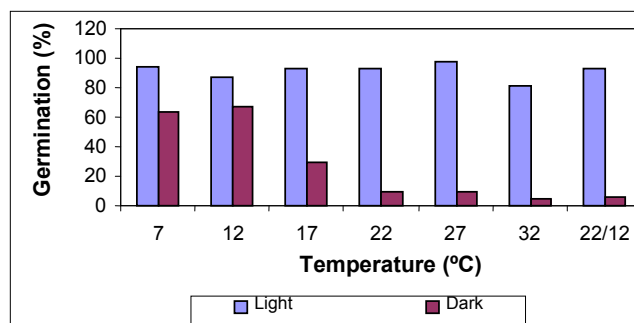
Senecio cardaminifolius



Cotula barbata

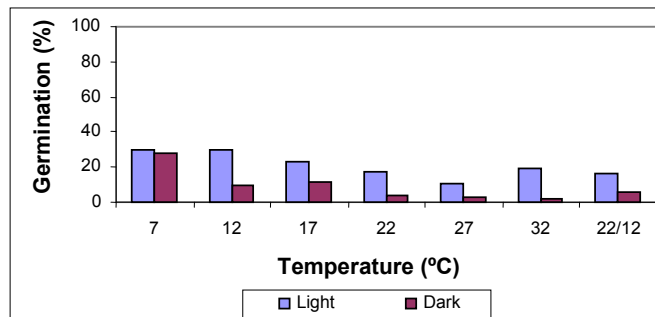


Ursinia cakilefolia (white achenes)

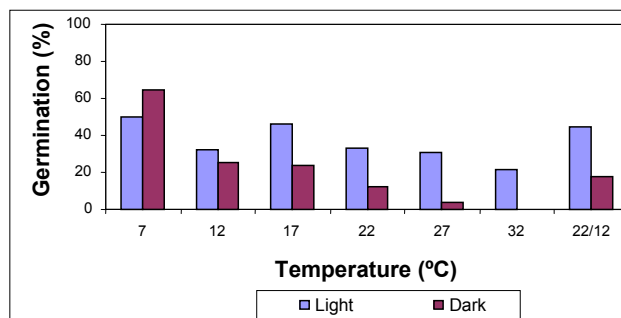


Cotula thunbergii

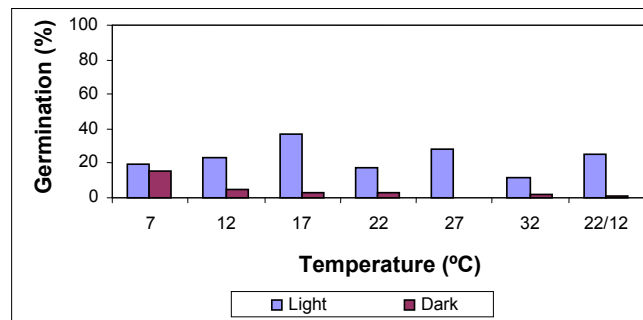
Figure 5.1 (Continued).



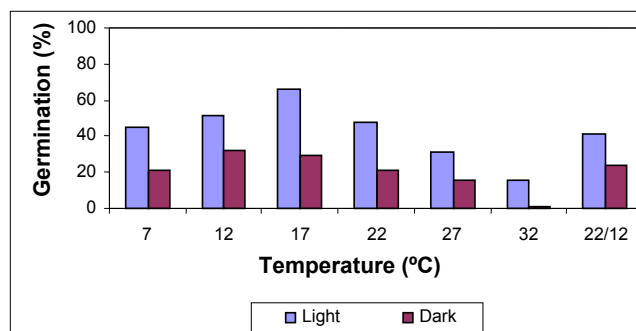
Foveolina dichotoma



Heliophila seselifolia

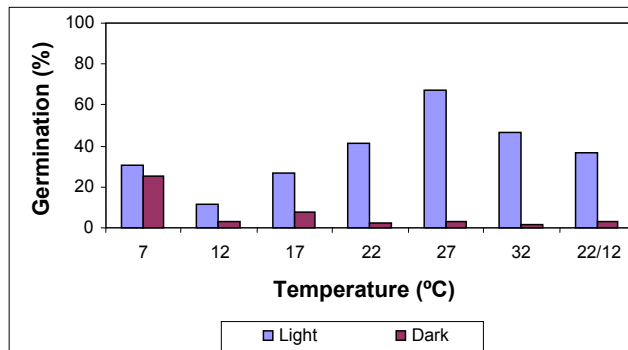


Oncosiphon grandiflorum

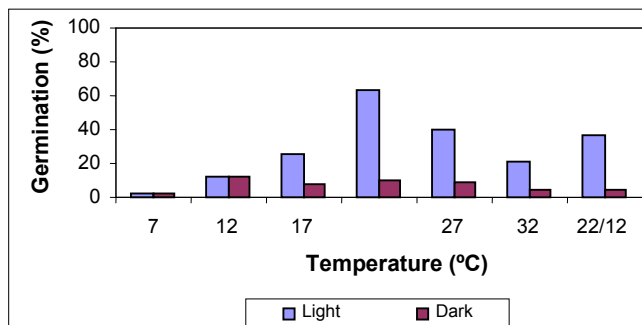


Ursinia calenduliflora

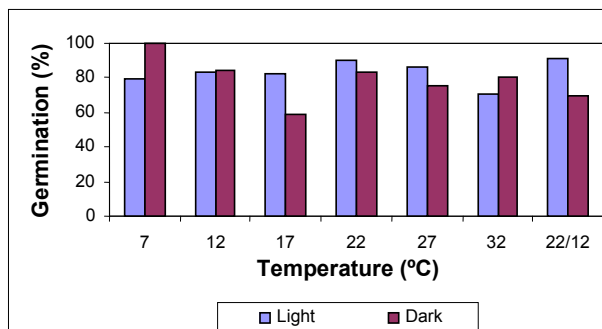
Figure 5.1 (Continued).



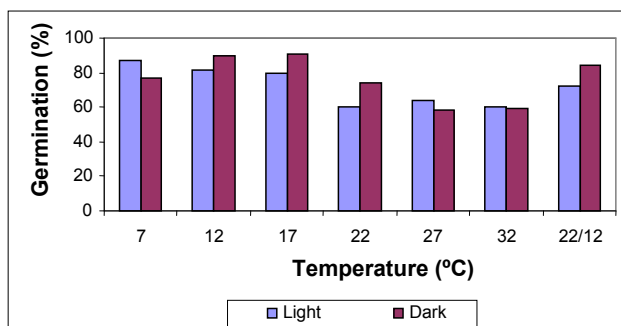
Senecio arenarius



Tripteris amplexans

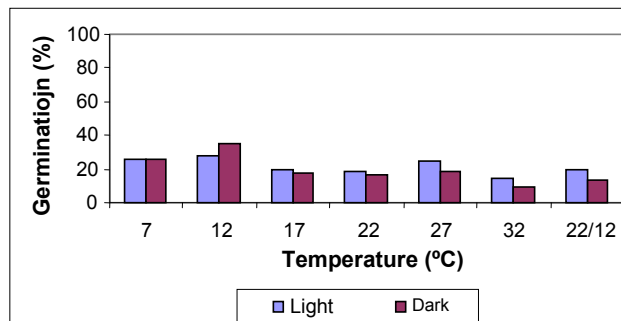


Senecio niveus

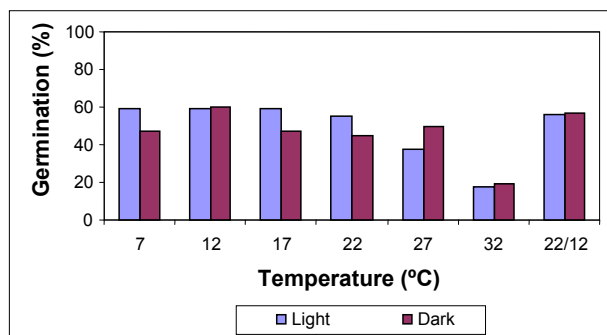


Gazania leiopodia

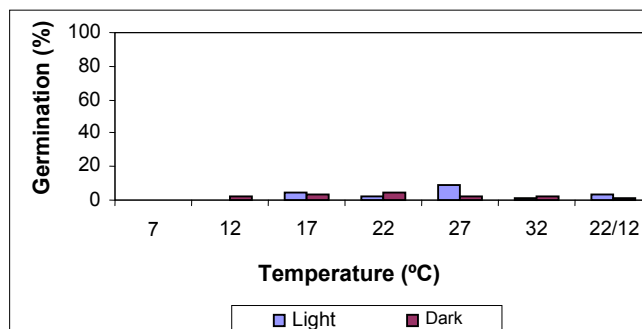
Figure 5.1 (Continued).



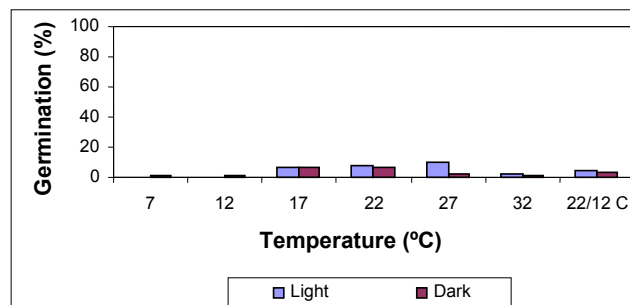
Gazania lichtensteinii



Tripteris sinuata



Pentzia incana



Tripteris hyoseroides

Figure 5.1 (Continued).

Table 5.2 Mean time to germination (days), of 23 myxospermic plant species of Namaqualand, at different temperature treatments under light and dark conditions. Within each species, values followed by the same letter are not significantly different at $p \leq 0.05$

	Light							Dark							Temp	Dark/light
	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C	7°C	12°C	17°C	22°C	27°C	32°C	22/12°C		
Mean time to germination was significantly shorter in light than in dark																
<i>Cotula thunbergii</i> (A)	12.4 ^g	7.1 ^{abcd}	5.3 ^{ab}	4.9 ^a	4.9 ^a	7.2 ^{abcd}	5.6 ^{ab}	14.0 ^g	9.7 ^{def}	10.0 ^{ef}	88.4 ^{1cde}	6.21 ^{abc}	20.7 ⁱ	7.8 ^{bcd}	0,000	0,000
<i>Foveolina dichotoma</i> (A)	8.9 ^{abc}	7.1 ^{ab}	5.5 ^a	5.8 ^a	6.7 ^{ab}	5.6 ^a	5.8 ^a	10.6 ^{bc}	13.0 ^c	12.7 ^c	10.1 ^{bc}	7.6 ^{ab}	6.3 ^{ab}	12.7 ^c	0,100	0,002
<i>Cotula barbata</i> (A)	11.9 ^{df}	6.7 ^{bc}	5.9 ^{abc}	5.5 ^{abc}	9.2 ^d	10.1 ^{de}	4.1 ^a	15.2 ^f	7.5 ^c	7.5 ^c	5.5 ^{ab}	11.5 ^{ef}	12.0 ^f	5.9 ^{abc}	0,000	0,000
<i>Gazania lichtensteinii</i> (A)	17.8 ^d	7.5 ^{ab}	5.9 ^a	7.6 ^{ab}	8.2 ^{ab}	10.2 ^{bc}	9.9 ^b	21.7 ^e	13.8 ^c	11.1 ^{bc}	7.8 ^{ab}	6.9 ^{ab}	7.4 ^{ab}	10.1 ^b	0,000	0,022
<i>Heliophila seselifolia</i> (A)	5.6 ^f	3.9 ^{de}	3.0 ^{cd}	2.9 ^{ab}	3.0 ^b	2.9 ^{ab}	4.3 ^a	6.3 ^g	3.7 ^{cd}	3.0 ^b	2.8 ^{ab}	2.3 ^a	-	3.3 ^{bc}	0,000	0,000
<i>Oncosiphon grandiflorum</i> (A)	7.6 ^{cd}	4.7 ^{abc}	4.5 ^{abc}	4.9 ^{abc}	5.6 ^{abc}	9.3 ^{de}	4.4 ^{ab}	7.1 ^{bcd}	7.4 ^{cd}	7.5 ^{cd}	10.7 ^e	-	14.0 ^f	4.0 ^a	0,002	0,040
<i>Senecio arenarius</i> (A)	6.7 ^b	5.1 ^{ab}	7.7 ^{bc}	5.3 ^{ab}	4.5 ^a	4.3 ^a	5.1 ^{ab}	6.8 ^b	4.8 ^a	7.5 ^{bc}	11.5 ^d	8.3 ^c	6.7 ^b	3.7 ^a	0,486	0,020
<i>Senecio niveus</i> (P)	10.6 ^e	6.1 ^{bc}	5.7 ^{ab}	5.1 ^{ab}	4.9 ^a	14.6 ^f	5.4 ^{ab}	9.9 ^{ade}	5.7 ^{ab}	5.6 ^{ab}	4.9 ^a	6.8 ^c	14.5 ^f	8.8 ^d	0,000	0,004
<i>Ursinia calenduliflora</i> (A)	10.2 ^{bcd}	7.6 ^{abc}	6.1 ^{ab}	6.3 ^{ab}	5.1 ^a	14.5 ^{ade}	7.6 ^{abc}	16.6 ^e	6.1 ^{ab}	10.0 ^{bcd}	9.4 ^{abc}	10.5 ^{cd}	16.0 ^e	7.7 ^{abc}	0,006	0,023
Mean time to germination was significantly shorter in dark than in light																
<i>Gazania leiopoda</i> (P)	10.1 ^g	7.1 ^{cde}	5.8 ^b	8.0 ^{df}	7.6 ^{de}	8.2 ^f	6.2 ^{bc}	9.2 ^{fg}	5.3 ^{ab}	4.6 ^a	4.5 ^a	6.7 ^{bcd}	7.8 ^e	5.2 ^{ab}	0,000	0,000
<i>Heliophila sp.2</i> (A)	7.5 ^d	7.2 ^d	3.6 ^{ab}	4.1 ^{abc}	5.4 ^c	3.0 ^{cb}	2.8 ^a	7.0 ^b	3.2 ^{ab}	3.4 ^{ab}	4.2 ^{ab}	3.1 ^{ab}	4.0 ^{abc}	3.1 ^{ab}	0,000	0,026
Mean time to germination not significantly affected by light or dark																
<i>Heliophila variabilis</i> (A)	5.0 ^e	3.3 ^{cd}	3.0 ^{bcd}	3.1 ^{bcd}	2.1 ^{ab}	2.6 ^{abc}	2.4 ^{ab}	4.7 ^a	3.7 ^d	2.3 ^{ab}	2.1 ^a	2.1 ^a	3.5 ^d	2.5 ^{ab}	0,000	0,464
<i>Tripteris hyoseroides</i> (A)	-	-	7.6 ^{ab}	6.7 ^{ab}	6.6 ^{ab}	19.6 ^c	8.7 ^{ab}	24.7 ^d	13.0 ^{bc}	11.1 ^{abc}	9.6 ^{ab}	8.5 ^{ab}	5.0 ^a	10.7 ^{abc}	0,663	0,327
<i>Pentzia incana</i> (P)	0.0	19.0 ^f	11.1 ^{cdef}	9.3 ^{bcd}	3.9 ^a	14.0 ^{ef}	16.0 ^{ef}	0.0	12.3 ^{def}	8.0 ^{abcd}	5.2 ^{ab}	6.3 ^{abc}	12.0 ^{def}	8.3 ^{abcd}	0,242	0,082
<i>Tripteris amplexans</i> (A)	16.0 ^c	10.0 ^{ab}	5.1 ^a	4.8 ^a	4.5 ^a	4.9 ^a	5.9 ^a	14.3 ^{bc}	8.8 ^{ab}	6.2 ^a	5.4 ^a	5.1 ^a	6.8 ^a	5.5 ^a	0,042	0,404
<i>Heliophila sp.1</i> (A)	5.5 ^e	3.2 ^c	2.6 ^a	2.5 ^a	3.1 ^{ab}	7.0 ^a	2.44 ^a	6.1 ^f	4.1 ^d	2.5 ^a	2.5 ^a	2.4 ^a	15.5 ^h	3.1 ^{bc}	0,092	0,729
<i>Ursinia cakilefolia black</i> (A)	6.4 ^{cde}	5.5 ^{abcde}	3.3 ^{ab}	2.9 ^{bca}	6.6 ^{de}	6.1 ^{bcd}	3.5 ^{abc}	6.3 ^{cde}	8.8 ^a	4.1 ^{abcd}	4.2 ^{abcd}	4.0 ^{abcd}	5.0 ^{abcd}	4.3 ^{abcd}	0,014	0,810
<i>Salvia dentata</i> (P)	16.7 ^{cd}	7.4 ^a	7.9 ^a	9.4 ^{ab}	14.9 ^{bcd}	19.6 ^d	8.6 ^a	14.8 ^{bcd}	10.5 ^{ab}	6.9 ^a	8.4 ^a	10.9 ^{bcd}	14.4 ^{bcd}	7.9 ^a	0,000	0,443
<i>Tripteris oppositifolia</i> (P)	15.6 ^a	8.5 ^{bc}	5.3 ^a	8.7 ^{bc}	12.2 ^d	8.5 ^{bc}	7.6 ^{abc}	12.4 ^d	8.7 ^{bc}	6.8 ^{ab}	6.83 ^{ab}	7.3 ^{abc}	10.0 ^{cd}	8.2 ^{bc}	0,000	0,095
<i>Tripteris sinuata</i> (P)	5.8 ^d	3.7 ^{abc}	2.3 ^a	3.1 ^{abc}	4.2 ^c	12.6 ^f	3.4 ^{abc}	6.5 ^a	3.7 ^{abc}	2.3 ^a	2.3 ^a	2.8 ^{abc}	8.9 ^a	2.7 ^{ab}		
<i>Senecio cardaminifolius</i> (A)	7.5 ^c	5.6 ^{abc}	3.4 ^a	4.3 ^{ab}	6.4 ^{abc}	3.5 ^a	4.9 ^{abc}	7.5 ^c	4.4 ^{ab}	4.8 ^{abc}	3.5 ^a	7.0 ^{bc}	-	4.5 ^{ab}	0,001	0,164
<i>Heliophila thunbergii</i> var <i>thunbergii</i> (A)	6.7 ^d	4.0 ^{abc}	3.8 ^{abc}	2.0 ^a	2.0 ^a	-	2.5 ^a	6.9 ^d	4.7 ^{bcd}	2.8 ^a	2.8 ^a	5.6 ^{bcd}	-	2.6 ^a	0,000	0,095
<i>Ursinia cakilefolia (white)</i> (A)	6.3 ^{cde}	5.6 ^{abcde}	3.2 ^a	6.6 ^{de}	6.2 ^{bcd}	8.5 ^{de}	4.2 ^{abcd}	6.4 ^{cde}	5.6 ^{abcde}	4.2 ^{abcd}	4.1 ^{abcd}	4.0 ^{abcd}	5.0 ^{abcd}	4.3 ^{abcd}	0,041	0,082
<i>Heliophila lactea</i> (A)	5.7 ^{eg}	4.2 ^{cd}	4.9 ^{de}	5.0 ^{de}	4.1 ^{bcd}	2.9 ^a	6.9 ^f	6.4 ^f	3.5 ^{abc}	3.8 ^{abc}	2.9 ^a	5.7 ^{ef}	3.0 ^{bab}	3.4 ^{abc}	0,000	0,118

- Treatment not used for this species.

A - Annual

P-Perennial

Table 5.3 Optimum germination temperatures (°C) calculated for 24 myxospermic species of Namaqualand

Species /seed type	Temperature(°C)	
	Light	Dark
Low temperature in light and dark		
<i>Heliophila</i> sp.1 (A)	14,20	14,00
<i>Heliophila thunbergii</i> var <i>thunbergii</i> (A)	11,80	14,60
<i>Cotula barbata</i> (A)	15,45	12,80
<i>Senecio niveus</i> (P)	15,25	13,97
<i>Ursinia cakilefolia</i> (black achenes) (A)	15,00	13,80
<i>Senecio cardaminifolius</i> (A)	15,88	12,06
Intermediate temperatures in light & low temperatures in dark		
<i>Oncosiphon grandiflorum</i> (A)	18,75	11,60
<i>Heliophila seselifolia</i> (A)	17,60	11,80
<i>Foveolina dichotoma</i> (A)	17,29	12,39
<i>Cotula thunbergii</i> (A)	19,60	12,87
<i>Gazania lichtensteinii</i> (A)	18,24	16,80
<i>Salvia dentata</i> (P)	16,18	14,89
Intermediates temperaures in light and dark		
<i>Ursinia calenduliflora</i> (A)	17,34	16,12
<i>Ursinia cakilefolia</i> (White achenes) (A)	15,31	16,42
<i>Heliophila</i> sp.2 (A)	16,32	16,59
<i>Tripteris sinuatum</i> (P)	17,14	17,65
<i>Gazania leiopoda</i> (P)	18,30	18,38
<i>Tripteris oppositifolia</i> (P)	15,31	15,27
High temperatures in light & low temperature in dark		
<i>Senecio arenarius</i> (A)	22,42	12,11
<i>Heliophila lactea</i> (A)	21,70	13,90
High temperatures in light & intermediate temperature in dark		
<i>Tripteris hyoseroides</i> (A)	23,50	19,76
<i>Tripteris amplexens</i> (A)	22,76	19,40
<i>Pentzia incana</i> (P)	20,10	19,60

A- Annual

P- Perennial

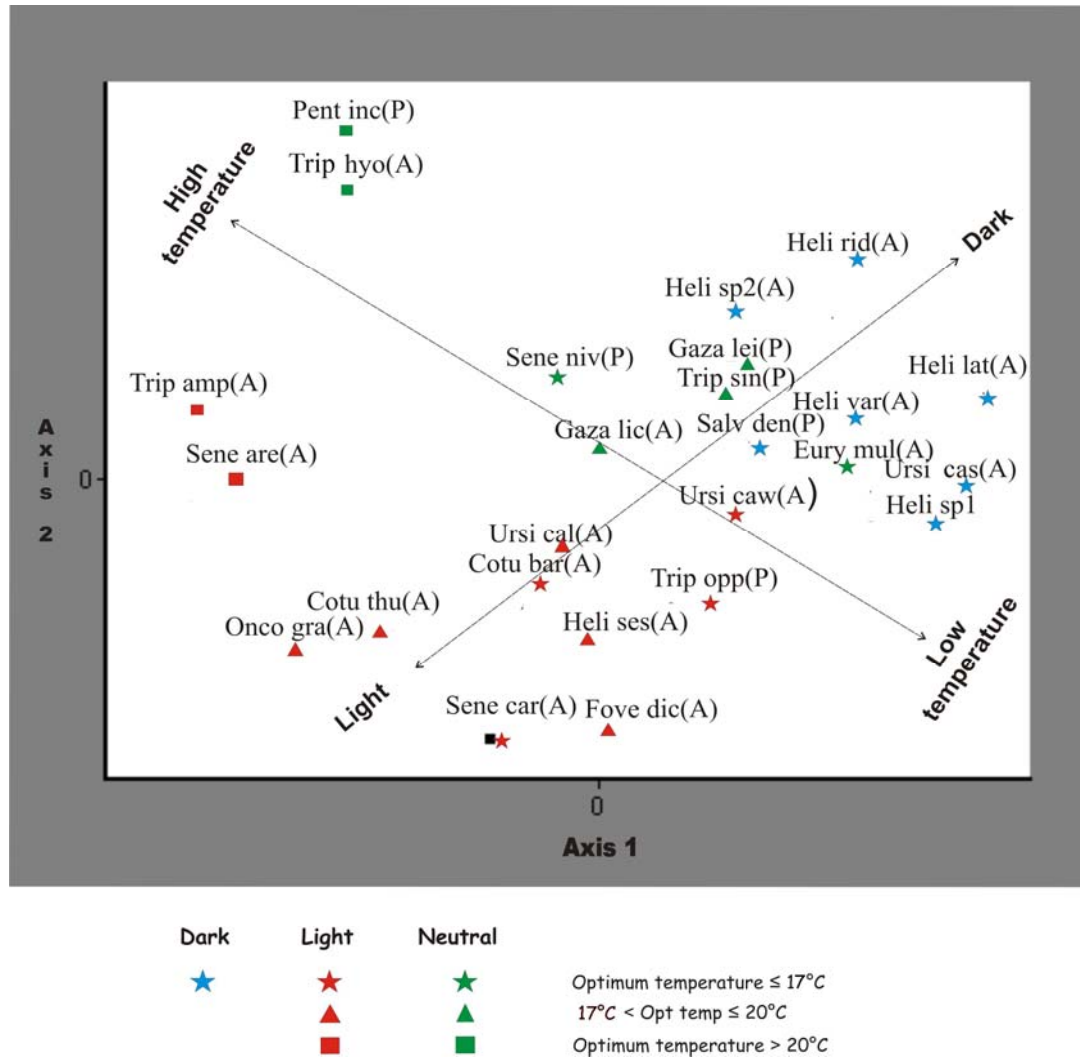


Figure 5.2 Ordination diagram based on a Principal Coordinate Analysis of the species germination percentages data with respect to two environmental variables (temperature, light/dark).

Nine species, mostly annuals, obtained significantly shorter mean germination times (days) in light than in the dark (Table 5.2), of which four also had the highest germination percentage in light. Four of these species obtained their shortest mean germination time (MTG) at intermediate temperature conditions (Table 5.2). The only perennial species in this group was *Senecio niveus* (Table 5.2).

Two of the species investigated obtained significantly shorter MTG in the dark (Table 5.2), of which the annuals *Heliophila* sp. 2 obtained the highest germination percentage in the dark. The germination percentage of the perennial *Gazania leiopoda* was not significantly different in light and dark (Table 5.2).

Mean germination time was not significantly affected by light in more than 50% of the species. This group included approximately a half of all annual as well as most of the perennial species investigated.

The alternating temperature did not show a particular trend in this study. Alternating temperatures did not significantly improve the mean germination percentages (Table 5.2) and the mean germination times of the species investigated above those at constant temperatures.

The principal coordinates analysis (PCoA) separated species according to their light and temperature requirements for optimal germination (Figure 5.2). Both factors had significant effects on seed germination, but the light requirement appears to be the dominant factor especially for annual species. Nevertheless the species with high temperature requirements can be differentiated from those with low and intermediate temperatures irrespective of the light requirement. But there is no clear separation between species that require low and intermediate temperature for optimum germination.

5.4 Discussion

Specific germination requirements can provide fine temporal niche partitioning, because these requirements are often far more restrictive than requirements for vegetative growth and reproduction (Bazzaz 1979). Overall desert plants from arid environments also require a high water availability for germination (Facelli *et al.* 2005) and have adaptations that allow them to time their germination to the most favourable, and often more predictable, part of the year (Baskin *et al.* 1993, Claus & Venable 2000).

Temperature requirements

Most species, both perennials and annuals in this study obtained their highest germination percentages and shortest mean germination time within the temperature range of 12-22°C (Table 5.1 & 5.2). The mean optimal germination temperature of 80% of species investigated occurred in the temperature range of 12-20°C in either light or dark. Many studies on seed germination and survival in the Succulent Karoo have found similar results (De Villiers *et al.* 2002a, Milton 2005).

Namaqualand is an arid winter rainfall region (Desmet and Cowling 1999). Annual species in an arid environment depend largely on seed germination during periods when the environment is suitable for completion of their life cycle (Van Rooyen 1999, Guterman 2002). After maturation seeds of winter annuals become conditionally dormant and undergo the process of afterripening during the hot and dry summer months (De Villiers *et al.* 2002b, Van Rooyen and De Villiers 2004). High temperature and low soil moisture conditions during summer promote loss of dormancy (Baskin and Baskin 1998). Occasional rainfall during this period does not induce germination, but as soon as the growing season approaches, the afterripening requirement has been satisfied and there is available moisture and suitable temperatures and germination can take place (De Villiers *et al.* 2002a, Van Rooyen and De Villiers 2004).

Additionally, winter annuals have developed phenological characters that prevent their seeds from germinating during summer because the maximum temperatures at which seeds can germinate are below those occurring in the habitat. Seeds germinate in autumn and early winter because at this season the temperatures are lower and conditions are relatively humid (De Villiers *et al.* 2002a, Milton 1995).

Most perennial species investigated in this study germinated over a wide range of temperatures and did not require light for germination (Table 5.1). They probably do not accumulate a persistent seed bank. This is supported by the findings of De Villiers (2000) on his study of some plants species of the Strandveld Succulent Karoo and by Smith *et al.* (1997) who reported that the seeds of some perennial species of other warm deserts have no dormancy and germinate in a wide range of low and intermediate temperatures. In the Succulent Karoo, where summer humidity is low and soil surface temperatures reach 64°C, selection has evidently favoured species whose germination is inhibited by high temperatures (Milton 1995). However, a high temperature reduces the percentage of seeds that remain in primary dormancy after their maturation, while germination in late autumn or winter would facilitate establishment during the moist winter period (Went 1949, Smith *et al.* 1996)

Although under natural conditions most seeds will germinate at low or intermediate temperatures, a reduced percentage of seeds might be able to germinate with late spring rains (Escudero *et al.* 1999). This might be the case with *Pentzia incana* that obtained its highest germination percentage at high temperatures.

Seeds of many species with low germination capacity at constant temperatures are stimulated by alternating temperatures (Baskin and Baskin 1998, Myers and Cooper 1989). Temperature fluctuation can act as a strong germination trigger, as diurnal fluctuation may be more important than light as environmental signal in sensing proximity to the soil surface because temperature, unlike light, is not attenuated as effectively by soil (Benvenuti *et al.* 1999). Alternating temperatures could also act as a season-sensing mechanism (Van Assche and Vanderberghe 1989). Sensitivity to periodic temperature fluctuation constitutes an important sensory system allowing plants to respond to daily variations in soil surface temperature. Alternating

temperatures interact with other environmental factors, including light, nitrate, substrate moisture level, oxygen concentration and level of active phytochrome to control germination (Gul and Weber 1999, Bewley and Black 1994). In other species, including those of this study, alternating temperatures had no positive effect on germination (Went 1979). The mucilage of the species investigated in this study largely prevent them from penetrating the soil, thus they do not face the problem of germinating from a great depth. In addition, temperature fluctuations during the winter season would be reduced.

Some species have mechanisms that insure that seed germination is spread over time, often over a period of years so called bet hedging (Venable and Lawlor 1980, Adondakis and Venable 2004). This is also found among heterocarpic species. The production of different types of seeds by one species is a common phenomenon found in unpredictable environments and arid environments to increase the chance of regeneration in the future (El-Keblawy and Al-Rawai 2006). The black seeds of *Ursinia cakilefolia* germinated better in the dark, while white seeds germinate better in light, but both obtained their highest germination percentages at low temperatures.

Light requirement

Non-dormant seeds of many species germinate equally well in light and darkness, others germinate to higher percentages in light than in darkness, and those of relatively few germinate to higher percentages in dark than in light (Baskin and Baskin 1998).

Light promoted germination of most annual species in this study. On the PCoA ordination species with a light requirement are clearly separated from the others. Various studies have demonstrated that light is one of the most important environmental signals in response to which seed germination is regulated (Guterman 1993, Zheng *et al.* 2005, Flores *et al.* 2006). In arid and semi-arid environments, sandy soils can modify the photon flux and light quality underground according the type of sand and soil moisture. Thus light can be relevant for triggering germination of desert plant seeds (Flores *et al.* 2006)

Seeds of many species are known to undergo a transition from primary to secondary dormancy during the burial period and then develop a light requirement to trigger germination (Gul and Weber 1999). The plant pigment phytochrome is the physiological sensor of light in seeds, and light-controlled seed germination is associated with this pigment. Another trait influencing the responsiveness to light is seed size (Baskin and Baskin 1998). Small seeds delay their germination until they are brought to the surface by soil disturbing agents to avoid fatal germination at depth in the soil (Schütz and Rave 1999).

Light sensitive seeds that are stimulated positively by light (positive photoblastic) and are situated on the soil surface may be exposed not only to light, but also to rapid dehydration after a rainfall that may stimulate their germination. However, the seeds of the mucilaginous species investigated, adhere to the soil surface which prevents them from being blown into dark cracks in the soil crust, thus conferring an advantage for species with a light requirement. The good contact between the soil and mucilage enables the seed to absorb the water in the surrounding soil and lubricate the area around the seed, thus making it easier for the root to penetrate the soil (Guttermann 2000).

Most perennial and a few of the annual species investigated acted indifferently towards light or dark, but on the PCoA ordination are closely associated with species that obtain their highest germination percentage and the shortest mean in the absence of light. Negative photoblasty implies that seeds require dark conditions and therefore need to be covered by sand in order to germinate (Guttermann 2002). The photo-inhibition mechanism can be considered to be an adaptation against surface seedling establishment in harsh habitats (Bell 1993). This group was mainly dominated annual species, particularly the genus *Heliophila*. Seeds with the potential to germinate in darkness at certain temperatures are induced into secondary dormancy if they are kept in darkness for prolonged periods of time at inappropriate temperatures for germination (Baskin and Baskin 1998).

5.5 Implications for management and conservation

The optimal management for increasing germination and seedling establishment differed among species, but in general most species obtained their highest germination percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons. Only a few species are inhibited by light. Most required light and others acted indifferent to light. For species with light requirements, the burial of seeds caused by the movement of sand or fauna may reduce their germination (Martinez-Sanchez *et al.* 2006).

Heavy grazing has been demonstrated to promote seed germination in tropical environments by removal of the relatively dense canopy (Derigibus *et al.* 1994). The vegetation in arid regions is less dense and should allow ample opportunities for light demanding species to germinate. The soil surface in arid regions however, is unstable and the presence of grazing animals could increase the instability. Keeping livestock on the field during summer months prior to autumn germination could promote the germination of some species because animal movement might bury seeds with negative photoblasty, however, it could also reduce germination of positive photoblastic seed by their burial.

Most of the species examined in this study have a relatively short mean germination time and are therefore fast germinators (Escuadero *et al.* 1997). It has been suggested by Van Rheede van Oudtshoorn and Van Rooyen (1999) that heavy dew falls, fog or small rainfall events that are not sufficient to cause germination, may produce conditions that induce a priming effect on mucilaginous seeds, which are then able to germinate immediately when there is sufficient water. It has been proposed that mucilaginous seeds in dormant seed banks have an advantage over non-mucilaginous seeds because the viability and longevity of the mucilaginous species is promoted by their prolonged wetting by dew (Van Rheede van Oudtshoorn and Van Rooyen 1999). This implies that if these seeds are deeply buried, their longevity will be reduced because the quantity of water produced by dew or fog could not penetrate the soil.

In concordance with what has been suggested in the preceding paragraph, with increasing climate change, conserving these species will be a difficult task, because the decrease in rainfall, dew and fog will affect the expansion of mucilage during late spring and early summer thus most seed would be carried by wind into depressions and few seeds might remain viable till the next growing season. Temporal wetting of the soil surface after seed maturation could be a possibility to maintain the seed bank.

Mucilaginous seeds have the same germination requirement as most desert seed, but their adhesion to the soil (often near the mother plants) provides them with the ability to germinate in a suitable environment. The germination and the establishment of seeds dispersed by water are uncertain because most of them will end up in depressions and be covered by soil.

5.6 References

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Chapter 6

Anatomical investigation of the mucilaginous diaspores of selected species of Namaqualand, South Africa

6.1 Introduction

Plants have developed many functional traits that allow them to adapt and survive in different environments. Seed dispersal is an important functional trait that influences the population structure and the spatial and temporal turnover of a plant community. The seed coat of some species has features that assist in seed dispersal. For example, the testa of seeds that are eaten by animals and man may be resistant to digestive processes and permit the seed to pass through the intestinal tract without damage (Fahn 1990).

Myxospermy is a functional trait where the epidermis of the diaspore (seed/fruit) contains mucilaginous cells, which swell and become sticky when in contact with water (Gutterman and Shem-Tov 1997, Van Rheede van Oudtshoorn and Van Rooyen 1999). According to Johri (1984) the mucilage-forming substance consists of secondary walls swelling after hydration.

There are many divergent ideas about the ecological importance of myxospermy, and it probably fulfills various functions. When wet, myxospermic diaspores adhere to the soil or to animals, and after drying out again remain glued to soil particles and thus resist being carried to unfavourable locations by wind. The good contact between the mucilage layer and the soil surface increases water absorption for germination and the water held by the mucilage could also serve as a water reservoir for seedling establishment (Gutterman *et al.* 1967, Van Rheede van Oudtshoorn and Van Rooyen 1999). Furthermore, the adherence of the seed to the soil by the mucilage prevents massive collection by seed predators and the repeated wetting of mucilaginous seeds during many nights with dew may affect the repair mechanisms of the DNA, cell membranes and organelles, thereby enhancing seed viability for many years (Van Rheede van Oudtshoorn and Van Rooyen, 1999). Mucilage may also control the germination process by excluding the passage of oxygen when the

moisture is in excess and could damage the emerging seedling (Guttermann *et al.* 1967, 1973, Guttermann 1996, Tamara *et al.* 2000). Little attention has thus far been given to the origin and chemical composition of mucilage of mucilaginous diaspores. Therefore, in this study the origin and the chemical composition of the mucilage of selected plant species of Namaqualand (South Africa) are investigated.

6.2 Background of species of which diaspores have been investigated

ACANTHACEAE

***Acanthopsis horrida* Nees.**

It is a dwarf perennial shrub up to 0.3 m high. The basal leaves are hairy, obovate and tapering into the leafstalk, with short spines on the margins. The flowerheads in which dense flowers are borne has very spiny bracts. It is found at altitudes of 460 to 500 m above sea level. It is an endemic species confined to the Northern Cape (Germishuisen *et al.* 2006).

***Blepharis furcata* (L.f.) Pers.**

It is a dwarf shrub of 0.1 to 0.5 m height. The flowers are in spikes with spiny bracts. It is found at altitudes of 200 to 1020 m above sea level in the Northern Cape (Germishuisen *et al.* 2006).

ASTERACEAE

***Cotula barbata* DC.**

A tufted annual herb growing 90 to 180 mm tall. The very hairy leaves are deeply divided and about 40 mm long. The flowerheads with only yellow disc florets are about 10 mm in diameter, and borne singly on a slender, hairless stalk. The involucre bracts are almost round and papery with a transparent margin. It is found in sandy places in the Richtersveld and Namaqualand klipkoppe (Le Roux 2005).

***Tripteris hyoseroides* DC.**

It is a glandular-hairy, aromatic annual herb of up to 0.5 m tall. The leaves are elliptical and irregularly toothed. The flowerheads are 30 to 50 mm in diameter, dark purplish in the center with orange ray florets surrounded by two series of bracts with membranous margins. Diaspores are three winged and are 7 to 8 mm long. It is

found in stony and rocky places throughout Namaqualand and also in other dry parts of the Northern, Western and Eastern Cape (Manning, 2003).

***Othonna cylindrica* (Lam.) DC.**

It is a shrub growing 0.5 to 1 m tall with narrow succulent leaves of 20 to 40 mm long. The flowerheads are about 20 mm in diameter and are borne in loose groups above the leaves. Each flowerhead contains about 10 green-veined, yellow ray-florets. The involucre bracts are in one row and joined at the base. It is found throughout Namaqualand and in the Western Cape and Namibia (Le Roux 2005).

***Senecio arenarius* (Thunb.)**

An annual herb growing about 0.4 m tall. The leaves with glandular hairs are up to 70 mm long and lobed into broad segments. The flowerheads are 25 to 30 mm in diameter with magenta-pink ray florets and yellow disc florets. The involucre bracts are free and in a single row (Le Roux 2005).

***Ursinia cakilefolia* DC.**

An annual herb growing up to 0.25 m tall. The leaves are up to 6 cm long, toothed and doubly-lobed into very narrow segments. The flowerheads are borne singly and are 25 to 35 mm in diameter. The ray florets are orange and disc florets are black. The involucre bracts are in many rows and the innermost bract is the largest with a conspicuous transparent tip. It is found in sandy places throughout Namaqualand and in the northern part of the Western Cape (Le Roux 2005).

***Pentzia incana* (Thunb.) Kuntze:**

An erect, densely-branched shrub growing up to 0.50 m high. The leaves are deeply divided, 2 to 6 mm long and covered with white hairs. The flowerheads have yellow disc florets only, are 6 mm in diameter and borne on leafless stalks. The involucre bracts are arranged in four rows and have membranous margins. An unpalatable plant to stock that grows on flats in the Richtersveld, Namaqualand klipkoppe and other arid regions in South Africa (Le Roux 2005).

***Oncosiphon grandiflorum* (Thunb.) Källersjö.**

A loosely-branched, annual herb growing 0.1 to 0.4 m tall. The leaves with a pungent smell are finely dissected, and up to 6 cm long. The flowerheads with yellow disc florets only are 7 to 10 mm in diameter and borne on a short, stout stalk. The involucre bracts are arranged in four rows with membranous margins. It is an unpalatable plant to stock. It is found in sandy places, often on ploughed land throughout Namaqualand, the Western Cape and in Namibia. (Le Roux, 2005).

***Foveolina dichotoma* (DC.) Källersjö.** An annual herb growing 0.2 to 0.3 m tall, branching mainly from the base. The leaves are doubly-lobed, sparsely covered with minute hairs and up to 2 cm long. The flowerheads have only yellow disc florets, are almost round, 5 to 7 mm in diameter, and borne singly on thin leafless stalks. The involucre bracts with membranous margins are in four rows. It is an unpalatable plant to stock. Found throughout Namaqualand and other dry parts of the Northern, Western and Eastern Cape (Le Roux 2005).

BRASSICACEAE

Heliophila thunbergii* (Eckl. & Zeyh.) Steud var. *thunbergii

This plant name has changed from *Heliophila latisiliqua*. The genus is native to South Africa, contains 70 species of annuals, perennials and subshrubs belonging to the cabbage family of which 26 occur in Namaqualand. *Heliophila thunbergii* var. *thunbergii* is an annual herb of 0.15 to 0.35 m tall. The leaves are simple or lobed. The four-petalled flowers are borne on racemes and are white, producing a colourful display in spring. It is found in sandy and rocky soils often on slopes in Namaqualand (Germishuisen *et al.* 2006).

LAMIACEAE

***Salvia dentata* Aiton**

A much branched shrub growing up to 1 m tall. The greyish leaves are up to 20 mm long and 10 mm wide and usually with toothed margins. The blue flowers are in groups on the ends of the branches and are up to 25 mm long. The calyx has rounded lobes and minute hairs. It is an unpalatable plant to stock, and is found along drainage lines and on rocky slopes in the Richtersveld and Namaqualand (Le Roux 2005).

6.3 Materials and Methods

Scanning electron microscopy

Dry seeds/achenes (henceforth referred to as seeds) were mounted on a stub and made conductive with RuO₄ vapour (Van der Merwe and Peacock 1999). For wet samples, seeds of each species were soaked in water for 24 hours before fixation. They were then fixed in 2.5% glutaraldehyde in 0.075 M phosphate buffer, pH 7.4, for one hour and rinsed three times (five minutes each) in 0.075 M phosphate buffer and dehydrated in an ethanol series with the respective concentrations of 30%, 50%, 70%, 90% and 100%. This was followed by critical point drying in liquid CO₂ and mounted on a stub and made conductive with RuO₄ vapour. Samples were viewed with the use of a JSM 840 scanning electron microscope (JEOL, Tokyo, Japan) and photographs were taken with the computer program Orion 6.60.4 (Belgium).

Light microscopy

Further studies were done on seeds or achenes where the origin of the mucilage could not clearly be establish with the scanning electron microscope. Dry samples were fixed in 4% (v/v) formaldehyde in 50% (v/v) ethanol (FAA) to prevent mucilage release (Tamara *et al.* 2000). The wet samples were immersed in water for 24 hours. Wet samples were fixed in 2.5% glutaraldehyde in 0.075 M phosphate buffer, pH 7.4 for 1 hour and rinsed three times (five minutes each) in 0.075 M phosphate buffer and dehydrated in an ethanol series with the respective concentrations 30%, 50%, 70%, 90% and 100%. Samples were then infiltrated over two days with pure LR-White, polymerised at 65°C for 24 to 36 hours. Sections were cut with a Reichert Ultracut E microtome. Each section was stained with toluidine blue (0.2% in 0.5% NaCO₃), mounted in immersion oil and viewed with a Nikon Optiphot light microscope (Tokyo, Japan). Photographs were taken with the Nikon Digital camera DXM 1200 (Tokyo, Japan) and the computer program Nikon ACT-1 (Tokyo, Japan).

Staining methods

Diaspore staining was done according to various manuals of microscopic staining (McClean and Ivimey Cook 1941, O'Brien and McCully 1981, Lawton and Ettridge 1986) the details of which are given in Table 6.1.

Table 6.1 Stains used for various compounds and expected results

Stain	Compound	Expected results
Methylene blue	Cellulose	Blue
Ruthenium red	Pectic substances	Red
Toluidine Blue	Polysaccharides	Pink –purple
Sudan 4	Lipids	Yellow
Phloroglucinol	Lignin	Pink
Aniline blue	Callose	Blue
Biuret solution	Protein	Violet

6.4 Results and discussion

The results suggest three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the outer cell wall of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs.

6.4.1 Epidermal mucilage

***Heliophila thunbergii* var. *thunbergii* (Brassicaceae)**

Scanning electron microscopy of dry seeds of *Heliophila thunbergii* var. *thunbergii* (Brassicaceae) reveals a circular seed (Figure 6.1A). The epidermal layer (e) consists of circular cells with a raised margin and a cavity in the centre (Figure 6.1B). The outermost layer (ol) seems to be filled with spongy content, probably mucilage (Figure 6.1C). The thin section of the dry seeds also reveals epidermal cells filled with mucilage (m) (Figure 6.1G). Once wet, the seed is covered by a gelatinous film (Figures 6.1D&E). The section of the wet seed reveals the epidermis with ruptured cells from which filaments of mucilage (m) emerge (Figure 6.1F). This is also visible in the thin section of the wet seed seen with the light microscope (Figure 6.1H). Upon wetting the mucilage swells and the epidermal cells become incapable of containing the excess mucilage and therefore rupture.

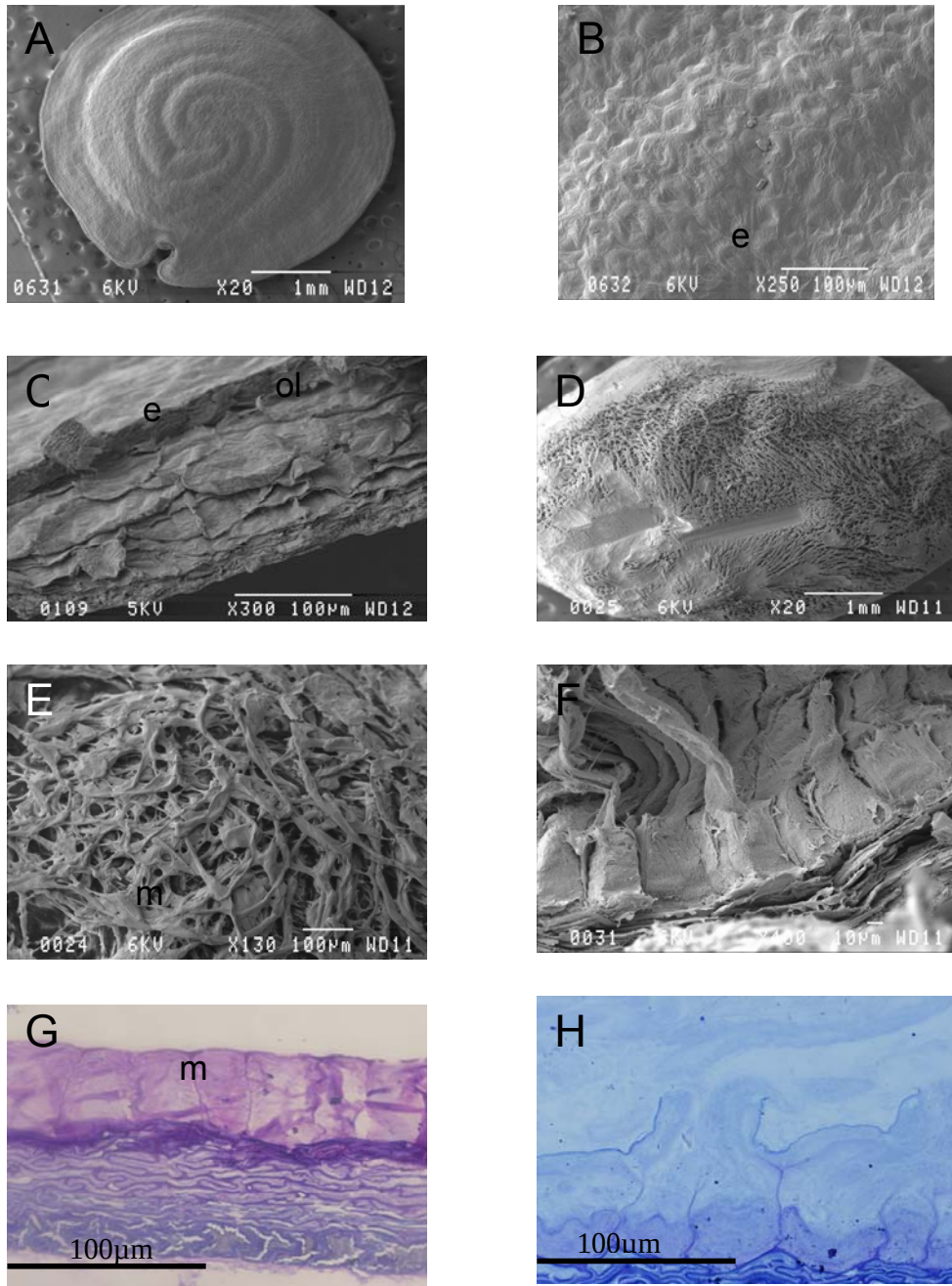


Figure 6.1 Scanning microscope (A-F) and light microscope (G-H) images of seeds of *Heliophila thunbergii* var. *thunbergii* : (A) Entire dry seed (scale bar = 1 mm); (B) high magnification of dry epidermis; (scale bar = 100 µm); (C) section of the dry seed (scale bar = 100 µm); (D) entire wet seed (scale bar = 1 mm); (E) high magnification of wet seed surface (scale bar = 100 µm); (F) section of wet seed (scale bar = 10 µm); (G) section of the dry seed (scale bar = 100 µm); (H) cross section of wet epidermis (scale bar = 100 µm). e = epidermal layer, m = mucilage, ol = outermost layer.

***Cotula barbata* (Asteraceae)**

In the dry state, the achene of this species does not have the same structure on both sides, the upper side is smooth (Figure 6.2 B) while the lower side is undulated (6.2.A) The phenomenon observed in *Cotula barbata* (Figure 6.2) is similar to the one of *H. thunbergii* var. *thunbergii*. When *C. barbata* achenes come in contact with water, the epidermal cells burst across the entire outer surface (Figure 6.2F) and not only the centre of the cell as in the case of *H. thunbergii* var. *thunbergii* (Figure 6.1H). This could be the reason for the mucilage appearing multi-layered (Figure 6.2E).

***Salvia lanceolata* (Lamiaceae)**

The scanning electron micrographs of the dry seed of *S. lanceolata* do not clearly reveal the structure of the mucilage in the epidermal cells (Figure 6.3A-C). The light microscopy cross section shows the epidermis filled and covered with mucilage (Figure 6.3G). After wetting the seed is covered with a thick mucilage layer (Figure 6.3D & E). Once in contact with water the outer layer of the epidermis absorbs water quickly, the epidermis cells swell, the cuticle ruptures and the contents are excreted in the shape of long, continuous threads. This is clearly visible on the wet sectioned seed (Figure 6.3F) and the thin cross section of the wet seed (Figure 6.3H).

Foveolina dichotoma*, *Oncosiphon grandiflorum* and *Pentzia incana

These three species are taxonomically related, all previously belonged to the genus *Pentzia*. Apparently these species have the same way to produce mucilage. The scanning electron microscopy shows that the epidermis of the dry achene of *F. dichotoma* consists of parallel longitudinal cells (Figure 6.4A & D). The epidermis of *O. grandiflorum* (Figure 6.4 B & E) and *P. incana* (Figure 6.4C & F) also reveals an epidermis that consists of longitudinal, more or less hexagonal, cells. Following wetting and freeze drying, the seeds are covered with a gelatinous film but the wings remain unchanged (Figure 6.5G, H, J). Light microscope sections show that the epidermal cells of the dry seeds are filled with mucilage (Figure 6.4K & L), which is released when the cells burst open upon swelling in contact with water (Figure 6.4 M).

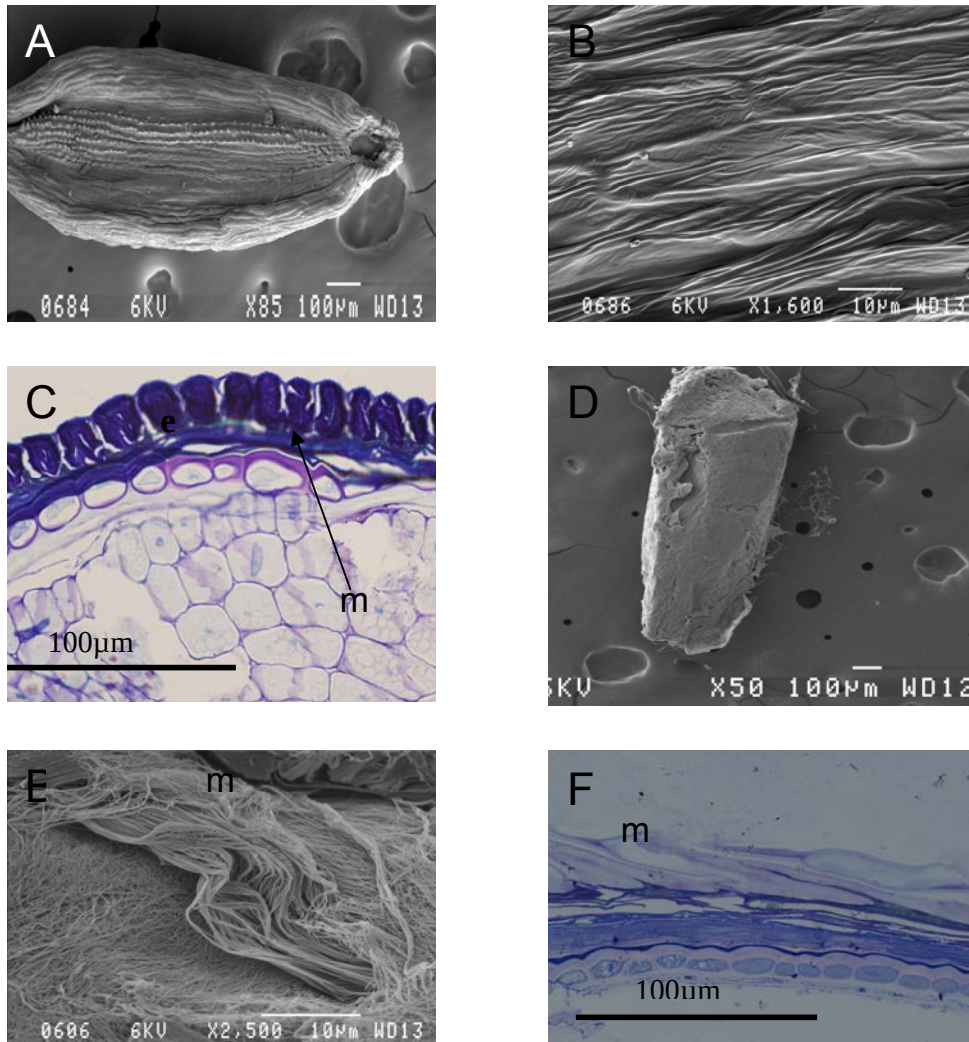
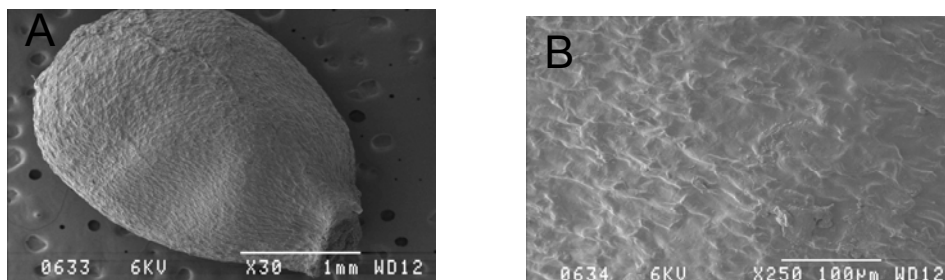


Figure 6.2 Scanning microscope (A- B, D, E) and light microscope (C, F) images of achenes of *Cotula barbata*: (A) Entire dry seed (scale bar = 100 µm); (B) high magnification of the epidermis (scale bar = 10 µm); (C) cross section of the dry seed coat (scale bar=100 µm) , with mucilage (arrow) retained in the epidermal layer; (D) entire wet seed (scale bar = 100 µm); (E) high magnification (scale bar = 10 µm) of wet epidermis covered with a thick layer of mucilage; (F) cross section of the wet epidermis of which the outer layer has burst, releasing mucilage from the epidermal cells (scale bar = 100 µm). e = epidermis; m = mucilage.



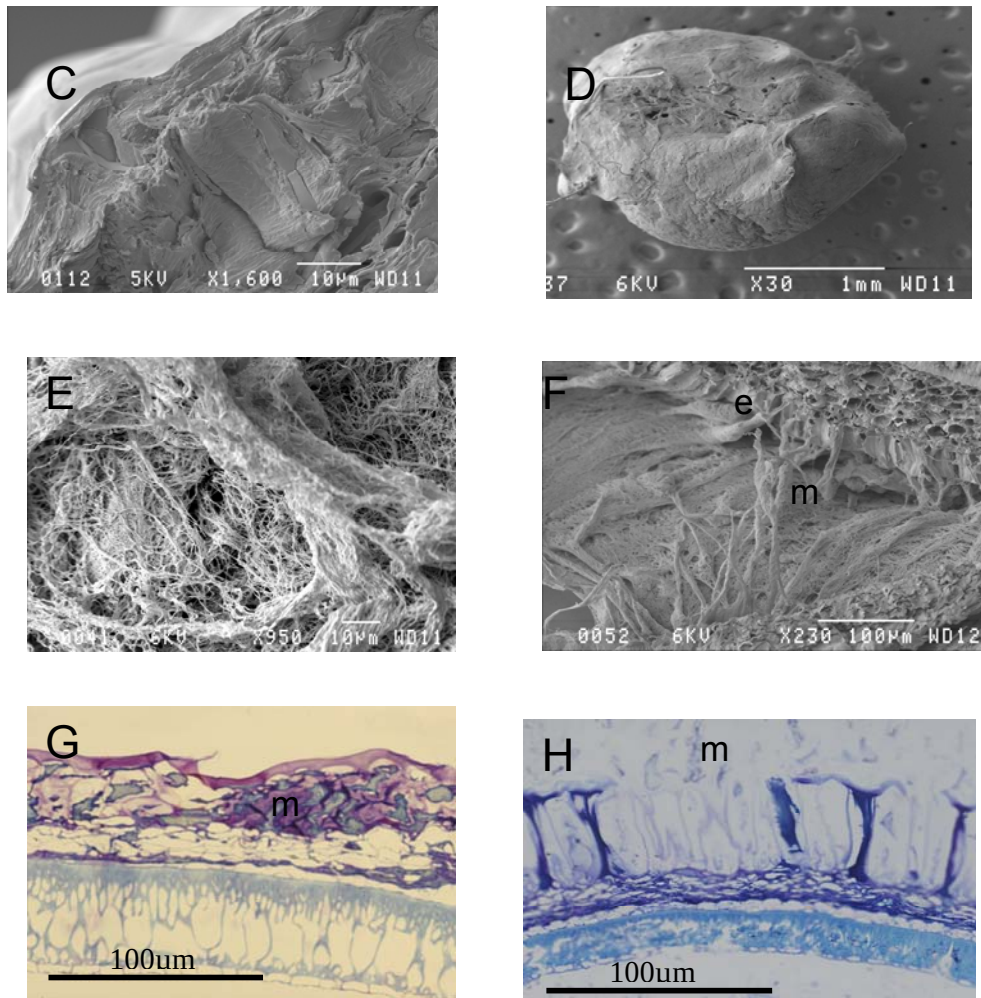
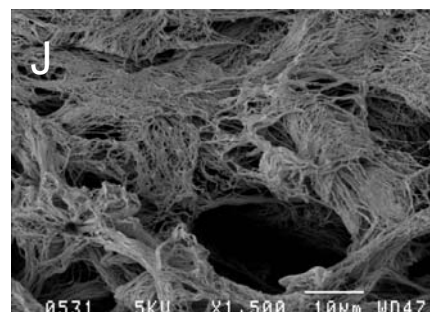
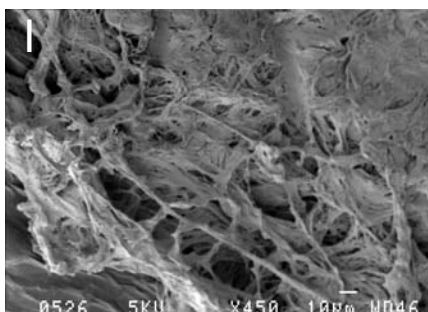
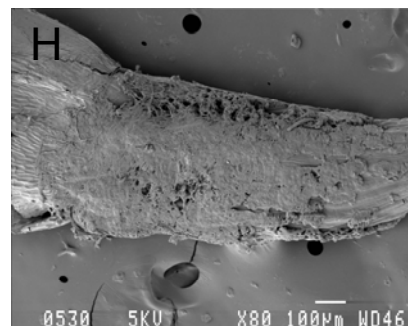
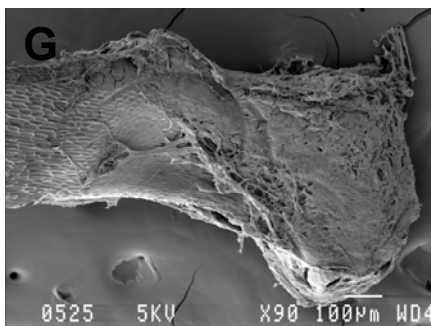
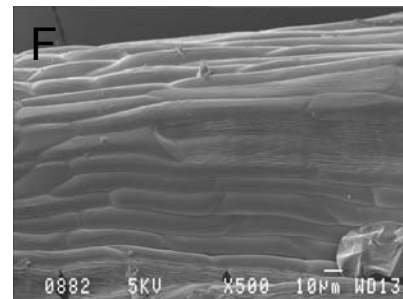
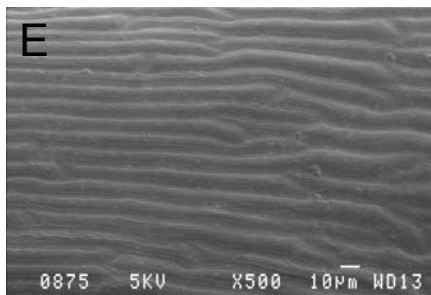
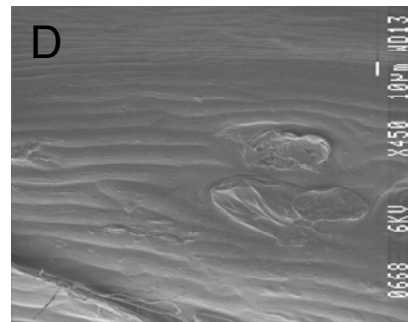
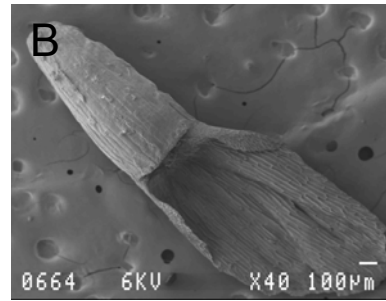
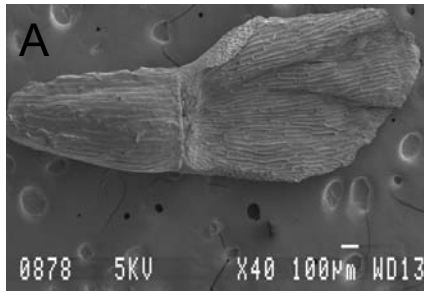


Figure 6.3 Scanning microscope (A-F) and light microscope (G,H) images of seeds of *Salvia lanceolata*: (A) Entire dry seed (scale bar = 1 mm); (B) high magnification of the dry epidermis filled with mucilage (scale bar = 100 μ m); (C) section of the dry seed (scale bar = 10 μ m); (D) entire wet seed covered with mucilage (scale bar = 1 mm); (E) high magnification of the wet epidermis covered with mucilage (scale bar = 10 μ m); (F) section of the wet seed with long strands of mucilage (scale bar = 100 μ m); (G) thin cross section of the dry seed with epidermal cells filled with mucilage (scale bar = 100 μ m); (H) thin cross section of the wet epidermis with an open cell that liberate mucilage (scale bar = 100 μ m), m = mucilage.



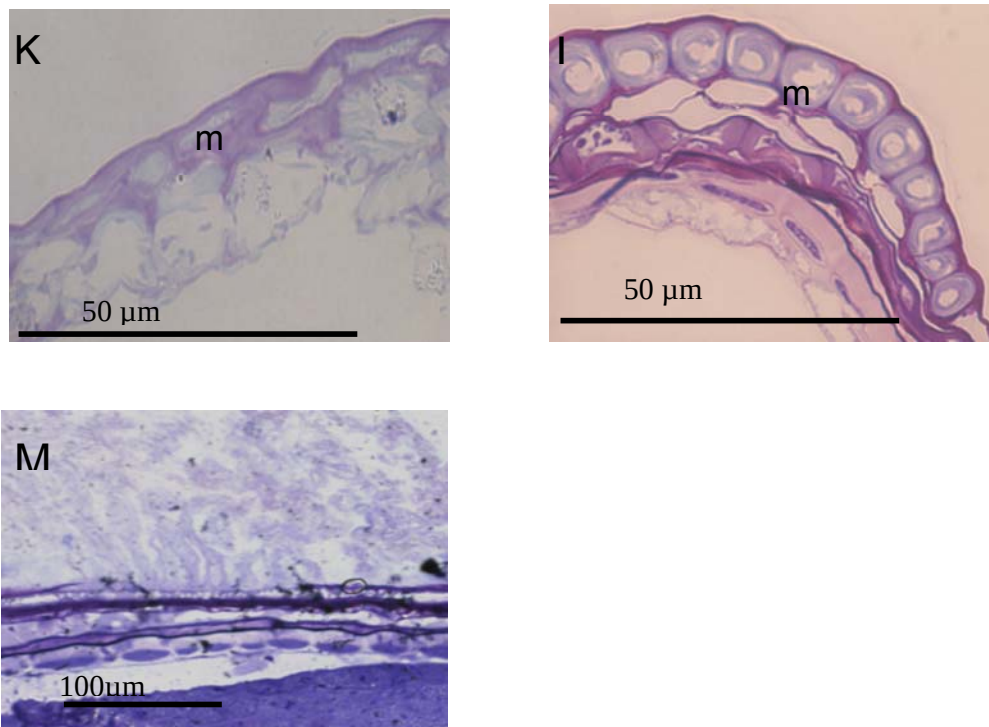


Figure 6.4: Scanning microscope (A-J) and light microscope (K-L) images of achenes of *Foveolina dichotoma*, *Oncosiphon grandiflorum* and *Pentzia incana*. (A) entire seed of *F. dichotoma* (scale bar = 100 µm); (B) entire dry achene of *O. grandiflorum* (scale bar = 100 µm); (C) entire dry achene of *P. incana* (scale bar = 1 mm); (D) high magnification of the epidermis *F. dichotoma* (scale bar = 10 µm); (E) high magnification of the epidermis of *O. grandiflorum* (scale bar = 10 µm); (F) high magnification of the epidermis of *P. incana* (scale bar = 10 µm); (G) entire wet achene of *F. dichotoma* (scale bar = 100 µm); (H) entire wet achene of *P. incana* (scale bar = 100 µm); (I) high magnification of the mucilage of *F. dichotoma* (scale bar = 10 µm); (J) high magnification of the epidermis of *P. incana* (scale bar = 10 µm); (K) thin cross section of dry epidermis of *F. dichotoma* (scale bar = 50 µm); (L) thin cross section of dry epidermis of *O. grandiflorum* (scale bar = 50 µm), and (M) thin cross section of wet epidermis of *O. grandiflorum* (scale bar = 100 µm) with broken epidermal cells that liberate mucilage.

6.4.2 Mucilaginous wings

Ursinia cakilefolia

Dry achenes of *Ursinia cakilefolia* (Asteraceae) have a winged pappus (Figure 6.5A), consisting of a single layer of radially elongated cells with helically thickened cell walls (Figures 6.5B & C). When the pappus comes into contact with water, the cells separate at the middle lamellae and the helical thickenings uncoil to form long strands of mucilage (Figures 6.5D & E). The different steps through which the pappus uncoils are clearly visible under the scanning electron microscope (Figure 6.5F).

Tripteris hyoseroides

Achenes of *Tripteris hyoseroides* (Asteraceae) are three-winged. The epidermis of the seed bearing part of the achene is undulate and does not become mucilaginous (Figure 5.6A). The section of the wings show hexagonally shaped cells completely filled with mucilage and separated by thick cell walls (Figure 6.6B). Upon wetting, the cells separate and the wings become completely mucilaginous (Figures 6.6C & D) and the long mucilage strands remain attached to the achene (Figure 6.6E).

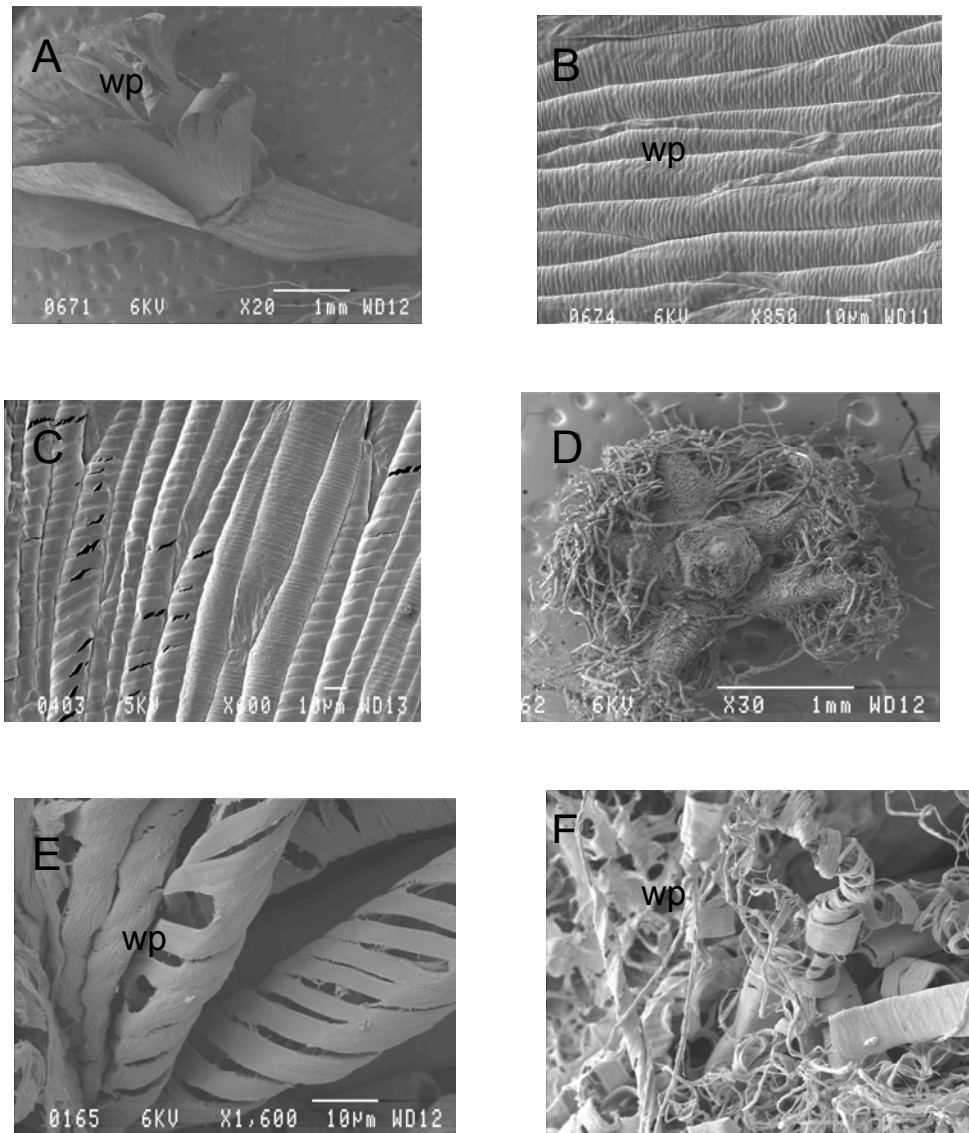


Figure 6.5 Scanning electron micrographs of the achenes of *Ursinia cakilefolia*. (A) Entire dry achene with wing pappus (scale bar = 1 mm); (B & C) High magnification of the dry winged pappus consisting of radially elongated cells (scale bar = 10 μ m); (D) entire wet achene with uncoiled winged pappus (scale bar = 1 mm); (E) high magnification of wet winged pappus (scale bar = 10 μ m); (F) long strands of uncoiled mucilage (scale bar = 10 μ m), wp = winged pappus.

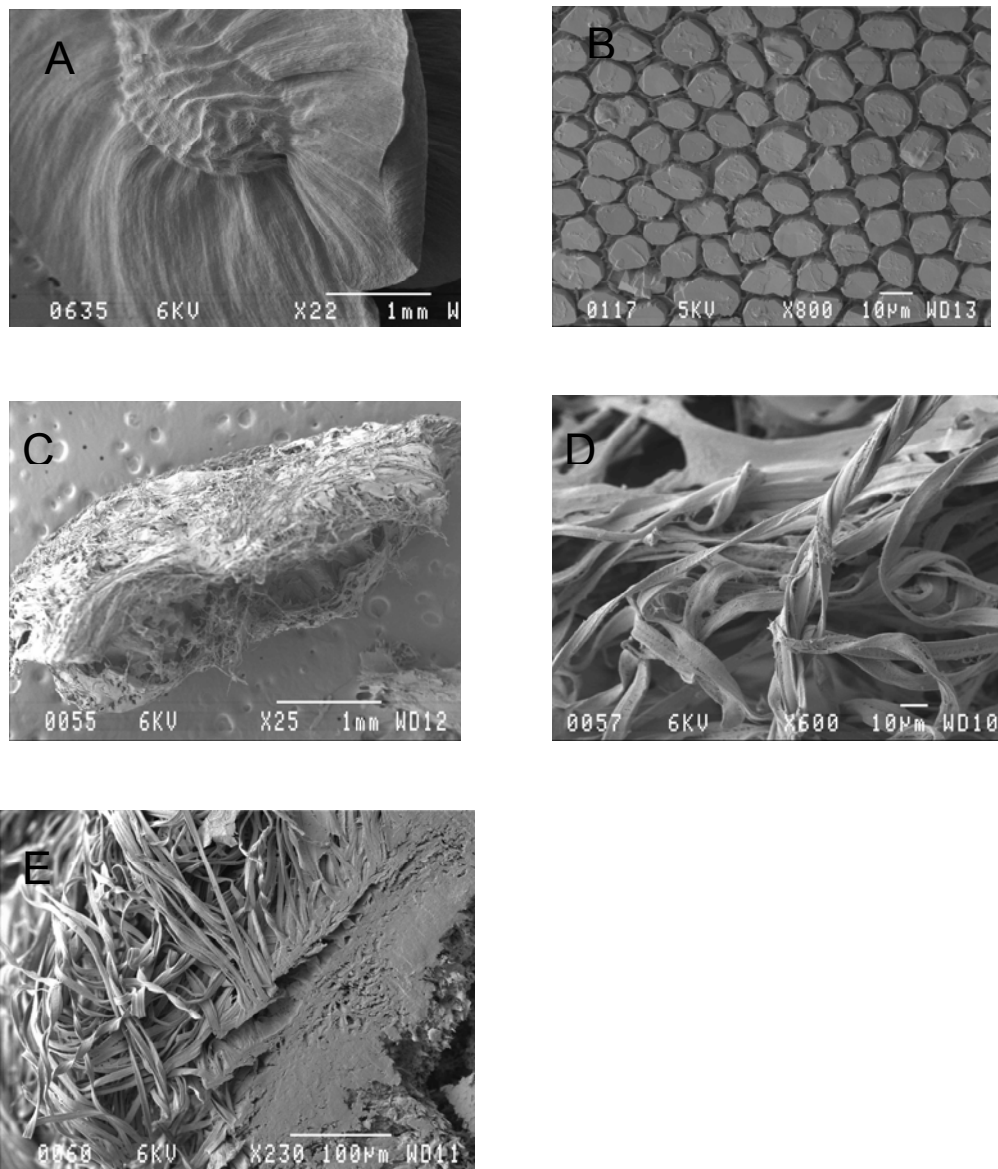


Figure 6.6 Scanning electron micrographs of the achenes of *Tripteris hyoseroides*. (A) Entire dry achene (scale bar = 1 mm); (B) high magnification of a section of the wings (scale bar = 10 μm); (C) entire wet achene with disintegrated wing (scale bar = 1 mm); (D) high magnification of long strands of mucilage (scale bar = 10 μm); (E) section of the wet seed with disintegrated wings (scale bar = 100 μm).

6.4.3 Mucilaginous hairs

Senecio arenarius

In the dry condition, the shiny white hairs, lie against the achene (Figure 6.7A) and have a finger-like shape. The interior of the hair seems to be filled with a coiled thread as seen at high magnification (Figure 6.7B & C). In the wet condition the hairs are orientated more or less perpendicular to the achene. Apparently, when the mucilaginous hairs absorb water the threads uncoil and become thin and long (Figure 6.7D). Under the light microscope, the hairs consist of two elongated cells attached to the epidermis (Figure 6.7F).

Othonna cylindrica

The dry achenes of *O. cylindrica* are covered with long white hairs (Figure 6.8A & B). When wet the tips of the hairs disintegrate to release an amorphous mucilaginous mass (Figure 6.8D). Apparently the hairs of *O. cylindrica* are covered and filled with a mucilage which, when in contact with water forms a firm gel (Figure 6.8E) that remains attached to the hair and produces long strands of mucilage that separate from the rest of the hair (Figure 6.8F). The bottom of the hair remains intact and firmly attached to the epidermis (Figure 6.8G).

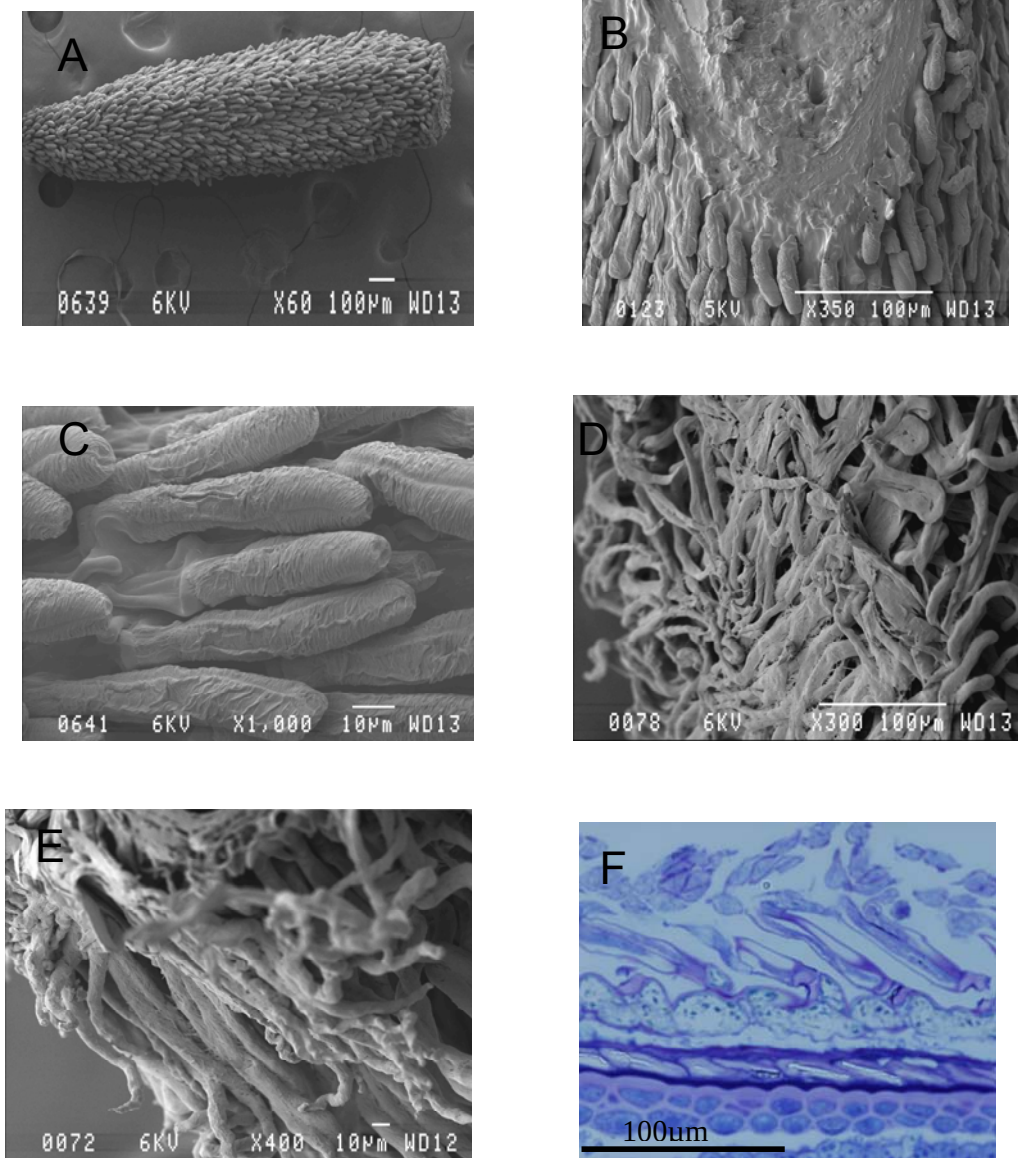


Figure 6.7 Scanning microscope (A-E) and light microscope (F) images of the achenes of *Senecio arenarius*: (A) Entire dry achene (scale bar = 100 µm); (B) dry section of the achene with hair lying against it (scale bar = 100 µm); (C) high magnification of hairs (scale bar = 10 µm); (D) entire wet achene (scale bar = 100 µm); (E) high magnification of wet achene with elongated hairs (scale bar = 10 µm); (F) cross section of wet achene with elongated bicellular hairs (scale bar = 100 µm).

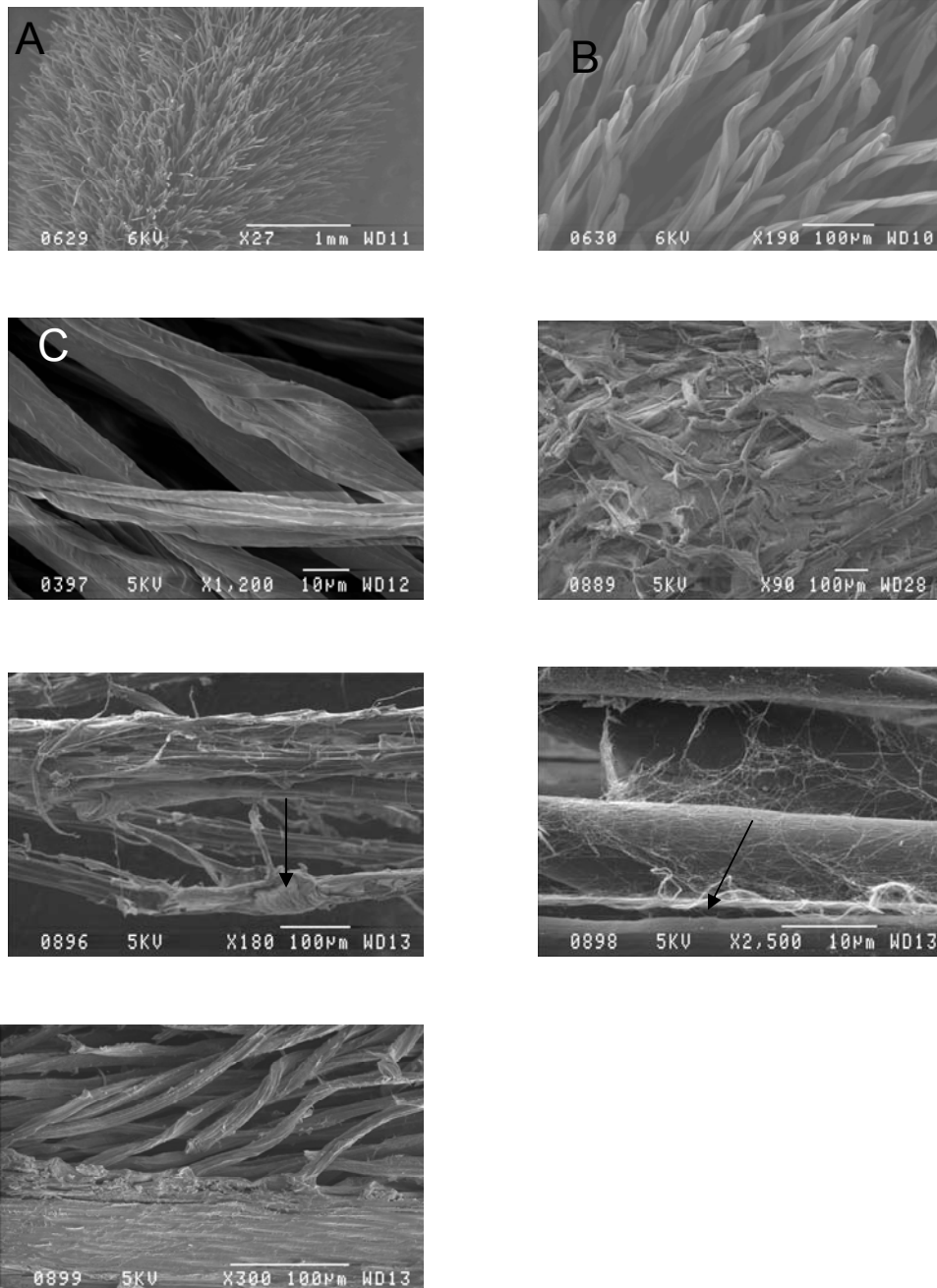
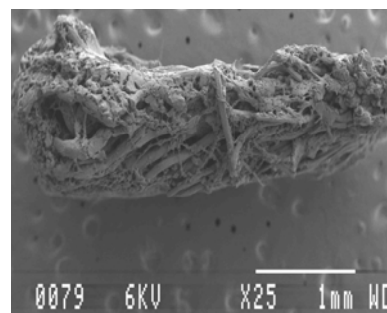
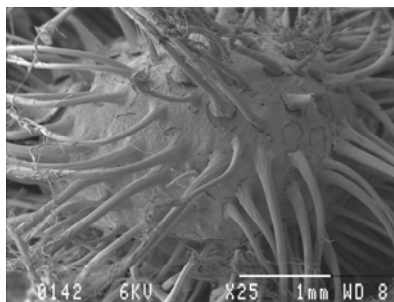
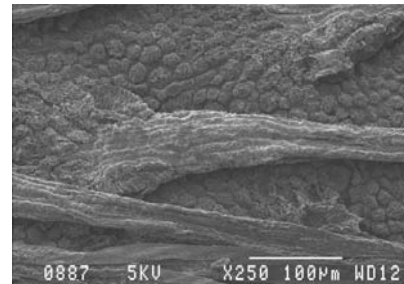
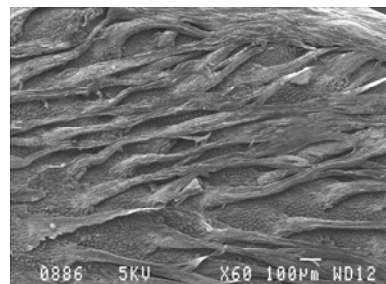
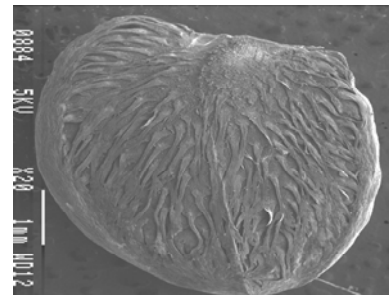
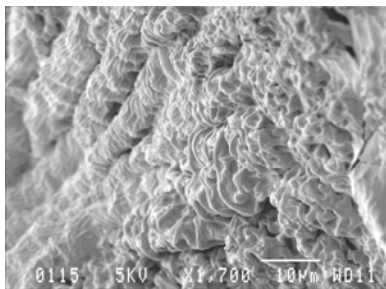
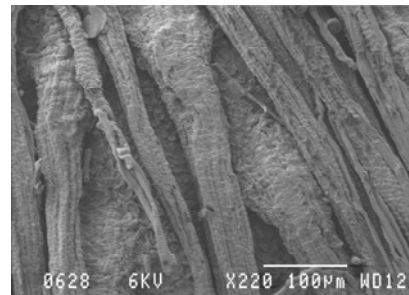
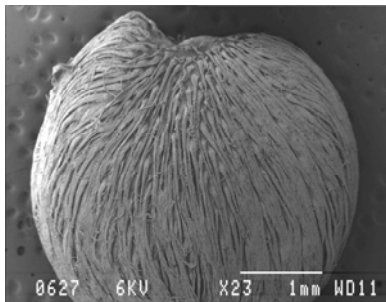


Figure 6.8 Scanning electron micrograph of achenes of *Othonna cylindrica*: (A) Entire dry achene (scale bar = 1 mm); (B) dry hair in high magnification (scale bar = 100 μm); (C) dry hair (scale bar = 10 μm); (D) entire wet achene (scale bar = 100 μm); (E) hairs covered with mucilage (arrow) (scale bar = 100 μm); (F) high magnification of wet hair with mucilage strand (arrow) (scale bar = 10 μm); (G) section of wet seed with the bottom of the hair attached to the epidermis (scale bar = 100 μm), m = mucilage.

***Acanthopsis horrida* and *Blepharis furcata* (Acanthaceae)**

In the dry condition the hairs on the seed surface of *Acanthopsis horrida* (Figure 6.9 A & B) and *Blepharis furcata* (Figure 6.9D & E) are tightly appressed to the seed coat and are covered with a thick deposit (Figure 6.9C & F). At high magnification it can be seen that these hairs contain coiled spirals (Figure 6.9 B). Once in contact with water the thick deposit expands, the hairs become swollen and orientate perpendicular to the seed coat (Figure 6.9G-I). The tips of the hair break open and release a multitude of strands of mucilage (Figures 6.9K-M). The bases of the hairs remain intact (Figure 6.9J).



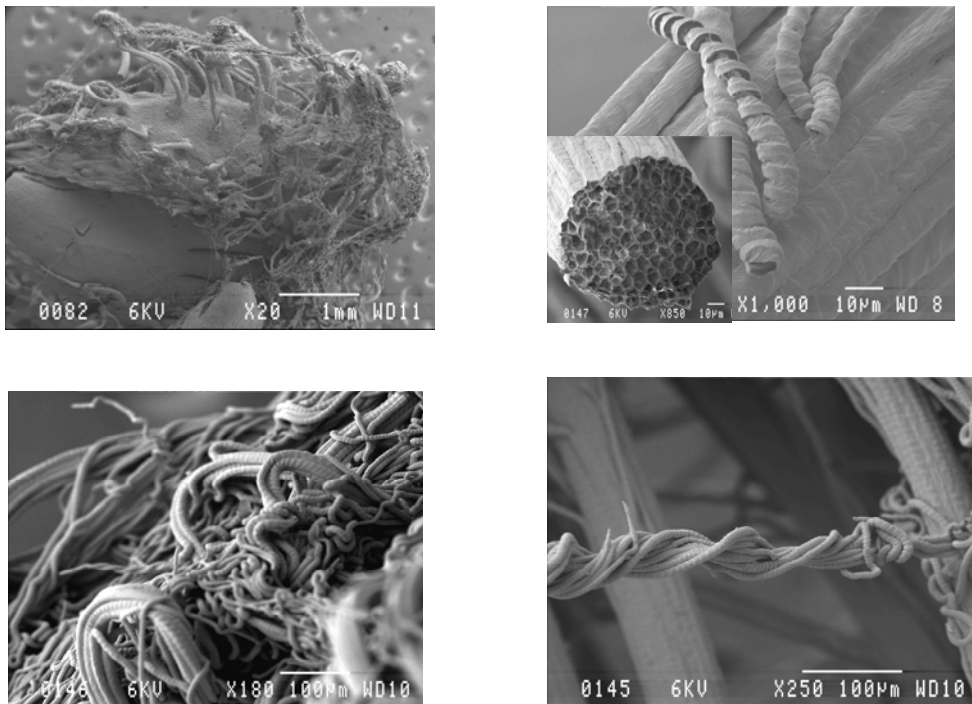


Figure 6.9 Scanning electron micrographs of seeds of *Acanthopsis horrida* and *Blepharis furcata*. (A) Entire dry seed of *A. horrida* (scale bar = 1 mm); (B) hairs of *A. horrida* (scale bar = 100 μm); (C) dry epidermis of *A. horrida* covered with thick deposit (scale bar = 10 μm); (D) entire dry seed of *B. furcata* (scale bar = 1 mm); (E) hairs of *B. furcata* (scale bar = 100 μm); (F) dry epidermis of *B. furcata* covered with thick deposit (scale bar = 100 μm); (G) wet seed of *A. horrida* (scale bar = 1 mm); (H & I) wet seed of *B. furcata* (scale bar = 1 mm); (J) bottom of a single wet hair of *A. horrida* made up of many strands (scale bar = 10 μm); (K) swollen hairs of *A. horrida* (scale bar = 10 μm); (L & M) uncoiled strands of mucilage of *A. horrida* (scale bar = 100 μm).

6.4.4 Staining

A positive reaction was only found with three stains: methylene blue for cellulose, ruthenium red for pectic substances and toluidine blue for polysaccharides. The rest of the stains did not react with the mucilage (see Appendix 1)

Table 6.1 Reaction of staining with the mucilage of each species

	Methylene blue	Ruthenium red	Toluidine blue
<i>Heliophila thunbergii</i> var. <i>thunbergii</i>	++	+	-
<i>Cotula barbata</i>	+	+++	++
<i>Salvia dentata</i>	+	+++	+
<i>Foveolina dichotoma</i>	+++	++	+
<i>Ursinia cakilefolia</i>	+++	++	+
<i>Tripteris hyoseroides</i>	+++	++	++
<i>Othonna cylindrica</i>	+++	+	+
<i>Senecio niveus</i>	++	+++	+++
<i>Acanthopsis horrida</i>	+++	+++	+++
<i>Blepharis furcata</i>	+++	+++	++

+ the number of symbol indicate the intensity of the reaction

Cellulose is the most abundant plant polysaccharide found in the form of microfibrils in cell walls and mucilage. It is a linear polymer of β -(1-4)-D- glucopyranose units. Different types of cellulose are found depending on the hydrogen bonding and hydrophobic properties. Dry amorphous and fibrous cellulose can absorb considerable amounts of water and becomes soft, flexible and viscous. Some cellulose is water-soluble and does not form a gel but forms open helical coils. Pectin is a heterogeneous grouping of acidic structural polysaccharides with the main molecules being the D-galacturonic acid residues. They do not possess exact structures and are complex. As for cellulose, pectin is a water binder, highly viscous and can form a firm gel when in contact with water (www.lsbu.ac.uk/water/hypec.html).

In all cases, the mucilage of these diaspores contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. This could be due to the presence of microfibrils of cellulose embedded in the pectin compounds forming a complex matrix. However, pectic substances and cellulose are also known to be the main component of the cell wall. In contact with water, hydrolytic enzymes such as pectinase, degrade the cell walls by breaking polymers into small subunits or breaking crosslinks. The reaction to the stains could partly be ascribed to the cell walls being present in the mucilage. There was no relationship between the structural origin of the mucilage and its chemical composition.

6.5 Conclusions

The structural origin and the chemistry of mucilage produced by diaspores are diverse. Diaspores that produce mucilage in the same way do not necessarily have the same chemical composition. Diaspores of myxospermous plant species might produce mucilage in different ways but this function is restricted to epidermal cells and other external appendages like hairs and wings. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions. This study has only given a broad scale of categories of compound that one could expect when working with mucilaginous diaspores. The chemistry of the mucilage is complex and needs a more detailed study to determine the exact type of polysaccharide forming mucilage in each diaspore.

6.6 Appendix 1

Images of microscope slides showing the reaction of mucilage with different stains

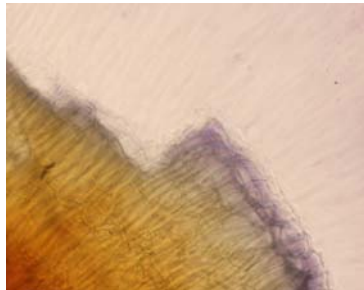
Heliophila thunbergii (Brassicaceae)



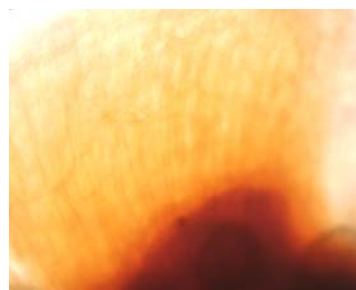
Methylene blue



Ruthenium red



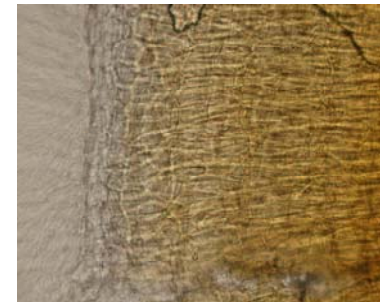
Toluidine blue



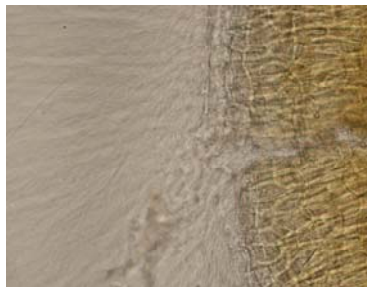
Aniline blue



Biuret solution



Phloroglucinol

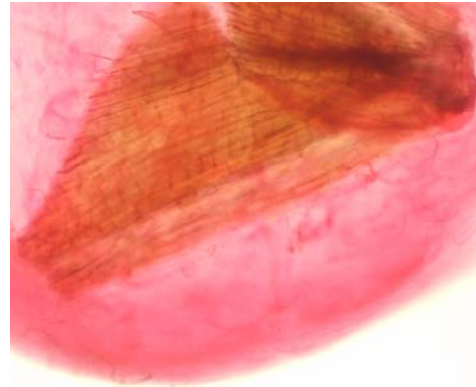


Sudan 4

Cotula barbata (Asteraceae)



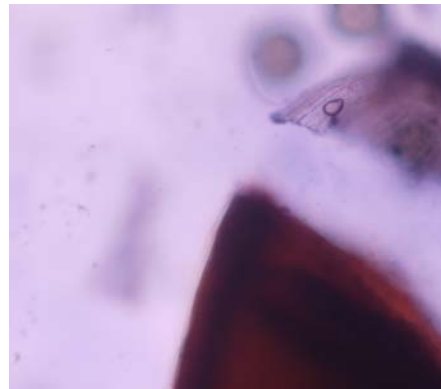
Methylene blue



Ruthenium red

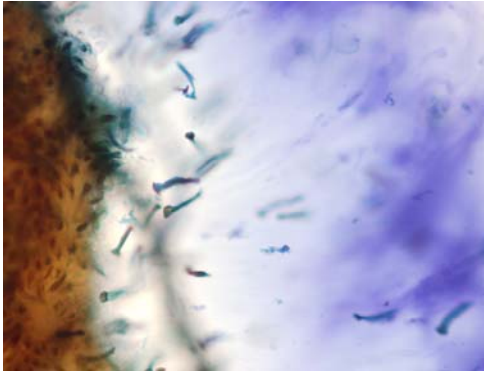


Toluidine blue

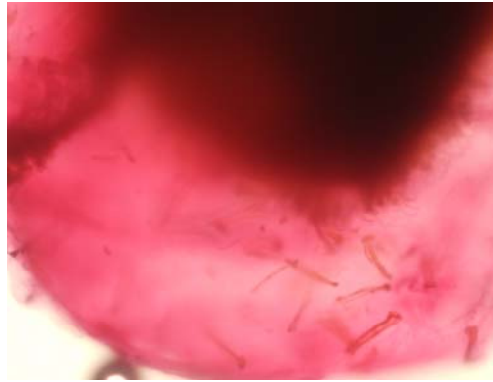


Aniline blue

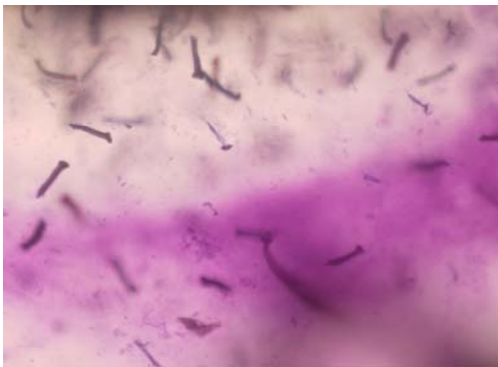
Salvia dentata (Lamiaceae)



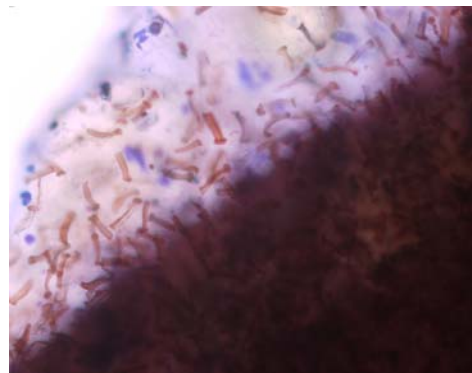
Methylene blue



Ruthenium red



Toluidine blue

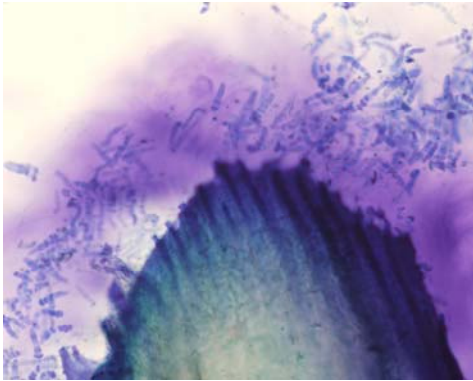


Aniline blue

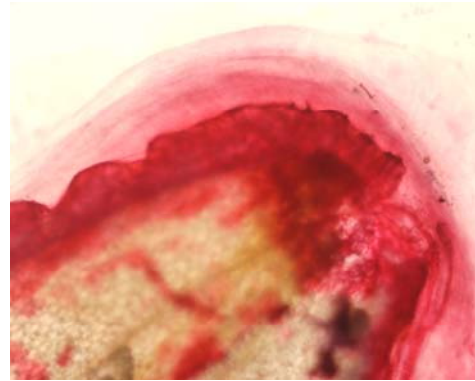


Phloroglucinol

Foveolina dichotoma (Asteraceae)



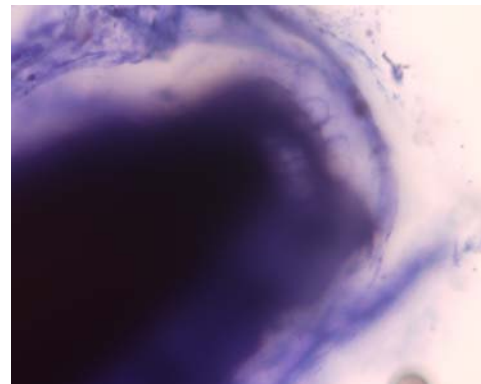
Methylene blue



Ruthenium red



Toluidine blue

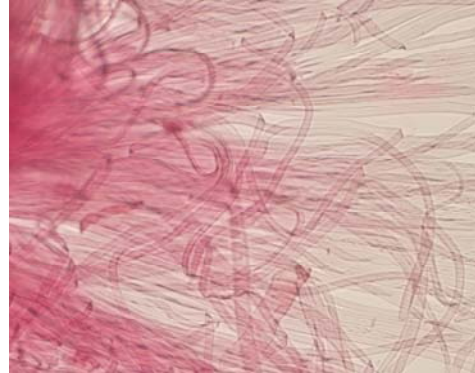


Aniline blue

Ursinia cakilefolia (Asteraceae)



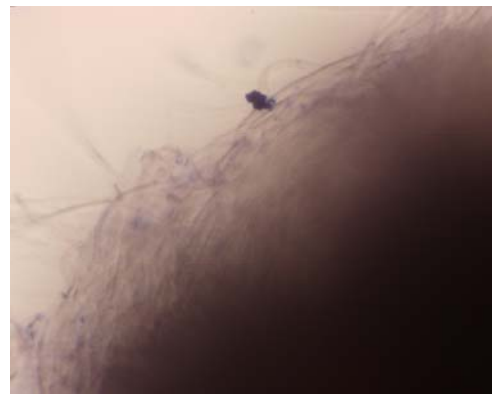
Methylene blue



Ruthenium Red



Toluidine blue



Aniline blue

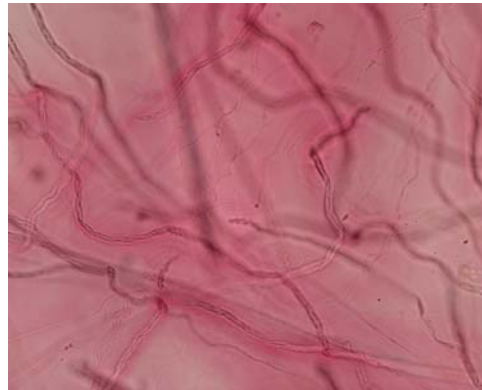


Biuret solution

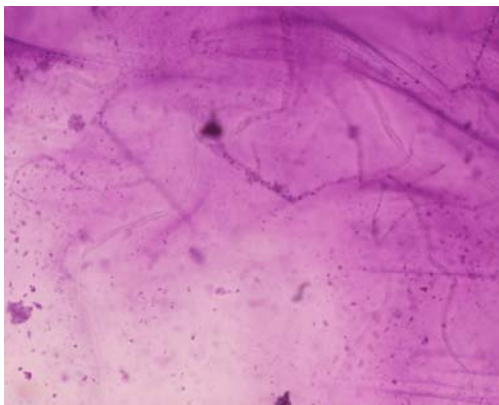
Othonna cylindrica (Asteraceae)



Methylene blue



Ruthenium red

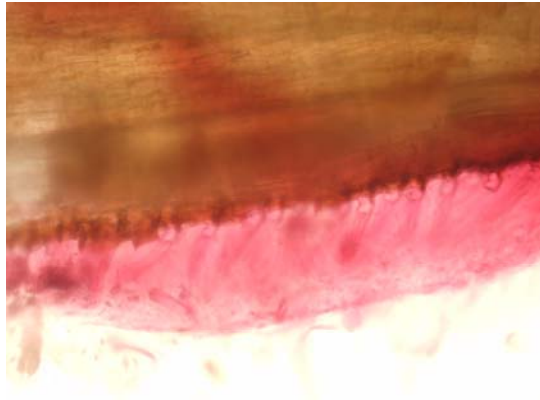


Toluidine blue

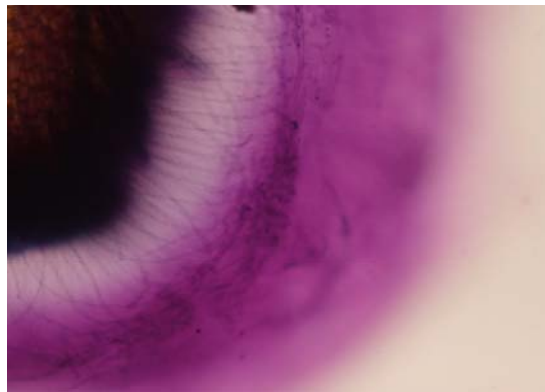


Biuret solution

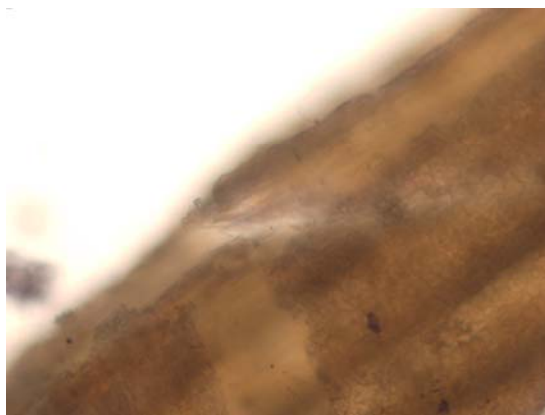
Senecio niveus (Asteraceae)



Ruthenium red

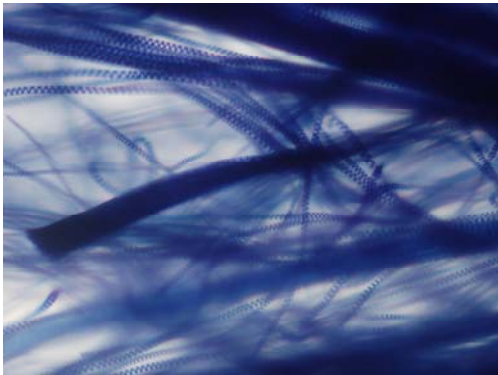


Toluidine blue

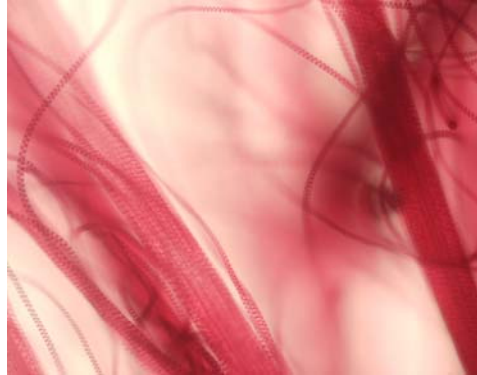


Aniline blue

Acanthopsis horrida (Acanthaceae)



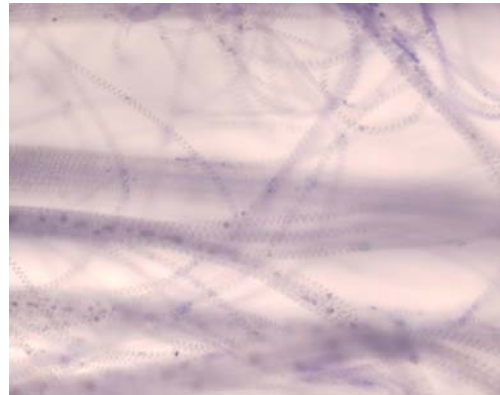
Methylene blue



Ruthenium red



Toluidine blue

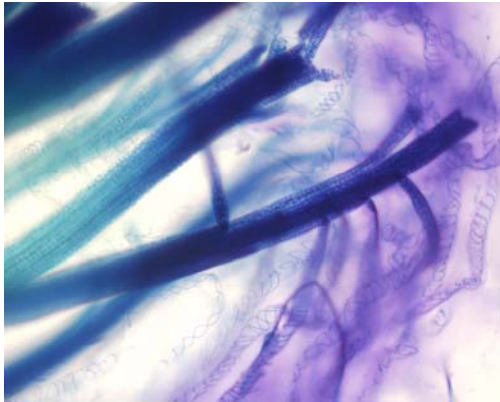


Aniline blue

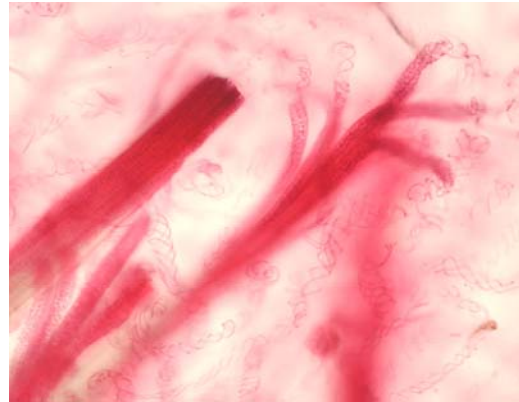


Phloroglucinol

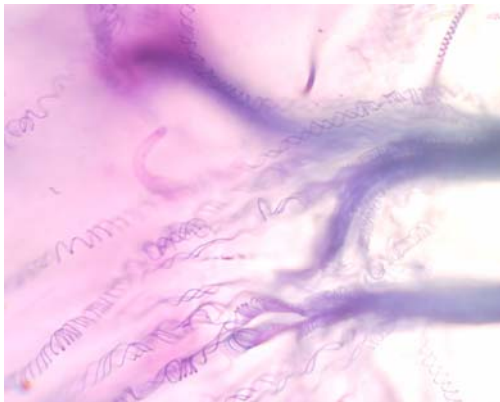
Blepharis furcata (Acanthaceae)



Methylene blue



Ruthenium red



Toluidine blue



Aniline blue



Phloroglucinol

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Chapter 7

General discussion and conclusions

The development of sustainable management systems for dry regions used for stock and crop production need to be underpinned by an understanding of the variety of functional adaptations, which characterize the system. Dispersal and disturbance are significant forces in the ecological and evolutionary dynamics of a population. Dispersal is a functional trait and plays an important role not only in range expansion but also in determining the spatial and genetic structure of populations at local and landscape scale (Levin *et al.* 2003). Livestock grazing has been identified as a major threat to the biodiversity in the Succulent Karoo Biome.

Based on the concept that vegetation is the most obvious external feature on which to classify ecosystems, a phytosociological classification of the vegetation of the study area was made. The six plant communities found largely reflect differences in land type, although the effect of different grazing intensity on communal and commercial rangeland is not excluded.

The mix of observed dispersal strategies is mirrored in the varied costs and benefits associated with different dispersal modes. In order to compile the dispersal spectra of the study area dispersal types were assigned to each species. The dispersal spectra of the two rangelands and communities were dominated by ombrohydrochory, autochory, plumed diaspores, dust diaspores and winged diaspores. Endozoochory was found to be significantly higher in communal land than in commercial land. Ombrohydrochoric, myxospermic, hygrochasic and woolly diaspores were significantly higher in commercial land than in communal land. At community level, endozoochory was significantly higher in the water course community (community 1) than in the plains community (community 3). Autochory and plumed diaspores were significantly lower in the watercourse community than in the sandy valley community (community 2). Ombrohydrochoric, autochoric, hygrochasic and woolly diaspores were significantly higher on the rocky slope community (community 5) and rocky hill community (community 6) than in the water-course community. In general, therefore the water course and sandy valley

communities differed most in their dispersal spectra from the other rockier communities.

Grazing, water, and landscape seem to be the major factors influencing the composition of different dispersal types. Herbivores can be important agents of dispersal for plants, even if they are not primarily seed eaters and their dung provides an ideal environment for germination of seeds and the growth of seedlings. Wind is a regular phenomenon in most desert areas and is minimally modified by vegetation acting as windbreak as is the case with a closed habitat. The lack of significant difference found in most anemochoric dispersal modes between the two rangelands is not surprising as desert plants are characteristically of low stature and allow wind circulation at all height levels. The genus *Eriocephalus* (shrubs) was the most dominant group with woolly diaspores. The low number of individuals with woolly diaspores in communal rangeland can be related to the decrease of *Eriocephalus* plants due to overgrazing by livestock. Furthermore, the movement of diaspores not only depends on the wind velocity but, also on the air humidity which is high in the water course habitat and therefore reduces the efficiency of dispersal. The significantly higher incidence of ombrohydrochory on the commercial land is attributed to the contributions of hygrochasy and trypanospermy. The main advantage of trypanospermy is the enhancement of water uptake due to increased seed-soil contact brought about by the burial of the diaspore. Most hygrochastic species possess a canopy seed bank from which diaspores are slowly released, depending on the amount and frequency of rainfall. This confers an advantage to these species to disperse their seeds at a favourable time for germination. The low number of hygrochasic species in communal land is as a result of indirect and direct effects of overgrazing on plant population dynamics.

Myxospermy was expected to contribute more on communal land than in commercial land given the proposed advantages that mucilage confers to seeds. Mucilage might confers resistance to some types of disturbance it does do not seem to confer resistance to overgrazing. The primary role of mucilage is linked to seed germination and seedling establishment. Although myxospermy acts after rather during the primary dispersal phase. Furthermore, the indirect effect of grazing might also influence the success of myxospermy as changes of the soil microtopography might

influence germination patterns of mucilaginous species. Livestock grazing is commonly considered a disturbance that affects ecological systems, especially if the grazing pressure is high. It may also affect the abiotic environment for example nutrient and water flow and loosening or compaction of the soil. Despite differences in trait spectra among rangelands and communities, all dispersal modes are represented in nearly all communities in the two rangelands. There was not a particular trend for species with telechoric, atelechoric and antitelechoric dispersal groups. Seed germination and seedling establishment are both crucial steps in the life cycle of a plant. The success of a species depends on every step of the life cycle; the interruption of one step might affect the survival negatively.

Mucilaginous diaspores produce a copious amount of mucilage once they come into contact with water. If they dry out, the seeds adhere to the soil. Information on the factors controlling the germination of these seed types will improve our limited knowledge on the survival of these plant species and could aid in the management and conservation of arid system. The temperature and light requirements for germination of 23 mucilaginous species of Namaqualand (24 seed types) were investigated. Significantly higher germination percentage in dark treatments were obtained for seven species with the majority being annuals and they all have a low ($\leq 17^{\circ}\text{C}$) optimal germination temperature. Almost half (11 species) of the species investigated required light for optimum germination and all of these species were annuals except the perennial *Tripteris oppositifolia*. The majority of the perennial species investigated and two annuals were not significantly affected by light at various temperatures. Nine species, mostly annuals, obtained significantly shorter mean germination times (days) in light than in the dark. The only perennial species in this group was *Senecio niveus*. Two of the species investigated obtained significantly shorter mean germination times in the dark. Mean germination time was not significantly affected by light in more than 50% of the species. This group included approximately a half of all annuals as well most of the perennial species. The alternating temperature did not show a particular trend in this study. Mucilaginous species have the same germination requirement as most desert species, but their adhesion to the soil (often near the mother plants) provides them with the ability to germinate in a suitable environment. The optimum conditions for germination differed among species, but in general most species obtained their highest germination

percentage at low and intermediate temperatures which in the field represent the autumn and winter seasons. For management purposes keeping livestock on the field during summer months prior to autumn germination could promote the germination of some species because animal movement might bury seeds with negative photoblasty, however, it could also reduce germination of positive photoblastic seed by their burial.

The various ideas that have being suggested about the ecological importance of myxospermy, and its ability to fulfill various functions led to the further investigation of the origin and chemical composition of mucilaginous seeds. The seeds of species of four families were investigated, i.e Acanthaceae, Asteraceae, Brassicaceae and Lamiaceae. Results have suggested three types of mucilage production which can be distinguished as follows: 1) epidermal and subepidermal mucilage production where the release of mucilage is correlated with the rupture of the cuticle of the epidermal cells, 2) species where the wings or the pappus disintegrate and become completely mucilaginous, and 3) species with mucilage excreting hairs. The chemical composition of the mucilage was found to be very complex and needs a more detailed study to determine the exact type of polysaccharide forming mucilage in each diaspore. However, the mucilage of all these diaspores investigated contained both cellulose and pectic substances exclusively or a complex of pectino-cellulosic compounds. There was no relationship between family, the origin of the mucilage and its chemical composition. Despite the diversity of the mucilage origin and structure, they accomplish more or less the same ecological functions.

Understanding the mechanisms of vegetation responses to environmental change is very complex and does not only required a floristic analysis but also the exploration of the multitude of plant functional traits implicated in the internal processes of the community. An in depth knowledge of the standing vegetation, and the various functional traits can aid decision making when considering management practices for conservation or farming.

Chapter 8

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