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UNTANGLING CLUMPS –
FACTORS INFLUENCING SEEDLING ECOLOGY IN A SEMI-DESERT,
AND THE IMPLICATIONS FOR RESTORATION ECOLOGY

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Thesis presented for the degree of Master of Science
in the Department of Botany, at the University of Cape Town.

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DEDICATION

Dedicated to the people of Namaqualand.

University of Cape Town

DECLARATION

I declare that *Untangling Clumps – Factors Influencing Seedling Ecology in a Semi-Desert, and the Implications for Restoration Ecology* is my own work, and that it has not been submitted for any other degree or examination at any other university and that all the sources I have used or cited have been indicated and acknowledged by complete reference.

Raldo Krüger

Date

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University of Cape Town

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To my God and Lord, Jesus Christ, thank You for the magnificent grandeur, and the intricate minutiae of the natural systems You created on earth. It speaks volumes of Your omniscience to conceive of such incredible complexity and Your omnipotence to make it all work together, despite our poor attempts to look after this natural wealth. Thank You for the opportunity, encouragement and strength You have given me during the time I worked in Namaqualand, and for the inspirational sunsets, floral displays and general beauty of the region, which kept me going during the many hot, cold, windy or rainy days!

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SUMMARY

Facilitation between plants and patch dynamics are two common ecological processes in semi-arid regions. I tested the relevance of these processes to seedling establishment of perennial species on degraded landscapes in Namaqualand, South Africa. The species were grouped into two functional guilds, Mesembryanthea (formerly the family Mesembryanthemaceae, but now part of the Aizoaceae; hereafter Mesemb), which rely on CAM to a variable degree and are shallow rooted, and non-Mesembryanthea (hereafter non-Mesemb) that utilize C3 photosynthesis and have deeper root systems.

I tested the hypothesis that non-resource factors of micro-sites affect seedling establishment by sowing seeds into unsheltered control plots and plots sheltered by transplanted adult shrubs, plastic tubes or square cardboard boxes. Survival of Mesemb seedlings was unaffected by shelter of adult shrubs or plastic tubes in Year 0, 1 or 2. Mesemb seedlings were also unaffected by box shelters in Year 0, but in Year 1 and 2 box sheltered plots had fewer seedlings, due to boxes collapsing onto seedlings. In a second experiment, the box methodology was improved so that they do not collapse, but seedling survival was still no different to unsheltered plots in Year 0. However, by Year 1 there were more seedlings in box sheltered plots, although these were smaller than those in unsheltered plots. Fewer non-Mesemb seedlings established under adult shrubs and more seedlings survived in plastic tube sheltered plots than in unsheltered ones in Year 0, 1 and 2. Box sheltered plots had more non-Mesemb seedlings than unsheltered plots in Year 0 only, while in Year 1 and 2 they had fewer seedlings due to collapsing boxes. With the improved box methodology, box sheltered plots had fewer non-Mesemb seedlings in both Year 0 and 1, however, these seedlings were taller than in unsheltered plots in Year 1.

I tested a second hypothesis, that seedling establishment is by affected micro-site resources (nutrients and water) by applying various soil treatments. Seedlings were cultivated in a greenhouse and transplanted into field plots where nutrients (N, P and K) were added to the soil at ecologically relevant quantities. In a further two experiments, seeds were sown into plots where nutrients (suite of macro and micro nutrients) were added and water availability was increased (through water-absorbing polymer gel, gravel or kelp fragments). Mesemb seedling establishment (survival and growth) was unaffected by nutrients in all three experiments. Increasing water availability by adding gel had no effect on survival of Mesemb seedlings, while kelp and gravel treatments had negative effects on seedling survival. However, the kelp treatment yielded taller Mesemb seedlings. Non-Mesemb seedling survival was increased by nutrients in two experiments and yielded taller seedlings in one. Increasing water availability by adding gel or kelp had no effect on non-Mesemb survival, but adding gravel increased seedling survival. The kelp treatment yielded taller non-Mesemb seedlings in Year 1.

Potential nurse species do not facilitate seedling establishment of Mesemb or non-Mesemb seedlings, concurring with other findings in the Succulent Karoo. Higher survival rates of Mesemb seedlings and greater growth rates of non-Mesemb seedlings when sheltered adequately indicate that there is some sheltering benefit, which can be applied to increase restoration success. Mesemb seedlings are unaffected by soil resources, and may establish better in open spaces between patches. Non-Mesemb seedlings benefit from additional soil resources, especially when the micro-site is also physically sheltered, typically found in patches in undisturbed vegetation. The results support the notion that seed dispersal mechanisms and seedling ecology are linked, and can inform restoration practices.

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Chapter 1

INTRODUCTION

PROBLEM STATEMENT

Seedling ecology is an important contributor to vegetation dynamics in natural systems, since where and how seedlings establish themselves determines where they will exist as adults (Boeken, 2008; Grubb, 1977). It is also crucial to understand this aspect of a plant's life cycle in order to successfully restore a degraded ecosystem and the processes that maintain it. There are at least two ecological processes that are prevalent in many arid and semi-arid systems, which may influence the seedling ecology of plants in these regions. The first relates to the uneven distribution of soil resources in arid regions, and the second relates to the potential benefits of physical shelter that is afforded by adult plants to establishing seedlings. While both of these processes are aspects of the nurse plant effect, and the broader concept of facilitation between plants, the former is also related to patch dynamics in semi-arid systems. Here I have used the convention of referring to processes relating to below-ground soil resources as patch dynamics, while above-ground processes related to the physical shelter provided by shrubs are referred to as the nurse plant effect.

Patch dynamics, where resources are concentrated in the soils below long-lived plants or clumps of plants (Aguiar & Sala, 1999), could lead to differential establishment success rates of seedlings (Harper, 1977). The higher resource levels in patches may allow seedlings that establish here to grow faster and larger than seedlings that establish in inter-patches where there are fewer resources, and thus have a greater chance of reaching adulthood. The physical shelter provided by shrubs from non-resource environmental elements could also be beneficial to seedlings that establish here, particularly in harsh environments such as semi-arid regions (Flores & Jurado, 2003). Nurse plants can shelter seedlings from harsh sunlight, strong winds, herbivory or trampling by animals (Callaway, 1995). However, the potential resource benefits and non-resource benefits that seedlings experience when establishing in patches or under nurse plants might also be countered by competition for resources with the adult shrubs. The net balance of the negative effects of competition and the positive effects of greater

resources or physical shelter will ultimately determine whether it is beneficial or not for seedlings to establish in these micro-sites (Callaway, 1995).

The prevalence of multi-species clumps in semi-deserts like Namaqualand indicates that the benefits of facilitation outweigh the costs of competition in these environments (Eccles *et al.*, 2001; Eccles *et al.*, 1999). While niche separation by different plant functional guilds has been used to explain the co-existence of adult plants (Carrick, 2003; Cody, 1986; Schenk *et al.*, 1999), the processes that lead to these clumps are poorly understood, partly due to the relative dearth of research on seedling ecology in the region. This thesis explored the factors that influence the seedling ecology of dominant perennial species in the Namaqualand Sandveld bioregion, in order to better understand the processes that lead to the formation of multi-species clumps. Facilitation by increased soil resources or shelter from non-resource elements are typical ecological features in semi-arid regions (Flores & Jurado, 2003), and the knowledge gained about Namaqualand's seedling ecology may be extended to other semi-arid regions. Furthermore, due to human-induced degradation, ranging from overgrazing to open-cast mining, there is a strong need to improve our knowledge of restoration ecology in the region. Understanding seedling ecology is valuable in developing guidelines for restoration interventions (Chambers, 2000), and the implications of these findings are discussed in light of restoring degraded landscapes in this region. This knowledge may well be applied to other semi-arid regions with some adaptation.

LITERATURE REVIEW

ARID SYSTEMS

Approximately 47% of the land surface of the earth is occupied by warm deserts (Evenari, 1986), also called drylands or arid and semi-arid regions. The most definitive feature of these regions is that very low amounts of water are available to the organisms that inhabit them. Drylands are defined as regions where the mean annual precipitation is 2/3 of the potential evaporative demand (Verstraete *et al.*, 2008). Persistent expansion of these drylands, called desertification, has at least partly been attributed to human activities. Anthropogenic climate change, unsustainable land use and extraction of mineral resources are among the main causes. According to the United Nations Convention to Combat Desertification, the phenomenon is a 'worldwide problem directly

affecting 250 million people and a third of the earth's land surface' (UNCCD, 2003). Thus the need to understand the processes that underpin ecology in arid regions has become more critical – both from a conservation and a restoration perspective.

Arid regions can occur in very hot, intermediate or very cold climates, mountainous or flat areas, rocky or sandy areas, and inland or close to the coast (Whitford, 2002). These factors have different effects on the plant communities that occur in these regions, and can either ameliorate or aggravate the effect of limited water input in these regions, by altering the potential evaporative demand. This will in turn have a strong influence on the selective regime under which plants exist, and the resultant adaptations to the conditions by plants (Ward, 2009). It is also important to understand these effects when restoration is attempted, so that the most critical limiting factors can be overcome in order to re-establish key ecological processes and ecosystem stability.

From a botanical and ecological point of view, plants in arid and semi-arid regions are of great interest since the conditions in which they occur represent the extremes of potential habitats that plants can occupy. Due to the extreme environmental conditions in arid regions plants often evolve similar solutions in order to survive (Ward, 2009). Indeed, there are a number of ecological concepts that are common in most arid or semi-arid systems. Below is an introduction to two of the most prevalent concepts, patch dynamics and facilitation by 'nurse plants'. Following that is an introduction to general seedling ecology, which highlights the relevance of the two ecological concepts to this important phase of plant life. The chapter concludes by introducing restoration ecology and reviewing examples of how patch dynamics and nurse plants have been applied to this field.

PATCH DYNAMICS

A common feature of arid or semi-arid systems is that plants do not occupy all the available ground surface area (Ward, 2009). This implies that plants in these systems are limited by some resource, since plants in more resource abundant systems often occupy all the horizontal area, and sometimes occupy several vertical layers too (e.g. canopy and understory layers in forests). While water is an obvious limiting resource in arid and semi-arid systems, there are often concomitant low levels of nutrients and organic matter due to the low productive potential of these systems. In semi-arid systems, plants tend to

compete for water when it is scarce (e.g. during the drying phase after a rain event), and for nutrients and light when water is abundant (Grubb, 1992). Competition, however, leads to the displacement or inhibition of neighboring plants (Tilman, 1987), and in low resource regions like semi-deserts, this leads to plants that occur within clumps separated by unvegetated, open areas. However, these open areas are not unused by plants, since they can extract the resources from them by various mechanisms, described below. This leads to an uneven distribution of soil resources in semi-arid systems, where high resource levels occur in soils under plant canopies and lower resource levels occur in the spaces between plant canopies (Aguiar & Sala, 1999).

The term 'patch dynamics' has been used to describe the process whereby areas of relative resource abundance develop in soils under plant canopies (Aguiar & Sala, 1999). These resource rich 'patches' occur within a matrix of resource poor 'inter-patches' from where resources are gathered. Other authors have used 'fertile islands' (Dean *et al.*, 1999; Stock *et al.*, 1999) or 'resource islands' (Camargo-Ricalde & Dhillion, 2003; Carrillo-Garcia *et al.*, 2000) to describe similar phenomena, and the term 'fetches' (Ludwig *et al.*, 1999) has been used instead of 'inter-patches'. Here I use the terms patches and inter-patches to avoid confusion, despite citing papers that use the terms 'nutrient islands', 'fertile islands' or 'fetches'.

The occurrence of higher soil resources in patches than in inter-patches has been recorded in arid and semi-arid systems in North America (Butterfield & Briggs, 2009; Tibbett, 2000; Titus *et al.*, 2002), South America (Aguiar & Sala, 1994; Aguilera *et al.*, 1999; Bisigato & Bertiller, 1999; Camargo-Ricalde & Dhillion, 2003), Eurasia (El-Bana *et al.*, 2003; Maestre *et al.*, 2001; Zaady *et al.*, 1996), Australasia (Ludwig & Tongway, 1996; Tongway & Ludwig, 1996) and Africa (Carrick, 2001; Dean *et al.*, 1999; Jones & Esler, 2004; Stock *et al.*, 1999). This prevalence has led to patch dynamics becoming one of the prominent frameworks within which arid land ecology is understood, while also providing a useful starting point for restoration research (Valladares & Gianoli, 2007). But why would this feature be so widespread in arid and semi-arid systems? The answer to this question lies in the sparse vegetation cover in these regions (Deblauwe *et al.*, 2008), where plants become focal points for resource accumulation (Garcia-Moya & McKell, 1970).

Several mechanisms that lead to a heterogeneous distribution of soil resources have been proposed. It has been suggested that patches occur in a banded pattern where water is responsible for aggregating resources, while spotted patch patterns are formed when wind is the dominant aggregating force (Aguar & Sala, 1999). Examples of both patterns have been discovered in many semi-arid regions. 'Trapping' of airborne particles by the plant canopy is a common mechanism in systems where winds are frequent. In the Tehuacan-Cucatlan Valley in Mexico, for example, endemic *Mimosa* species (Fabaceae-Mimosoideae) have greater levels of nutrients in the soil below their canopies (Camargo-Ricalde & Dhillion, 2003). It is likely that spores of arbuscular mycorrhizae, which aid in nutrient uptake, are trapped by the plant canopies and deposited on the soil below the canopy, resulting in a greater abundance under trees (Camargo-Ricalde & Dhillion, 2003). In the northern Sinai desert, nutrient rich soil sediments are deposited within and around plant canopies to the extent that mounds are formed (El-Bana *et al.*, 2003). These mounds, or 'nebkhas', create patches with higher nutrient levels in which other plants are able to grow. The accumulation of leaf litter below a plant (whether from the plant itself or from other plants in the landscape) also leads to higher nutrient levels in patches (Tongway & Ludwig, 1996; Zaady *et al.*, 1996).

Animals associated with plants can also contribute to the increase of resources in patches. In the Kalahari semi-desert in southern Africa, *Acacia erioloba* trees are focal points for animal activity, resulting in higher nutrient levels under the trees due to decomposition of faeces, fallen nests and carcass remains under the trees (Dean *et al.*, 1999). Soil micro-organisms associated with plant roots may also contribute to higher nutrient levels in soil below plants (Aguilera *et al.*, 1999). It has also been suggested that animals can initiate the process of creating resource rich patches that are subsequently inhabited by plants. For example fossorial rodents (Desmet & Cowling, 1999b) and harvester ants (Dean, 1993; Midgley & Musil, 1990) play this role in Namaqualand. Plants themselves can be directly responsible for creating the resource rich patches. Roots of arid or semi-arid plants often extend beyond their canopies (Esler *et al.*, 2002), thereby accessing the nutrients in the inter-patches and drawing them into the patches, and returning them to the soil below their canopies through plant litter decomposition (Zaady *et al.*, 1996).

These mechanisms mainly contribute to higher levels of nutrients within the patches, but patches have also been shown to have a higher water input than inter-patches. In Australia, where much of the landscape is gently sloped, the importance of patches that obstruct surface flow of water from inter-patches has been noted (Ludwig *et al.*, 1999). Water (and organic matter and nutrients that are carried by the water) input is higher in these patches, that often assume a banded pattern (Aguiar & Sala, 1999). In a review of patchy semi-arid vegetation types in Australia, Europe and North America, it was found that patches store significantly more water, produced greater growth, and had greater infiltration rates than inter-patches (Ludwig *et al.*, 2005). This is often due to the accumulation of leaf litter in patches (Boeken & Orenstein, 2001), or the presence of biological crusts (Eldridge & Greene, 1994), both of which decrease the run-off rate and therefore increase the infiltration rate. Furthermore, biopedturbation under plant canopies can lead to greater water infiltration rates (Whitford & Kay, 1999), when, for example small mammals or arthropods burrow under plants, loosen the soil and in so doing increase soil microtopography which in turn increases infiltration. These digging sites are known to be favorable micro-sites for seed germination in desert systems (Gutterman, 1993). In systems where fog or mist occurs regularly, some plants can harvest the water indirectly through condensation forming on their leaves and dripping onto the soil below, or directly by absorbing water into their leaves via epidermal hydathodes that enter the stomatal openings (Martin & von Willert, 2000).

While plants themselves are the driving force behind patch dynamics, the resultant unequal distribution of soil resources also influences seedling recruitment. The spatial heterogeneity of resources offers seedlings a variety of potential establishment niches. Seedlings with different ecological traits can exploit these niches differentially (Harper, 1977), thereby affecting vegetation patterns. Thus a feedback loop exists, which influences the spatial distribution of plants and structure of plant communities (Levin *et al.*, 2003; Nathan & Muller-Landau, 2000; Tilman & Kareiva, 1997). Patch dynamics are therefore a fundamental ecological process that drives ecosystem functions and long-term stability in arid and semi-arid regions, and should be considered in ecological and restoration research (Valladares & Gianoli, 2007). It is also important to understand fine scale processes such as redistribution of resources from inter-patches to patches, in order to grasp the complexity of patterns and dynamics at a landscape level (Peters *et al.*, 2006). In this thesis I investigated the effects of the two main features of resource rich

patches, greater nutrient and greater water availability, on the establishment of seedlings of the dominant species in a semi-desert in South Africa.

NURSE PLANTS

COMPETITION AND FACILITATION BETWEEN PLANTS

Plants in close proximity to each other interact to varying degrees, and these interactions also strongly influence the community structure and dynamics (Padilla & Pugnaire, 2006). Plant interactions can be broadly divided into negative or positive. Negative interactions have received the most attention from ecologists (Brooker *et al.*, 2008), and are probably the most frequent type of interaction between plants. Competition between plants for limited resources has been well established over the last 60 to 70 years (Callaway, 1995), with light, water and nutrients being the main limiting resources. In semi-arid regions, light is usually not a limiting factor between adult plants, since vegetation is sparser and shorter than in higher rainfall regions. Water is an obvious scarce resource in these systems, while competition for nutrients is thought to be equally intense whether it occurs in low or high concentrations (Tilman, 1987). Negative interactions between plants arise as a result of competition for these two resources in the soil profile. This can lead to a reduction in overall fitness of the plants through a decrease in growth rates or reproductive success, and in extreme cases, through mortality.

Positive interactions, or facilitation, between plants have received less attention than negative interactions (Brooker *et al.*, 2008). Before the mid 1980's much of the evidence was anecdotal (Callaway, 1995). However, there has been a marked increase in the amount of experimental evidence supporting facilitation between plant species (Brooker *et al.*, 2008), and it is thought that it may be a fundamental process in shaping spatial distributions within plant communities. Positive interactions must be beneficial to one or both plants, without being detrimental to either. These relationships can be described as positive-positive (+/+) where both plants benefit ('mutualism') or positive-neutral (+/0) where one benefits and the other is unaffected ('commensalism'; Brooker *et al.* 2008). Parasitic relationships, where one plant benefits to the detriment of another (positive-negative associations), are not included in the concept of facilitation.

There are many ways in which plants can benefit from being in close proximity to neighboring plants. These benefits arise through resource modification, substrate

modification, physical protection, pollination benefits, concentration of propagules and concentration of associated soil microorganisms (Callaway, 1995). Resource modification may occur as a result of several different processes including: (a) shading from sunlight, which reduces water loss through transpiration, and smaller temperature fluctuations; (b) increasing available soil moisture through reduced ground surface evaporation due to shading or the concentration of leaf litter, or increased infiltration; (c) increasing available nutrients through several mechanisms such as nitrogen fixation and 'nutrient pumping' by deep rooted species, as well as by the trapping and deposition of nutrient-rich airborne particles by the canopy, increased litter fall and decomposition and oxygenation of the soil (especially in wetlands; Callaway 1995). Substrate modification can occur when a plant changes soil properties (such as dry bulk density) by litter deposition and root penetration, or trapping of fine wind-borne particles. Palatable species may be offered protection from herbivores by unpalatable species (Callaway *et al.*, 2005; El-Bana *et al.*, 2003) or species with inaccessible architecture or spinescence (King & Stanton, 2008). Plants can also provide mutual protection to one another from the physical effects of wind or trampling by animals (Eccles *et al.*, 2001).

In reality, plant-plant interactions are highly complex. Plants in close proximity could experience competition and facilitation simultaneously (Brooker *et al.*, 2008; Callaway, 1995). It is possible to envisage how plants could compete for one resource while benefitting in an unrelated way. For example a tree may provide shelter from strong sunlight to herbaceous plants growing beneath it, while simultaneously competing for soil resources, particularly where the tree also has a shallow root system. However, plants can also experience competition and facilitation in relation to the same resource. For example if the tree in the previous example also provides greater nutrients in the soil profile due to nitrogen fixation and increased litter fall, then the tree and the associated herbs would compete for the same nutrients. The sum or balance of all the negative and positive interactions plants experience determines whether the overall interaction is negative or positive (Brooker *et al.*, 2008). These are often very finely poised, and can change in one direction or the other depending on the time of day, time of year, the respective life stages of the plants or the location and prevailing environmental conditions (Armas & Pugnaire, 2005). It is therefore difficult to quantify the overall positive or negative interactions between species, and to suggest that these are static in time, since most experimental studies provide a snapshot view of these dynamics.

However, the overall nature of the relationship between two species can be inferred from the spatial distribution of plants and their sizes. At a community level, net competition is inferred if plant size increases with increasing distance with its nearest neighbor, while net facilitation can be inferred if plant size increases with decreasing distance to its nearest neighbor (Carrick, 2003).

FACILITATION OF SEEDLINGS BY ADULT PLANTS

The nurse plant effect (Niering *et al.*, 1963) is a special case of facilitation, where the benefactor is typically an adult plant and the beneficiary plants are seedlings. Nurse plant relationships are generally positive-neutral, where the nurse plant creates a favorable environment for the beneficiary plants, while it is unaffected. The interaction may remain mutually beneficial or shift towards greater competition with the nurse plant as the seedlings grow into adults. The latter case occurs in the context of Clementian succession (Connell & Slatyer, 1977), where early succession species are nurse plants for the seedlings of later succession species and when the latter become adults they outcompete the former. However, nurse plants have also been identified in stable, 'climax' communities, where they co-exist with the species that are nursed by them (Brooker *et al.*, 2008). In such communities, cyclical changes in the spatial distributions of the nurse and beneficiary species maintain a dynamic yet stable community over time (Yeaton & Esler, 1990).

Nurse plants facilitate the establishment and growth of seedlings in similar ways to the general case of facilitation between any two plants, with the main mechanisms relating to physical protection, greater water and nutrient availability and improved microclimates by buffering environmental extremes (Flores & Jurado, 2003; Padilla & Pugnaire, 2006). In the Sonoran Desert in North America, the Saguaro cactus (*Cereus giganteus* and *Carnegiea ginatea*) is a well-known example of a species that employs nurse plants to establish itself. These giant cacti are associated with Paloverde trees (*Cercidium microphyllum*) and other desert shrubs that protect them from grazers such as rabbits and rodents, and even frost death in their early years (Niering *et al.*, 1963). Seedlings of the Saguaro can take 10 years to reach a height of 2 cm, and the nurse plants shelter them during their long 'juvenile' phase.

There is clearly some overlap in the concepts of patch dynamics and nurse plants, since the very existence of resource rich patches is related to long-lived adult plants that accumulate resources, and nurse plants are typically long-lived adult plants. Some beneficial features of a nurse plant to seedlings may be consistent with the concept of patch dynamics, but not all. Patch dynamics relate chiefly to the greater availability of resources needed by plants, and these may be provided by nurse plants too. However, nurse plants may provide physical protection or shelter from biotic or abiotic elements, which is sometimes but not necessarily the case with resource rich patches. In order to investigate the influence of these ecological concepts, it is necessary to separate the possible mechanisms that exist. A useful distinction can be made between the benefit of resource factors (such as nutrients and water) and non-resource factors, such as physical damage by herbivory, trampling or strong winds (Grace, 1991; Maestre *et al.*, 2009). This distinction both incorporates and transcends the ecological concepts of patch dynamics and nurse plants, and it allows explicit falsifiable hypotheses to be set up. In this thesis I investigated the effects of both non-resource (Chapter 3) and resource (Chapter 4) factors on the establishment of seedlings of dominant perennial species in a semi-desert in South Africa, and attempt to distinguish the relative importance of these factors in this system.

SEEDLING ECOLOGY

Seeds are often very resilient to harsh conditions, such as extreme temperatures and drought (Leck *et al.*, 2008). Plants often use the seed stage of a plant's life cycle to carry their genes through periods that are unfavorable for juvenile or adult plants. These include dry seasons or even drought years or extended drought periods. Furthermore, most adult plants are generally more resilient to environmental stresses than their seedling counterparts (Leck & Outred, 2008). Some of the reasons for this are that they have larger root systems and therefore greater access to soil resources such as water and nutrients, and they have larger above and below ground structures that serve as reservoirs for essential resources. Many plants have specially adapted strategies to cope with unfavorable environmental conditions, whether these are seasonal droughts or extended drought periods. Besides the strategy of bridging these periods with a seed phase (used commonly by ephemeral plants to bridge the dry season), plants could senesce, die back, resprout from roots, slow down metabolic activities, or create stores of resources for lean times.

In contrast to the seed and adult stages of a plants' life, a plant is generally at its most vulnerable to drought, flooding, lack of resources, herbivory and parasitism during the seedling stage (Karban & Thaler, 1999; Leck *et al.*, 2008). Individual seedlings with some advantage will stand a greater chance of surviving through to adulthood than others. This advantage can be inherent, such as the size of the seeds from which they germinated, i.e. large seeds have more stored resources for seedlings to draw on (Coomes & Grubb, 2003; Westoby *et al.*, 2002), a result of the position of the seed in the inflorescence, on the plant or even the age of the mother plant (Gutterman, 1993), or may be a result of several additional factors that contribute to the germination of seeds (Baskin & Baskin, 2001; Bewley & Black, 1994). External factors, such as the apparently stochastic dispersal events that determine the precise locality and environment in which seeds germinate can also influence their survival (Gutterman, 1993; Harper, 1977). However, some external factors are not entirely stochastic, since plants have developed different dispersal strategies which increase the likelihood of the seeds being dispersed to favorable micro-sites. Plants have 'preferred pathways of dispersal' (Gustafson & Gardner, 1996) or 'directed dispersal' (Levin *et al.*, 2003), which typically utilize wind, water, or animals, with each resulting in dispersal to a different type of micro-site. While species in arid regions tend to have short dispersal distances (Pueyo *et al.*, 2008), some species utilize the low vegetation cover and frequent winds to disperse their seeds further (Chambers *et al.*, 1991; Gutterman, 1993). Wind dispersed seeds (anemochory) tend to have structures (like wings or papii) that increase their surface area:volume ratio so that they are more easily moved by wind (Gutterman, 1993; van Oudtshoorn & van Rooyen, 1999). These seeds usually collect in areas where wind speed is reduced, or where they are obstructed from being blown further. The same structures also result in them getting caught up in low hanging branches of shrubs or plant debris. Besides the typical case of water dispersal (hydrochory) via a river or a stream, seeds can also be dispersed by water in non-riverine systems. This typically occurs by sheet flow (bithisochory) over the ground surface when the rainfall exceeds the water infiltration rate (Gutterman, 1993; Schulze *et al.*, 2005; van Oudtshoorn & van Rooyen, 1999). Seeds that are water dispersed are often small, and may develop a mucilaginous substance on the seed coat when it starts absorbing moisture in order to make them more buoyant (Leck & Outred, 2008). Water dispersed seeds are inevitably dispersed to areas where water flow is obstructed, such as areas of local depression where water pools before it eventually infiltrates. Animal dispersal (zoochory) is less common in arid regions (van Oudtshoorn & van Rooyen, 1999).

However, in species such as the Saguaro cactus (*Cereus giganteus* and *Carnegiea gigantea*), birds are attracted to the fleshy fruits that are produced. This ensures a high likelihood that seeds will be deposited under other shrubs or trees, as the birds perch on these while defecating (Niering *et al.*, 1963). In the Karoo in South Africa, it was found that there are three times more seeds in micro-sites under shrub canopies than in open micro-sites (Jones & Esler, 2004), most likely a consequence of the dispersal mechanisms that are prevalent in this region which 'direct' their seeds to favorable micro-sites.

While the qualities that increase the resilience of adult plants to unfavorable conditions are probably inherent to their seedlings, the latter's ability to implement them to survive these conditions is undoubtedly less than that of adults. It has long been recognized that favorable micro-sites have a positive effect on seedling survival (Harper, 1977; Leck & Outred, 2008). Characteristics that make micro-sites favorable will vary greatly from ecosystem to ecosystem, and also from species to species. Favorable micro-sites are broadly defined as having greater levels of resources that may be limiting in that system, or areas that are more sheltered from negative environmental elements. In semi-arid ecosystems, where soil resources are limiting, favorable micro-sites are generally those where these resources occur in greater abundance in the soil. Soil resources such as water and plant litter are concentrated in small scale local depressions due the gravitational flow of water into these depressions. In the Karoo for example, holes dug by mammals in inter-patches accumulate detritus, seeds and water, thus creating favorable micro-sites for seed germination (Dean & Milton, 1991). Furthermore, the patch dynamics evident in many semi-arid systems result in favorable micro-sites beneath plant canopies, since soil resources are concentrated here (Aguiar & Sala, 1994; Stock *et al.*, 1999). Leaf litter from the adult plants is also dropped underneath the canopy, where it forms mulch that slows the evaporation of soil moisture while also decomposing and adding nutrients back to the soil (Collins *et al.*, 2008). It is also possible that greater moisture input under adult plants can occur due to condensation of fog on their leaves that results in water dripping onto the soil below. Furthermore, rainwater that runs down the main stem of the plant ensures deeper infiltration, resulting in less evaporation and thus greater water availability (Whitford, 1999).

Given the importance of the seedling stage of a plant's life in determining where adult plants exist (Grubb, 1977), it is crucial to understand the dynamics that affect seedling

establishment when attempting to understand vegetation patterns and dynamics of adult plants (Boeken, 2008). Understanding the dynamics that govern seedling ecology and establishment is also crucial in formulating methods for restoring degraded areas by applying ecological principles and knowledge (Boeken, 2008; Chambers, 2000). In this thesis, I investigated the ecological factors that influence the establishment (survival and growth) of seedlings of the dominant perennial species in a semi-desert region in South Africa.

RESTORING SEMI-ARID SYSTEMS BY APPLYING ECOLOGICAL KNOWLEDGE

Due to increasing demands on natural systems, global climate change and the utilization of mineral resources, arid and semi-arid systems are subject to increasing pressure (Reynolds & Stafford Smith, 2002). The scale of human induced degradation, whether through climate change, overgrazing, cropping, or mining, has increased substantially in recent decades. The concurrent increase in the need to conserve existing natural landscapes and restore degraded ones has been hampered by slow development of sufficient ecological understanding in each region or ecosystem. Fortunately, the concepts described above are virtually ubiquitous in semi-arid systems, and they provide a framework for more specialized research to be conducted. Together with the increase in ecological research in recent decades, there is new hope for degraded landscapes in arid and semi-arid regions. The challenge for restoration ecologists is to integrate good scientific research with a practical application of these findings and to implement such applications within the institutional and policy framework at national, regional and local levels (Hobbs & Harris, 2001).

The aim of ecological restoration is to “repair ecosystems with respect to their health, integrity, and self-sustainability” (Society for Ecological Restoration International Science and Policy Working Guild, 2004). These three aspects of restoration do not merely encompass species numbers or diversity, but require the return of ecological function and with it greater resilience to fluctuations in environmental conditions and external disturbances. Restoration ecology has been called an ‘acid test’ for understanding ecosystems, since it is necessary to understand the processes that maintain them in order to re-create them after degradation (Bradshaw, 1983). Attempts at restoration in semi-arid systems that do not focus on the return of ecosystem function generally require more intervention, are more costly to implement and do not result in long-term success.

For example, many restoration efforts have aimed to reduced competition from existing vegetation in order to promote the establishment of 'target' or favorable species (Gomez-Aparicio, 2009). However, this ignores the principles of facilitation and succession which are both important processes in natural systems. Not only is clearing of existing pioneer vegetation an unnecessary input of time and effort, it can actually decrease the overall success of restoration because later succession species often require a cover of pioneer species in order to establish. However, increasing awareness of ecological dynamics, such as patch dynamics and facilitation, has led to these being implemented in restoration efforts more widely.

The importance of creating favorable micro-sites or 'safe sites' for seedling establishment when restoring degraded areas has been recognized (Galatowitsch, 2008). Taking into account the greater frequencies of positive plant interactions in semi-arid systems (Gomez-Aparicio, 2009), it is important to consider the effects that plants have in creating favorable micro-sites for seedlings. Restoration practices that mimic these processes have a greater chance of being successful.

EXAMPLES OF USING PATCH DYNAMICS IN RESTORATION

There are numerous examples of restoration practitioners who have attempted to initiate ecological processes on degraded landscapes in order to achieve restoration (Galatowitsch, 2008). Patch dynamics in semi-arid systems result in a heterogeneous distribution of resources that are useful for plant growth. While plants themselves are largely responsible for generating this pattern of resource distribution, they are absent or far less abundant in degraded landscapes. Furthermore, the plants that are likely to be present or most abundant on degraded landscapes are pioneer or early succession plants, which are not typically responsible for creating long-lived, heterogeneous patches in the landscape due to their short life spans (Stock *et al.*, 1999). Depending on the type and degree of degradation, it is also likely that patches of high resource concentration are also no longer present on degraded landscapes (Galatowitsch, 2008). This is particularly the case where soil is removed, such as during open cast mining (Mahood, 2003; Schmidt, 2002), or homogenized, such as during tilling for crop farming (Allen, 1988; Allen & Macmahon, 1985). Even where overgrazing results in a loss of perennial shrubs it is likely that the resource rich patches will disappear over time (Allen & Macmahon, 1985). While the resources are not necessarily lost from that landscape, they are spread out more

evenly across the landscape and the aggregation at micro-sites may no longer occur at sufficient levels to sustain seedling establishment and growth through to adulthood (Whisenant *et al.*, 1995).

Various attempts have been made at pooling resources in order to restore degraded landscapes. Water is perhaps the easiest resource to gather on a homogenous landscape. Since run-off water often transports organic matter and nutrients too, pooling it effectively can contribute to creating resource rich patches. By simply altering the soil topography, water will run off from local high lying areas and collect in local depressions or catchments. The overall topography can be used to determine the scale at which depressions are constructed (Ludwig *et al.*, 2000). For example, in New South Wales, Australia, where rangelands with slopes of less than 0.4% have been severely degraded by overgrazing, mechanically constructed large-scale macro-catchments have proved successful in encouraging the establishment of indigenous vegetation (Thompson, 2008). Each 'waterpond', consisting of circular or horseshoe shaped ridges, encloses an area of approximately 0.4 ha. On these gentle slopes the water catchments can be large, since runoff rates are much lower. However, on more uneven terrain, catchments may be much smaller. For example, in Texas in the United States of America, seedlings of two shrub species that were planted in 1.5 m² micro-catchments showed greater survival and standing biomass than those planted in unaltered micro-sites (Whisenant *et al.*, 1995). In the uplands of Namaqualand, where local topography is irregular, c.0.3 m² triangular micro-catchments were constructed on severely overgrazed rangelands (Simons, 2005). Although no significant difference of soil moisture levels could be detected between these and open sites, the micro-catchments did collect higher amounts of organic matter in some cases and yielded higher rates of natural recruitment of ephemerals (Simons, 2005). Rather than changing the actual soil topography in order to catch and retain water, impeding water flow by strategically placed plant debris has been used effectively to increase soil water moisture and plant growth in Australia (Ludwig & Tongway, 1996; Tongway & Ludwig, 1996). However, Simons (2005) found that this method was ineffective in Namaqualand. Water catchments have also been used in desert restoration in North America (Edwards *et al.*, 2000; Fidelibus & Bainbridge, 1994). In this thesis, I have not attempted to validate the beneficial effect of micro-catchments on seedling establishment, since it has been well established elsewhere. However, I have used micro-catchments for all plots and treatments in all but one of the experiments (Experiment 3).

Micro-catchments aimed at increasing soil moisture frequently gather other resources too, e.g. nutrients, organic matter and seeds. The positive effects of nutrients on seedling growth are well-established, and have been utilized to improve restoration success (Walker, 2002). Most restoration attempts are viewed as agricultural or horticultural exercises, instead of as ecological endeavors, and thus broadcast fertilizing (and seeding) is often favored. This practice, however, is wasteful in most cases in semi-arid regions, since seeds and seedlings do not only require nutrients to be successful, but also micro-sites that provide greater water input and shelter from harsh conditions. For this reason, only a small fraction of broadcast fertilizers (and seeds) will contribute to successful plant establishment.

Indirect methods of increasing water and nutrient availability have also been implemented. The application of an organic mulch releases nutrients into the soil as it decomposes (Galatowitsch, 2008). It may also increase water availability by absorbing water and reducing evaporation by shielding soil from the sun (Went & Sheps, 1971). In Australia, seedling recruitment was optimal where a canopy derived mulch was applied in restoration of *Banksia* woodlands (Rokich *et al.*, 2002). In the Karoo, restoration trials indicated that organic mulch increased water infiltration and yielded significantly higher seedling numbers from seeds sown in mulch plots (Beukes & Cowling, 2003). Another indirect method of increasing nutrients on degraded landscapes is by introducing nutrient fixing micro-organisms. Pot experiments where soil was inoculated with plant-growth-promoting bacterium *Azospirillum brasilense* resulted in significantly greater dry shoot mass (60%) and root length (100%) of Giant cactus (*Pachycereus pringlei*) in nutrient poor soils of the Sonoran Desert (Carrillo-Garcia *et al.*, 2000). In another study, ectomycorrhizal fungi increased growth of oak seedlings significantly, but only when the pot soils were also organically enriched (Lunt & Hedger, 2003).

However, direct or indirect addition of nutrients does not always impact seedlings positively. In a pot experiment with prairie bunchgrass, it was found that although initial growth was highest in fertilized and mulched pots, after three years these treatments had the lowest survival rate and the greatest number of weeds (Ewing, 2002). It is likely that the amount of fertilizer and mulch that was added in these experiments were not ecologically relevant to this species, resulting in excessive weed growth and eventual

suppression of the grass seedlings. This highlights the importance of adding resources at amounts that are ecologically relevant to the species being targeted.

In this thesis, I investigated the effect of the availability of two soil resources, nutrients and water, on the establishment (survival and growth) of seedlings on a range of degraded sites in a semi-desert in South Africa (Chapter 4). I used this knowledge to firstly understand the role of nutrients and water in the dynamics of undisturbed vegetation and secondly, in improving the success of restoration efforts in degraded landscapes in the region (Chapter 5).

EXAMPLES OF NURSE PLANTS IN RESTORATION

Adult plants are largely responsible for uneven soil resource distribution in undisturbed landscapes (Aguilar & Sala, 1999; Flores & Jurado, 2003), making them prime candidates for generating resource rich patches in degraded landscapes. However, the successful use of nurse plants in restoration is more likely associated with the benefit of providing shelter to seedlings than necessarily increasing soil resources. This is because resource accumulation in patches under adult plants is a slow process that occurs over the lifetime of a plant (Stock *et al.*, 1999). Transplanted adult plants will therefore not confer a greater resource benefit to seedlings underneath it immediately, but they could provide physical shelter right away.

Published evidence of successful use of nurse plants in restoration of target species has only emerged relatively recently, and is not plentiful (Padilla & Pugnaire, 2006). Castro *et al.* (2002) first showed that nurse shrubs decreased seedling mortality in two mountain pines without inhibiting their growth in the Sierra Nevada range in Spain. Research in semi-arid areas of China has demonstrated that micro-sites below transplanted shrub nurse plants have a range of improved qualities, such as higher organic matter, total and available nitrogen and phosphorus, soil moisture and soil seed densities, which contributed to higher seedling densities, heights, cover and biomass under the nurse plants (Zhoa *et al.*, 2007). However, in Namaqualand, seedling emergence from sown seeds on previously mined sites was higher under transplanted shrubs than in open areas, but not significantly so (Schmidt, 2002). In Mexico, it was found that oak seedlings did not survive better beneath nurse shrubs unless they were irrigated, and that irrigated oak seedlings in the open did not survive better than those under nurse plants that were not

irrigated (Badano *et al.*, 2009). Thus, in above average rainfall years, oak seedlings would be expected to survive better under nurse plants than open areas without being watered.

In this thesis I have examined the possible benefit of physical shelter to seedlings of the dominant perennial species in a semi-desert in South Africa (Chapter 3). Physical shelter may provide protection for seedlings from a number of environmental elements, such as herbivory, trampling by large animals (Eccles *et al.*, 2001), high irradiance from the sun, strong winds and sandblasting. I investigated the potential benefit derived by seedlings establishing under nurse plants (adult shrubs) and artificial shelters that provide physical shelter but do not compete with the seedlings for soil resources. I have not distinguished between the type of elements that the seedlings are sheltered from, but rather whether there is an overall benefit to seedlings from being sheltered. The provision of shelter with competition for soil resources (nurse plants) and without competition for soil resources (artificial shelters), sheds light on the balance between the potential facilitation benefit of shelter from the negative impacts of competition. This is important for understanding both seedling dynamics as well as the development of vegetation patterns (Kollmann, 2008). Such information can also be used in the application of restoration methods in degraded semi-arid landscapes (Chapter 5).

KEY OBJECTIVES AND RESEARCH THEMES

The focus of this thesis is on the ecology of the seedling phase of the dominant perennial species of the Namaqualand Sandveld bioregion (Mucina & Rutherford, 2006). The key objectives of the thesis are not only locally applicable but are relevant to other semi-arid ecosystems, since they are based on broad ecological concepts. The first objective is explored in the two data chapters, while the second objective is addressed in the final synthesis chapter.

Key objectives:

- 1) Determining the main factors that promote seedling establishment in semi-deserts** (Chapter 3 & Chapter 4)
- 2) Examining how knowledge of seedling ecology can be applied to restore degraded landscapes in semi-deserts** (Chapter 5)

Testable hypotheses were derived from the first objective. These broadly relate to the effects of facilitation by non-resource factors (Chapter 3) and resource factors (Chapter 4) on seedling establishment (survival and growth). Maestre *et al.* (2009) argue that the nature of the stress factor will have a bearing on the nature of facilitation between plants. When the stress component is promoted by non-resource factors (such as temperature, wind, herbivory or trampling), one would expect facilitation to be driven by architecture-mediated protection to the seedlings (Maestre *et al.*, 2009). Chapter 3 explores the benefit of above various ground shelters on the establishment (survival and growth) of seedlings of the dominant perennial species in a semi-desert in South Africa.

Hypothesis: Non-resource factors (such as wind and temperature) of micro-sites affect seedling establishment.

When the stress component is promoted by competition for resources (such as water or nutrients), one would expect that facilitation to be driven by niche separation (cf. Cody, 1986). Chapter 4 explores the effects of altering nutrient and water availability on the establishment (survival and growth) of seedlings of the dominant perennial species in a semi-desert in South Africa.

Hypothesis: Resource factors (such as nutrient and water availability) of micro-sites affect seedling establishment.

Each hypothesis was tested with a number of experiments. The experiments were conducted on a variety of degraded sites that are typical of post-mining landscapes (one of the most severe forms of ecological degradation) in the winter rainfall region of Namaqualand, a semi-desert on the west coast of South Africa (see Chapter 2). They were also initiated in three different calendar years (2005, 2006 and 2007), thereby accounting for inter-annual climatic variability that is present in any natural system. The second objective has been examined by extending the conclusions of the first key question to restoration ecology (Chapter 5).

LIMITATIONS OF THE THESIS

The data for this thesis were collected during four years of the Namaqualand Restoration Initiative (NRI), a research, advocacy and implementation project which had specific objectives and constraints that guided the research. One of the objectives was to develop practical restoration methods for mining operators in Namaqualand, within this period. The focus of the research was therefore to make incisive advances in the restoration knowledge for Namaqualand, with the aim of gaining practical answers. The main aim of the thesis is to contribute to the ecological understanding of recruitment dynamics and its contribution to vegetation patterns in Namaqualand, by drawing out the ecological implications of the results.

Another factor that influenced the experimental design and statistical analyses of the experiments described in this thesis, was the difficulty in selecting analogous or comparable sites where the experiments could be repeated. This is a result of the mining process which occurs rather haphazardly, resulting in sites of varying ages and disturbance histories. Rather than viewing individual sites as replicates, the approach was to apply the experimental treatments to a range of possible conditions that occur within the mining area, and as such provide conclusions and solutions that are more broadly applicable. These challenges and the research and statistical approach necessitated by them are described in more detail in Chapter 2.

THESIS OUTLINE

This first chapter is devoted to a broad literature review on the ecology of arid systems, introducing the two principal ecological concepts related to facilitation, i.e. patch dynamics and physical shelter provided by nurse plants. The focus then shifts towards seedling ecology in these regions and key drivers of establishment success such as drought and stochastic dispersal events. The relevance of this is linked to the two overarching potential benefits of patch dynamics and nurse plants to seedling establishment, namely resource and non-resource benefits. Lastly, restoration ecology in arid and semi-arid regions is introduced, and examples are given of how ecological concepts can be applied in restoration interventions. Following this is a statement of the key objectives of this thesis that led to the development of specific hypotheses.

Chapter 2 describes the Namaqualand region, including the natural abiotic and biotic factors that are relevant to plant ecology, as well as the anthropogenic factors relevant to restoration ecology in the region. The dominant perennial species in the Sandveld bioregion of Namaqualand are introduced, as well as the rationale for using two broad 'functional guilds' (i.e. Mesemb and non-Mesemb) to evaluate hypotheses throughout this thesis. An overview of the mining process is given to create a context for the sites where experiments were conducted. The research approach is introduced, together with the location and descriptions of field sites that were used for the experiments.

There is a high incidence of multi-species clumps in the Sandveld bioregion of Namaqualand. Clearly there is a benefit to individual plants to occur in clumps with other individuals, but there are also costs. Chapter 3 explores the benefit of physical shelter to Mesemb and non-Mesemb seedlings. It includes a detailed literature review on competition and facilitation between adult plants and seedlings, and the theory and evidence for 'nurse plants' in semi-arid regions. The experiments are described, and their results are discussed in light of their implications for ecology in Namaqualand.

There is considerable evidence that plants or clumps of plants create patches that are more resource rich ('fertile islands') in arid or semi-arid systems. Chapter 4 addresses soil resource (nutrients and water) dynamics and their influence on seedling establishment and survival, both in the presence and absence of physical shelter. A detailed literature review of the subject is given. The experiments used to evaluate the hypothesis are described and the results are discussed in the context of ecology in Namaqualand.

In Chapter 5 the main findings of the thesis are summarized. These conclusions are used to extrapolate the ecological knowledge to restoration practice along the themes of this thesis. These include the specific use of patch dynamics and nurse plants in restoration endeavors, as well as the underlying theme that physiological traits are responsible for ecological functions in plants. The chapter concludes by exploring the broader idea of using natural processes to complement restoration efforts in semi-arid regions.

Chapter 2

REGIONAL OVERVIEW AND SITE DESCRIPTIONS

INTRODUCTION TO THE REGION

Namaqualand is situated in north-western South Africa. It is a semi-arid, winter rainfall region that occupies about 50 000 km² (Cowling *et al.*, 1999) and is part of the greater Succulent Karoo biome (Figure 2.1) which covers about 100 000 km² (Esler *et al.*, 1999). The Succulent Karoo has the highest species diversity at local and regional scales of any semi-arid region in the world, with 6 356 vascular plant species in 168 families and 1 002 genera (Desmet, 2007). The Succulent Karoo biome is one of only two desert regions recognized as a global biodiversity hot-spot (Myers, 2003; Myers *et al.*, 2000), highlighting its exceptionally high species diversity and urgent need for conservation. Although it is comparable to other semi-arid regions worldwide in terms of the range of physical environments and topography, it differs in that it is much smaller in extent and because of this relatively steep environmental gradients occur over shorter distances (Whitford, 1999), which results in greater niche differentiation over smaller areas.

Namaqualand has been divided into a number of bioregions (Figure 2.2). The study sites where experiments were conducted are located within the Namaqualand Sandveld bioregion (Mucina & Rutherford, 2006), and occur on the level plains that are bordered by the Atlantic Ocean to the west, and the Namaqualand Hardeveld bioregion to the east. The low undulating landscape of the Namaqualand Sandveld bioregion is fairly homogenous, interrupted by occasional sand plumes, rocky outcrops and vlei or wetland areas. The narrow strip stretches from the Olifants River in the south, to just south of Alexanderbaai in the north, ranging in width from a few hundred meters to about 50 km.

CLIMATE

Namaqualand is primarily a winter rainfall region, with an extended summer drought period. Annual rainfall varies from about 50 mm in the north-west to more than 400 mm in the uplands of the Kamiesberg (Cowling *et al.*, 1999; Desmet, 2007; Myers, 2003). In

the Namaqualand Sandveld, where the study sites are located, the annual rainfall varies from about 50 mm in the north to 150 mm in the south (Cowling *et al.*, 1999). A unique feature of Namaqualand rainfall is that it is predictable (Hoffman & Cowling, 1987) relative to other winter-rainfall regions worldwide (Esler *et al.*, 1999), and this reliable water input is thought to contribute greatly to the biological patterns and processes in the region (Cowling *et al.*, 1999). Along the coast the low rainfall is also supplemented by coastal fog, mostly in the summer months (Desmet, 1996). At Hondeklipbaai, where 2 of the 5 experiments described in this thesis were conducted, the long-term mean annual rainfall is 96.5 mm, with a coefficient of variation (CV) of 40% (n=39; South African Weather Bureau). There is no official long-term weather station at Kleinsee, where the remaining 3 experiments were conducted. However, rainfall data from a local resident who has been recording the rainfall, indicates that the mean annual rainfall at Kleinsee is 101.5 mm with a CV of 38% (n=46; *pers. comm.* A. van Wyk). Annual rainfall in the years during which the experiments at Kleinsee were monitored was above the long-term annual mean, but within the CV range (Figure 2.5). For the experiments at Hondeklipbaai, annual rainfall during the first year was well above the long-term mean and outside the CV range, while in the second year it was very similar to the long-term mean (Figure 2.5).

Namaqualand is a relatively mild desert due to its close proximity to the moderating effect of the cold Benguela Current in the Atlantic Ocean (Desmet & Cowling, 1999a). Temperatures are especially mild on the coastal plains where the study sites are located. Unfortunately no temperature data exist for Kleinsee. At Koingnaas, which is close to Hondeklipbaai (Figure 2.2), the absolute minimum and maximum temperatures are about 11°C and 32°C in summer and 3°C and 31°C in winter (South African Weather Bureau, data from 2000-2005). The similarity in the summer and winter temperature maxima is due primarily to the regular 'berg winds' that bring hot, turbulent air from the inland plateau during the winter months (Cowling *et al.*, 1999).

Coastal Namaqualand has a relatively strong wind regime. The dominant winds in summer are south, south-westerly and in winter the frequent 'berg winds' come from a north-easterly direction. The latter winds have been known to noticeably desiccate plants within a few days of blowing, and is a major challenge to restoration (Botha *et al.*, 2008). The summer winds present a different challenge to plants, in that the sandy nature of the surface soils makes them highly mobile, especially when they are dry. At Koingnaas, close

to Hondeklipbaai, wind data indicates that in summer a large proportion of the wind is stronger than 9 m.s^{-1} , and that the dominant wind direction is southerly (Figure 2.6; M.S. Botha, R. Krüger, P.J. Carrick, *in prep.*). In winter, the wind is not as strong (mostly between 3 and 9 m.s^{-1}), with most winds coming from the south or the east.

VEGETATION

SPECIES AND VEGETATION TYPES

Namaqualand has 3 500 vascular plant species, in 135 families and 724 genera (Desmet, 2007). As with the rest of the Succulent Karoo, the majority of the vegetation in Namaqualand consists of small to medium sized shrubs. An unusually high proportion of these shrubs are succulent species (Cowling *et al.*, 1994), representing about 10% of the world's succulent flora (Cowling *et al.*, 1999). The degree and type of succulence varies considerably, with strong leaf succulence being the most common type. Non-succulent woody shrubs make up most of the remaining vegetation, although there is a large component of bulbs and dwarf succulents, and a lesser component of annual and pauciennial herbaceous plants. Where the natural vegetation has been disturbed, particularly by cultivation, annual and pauciennial species dominate creating the spectacular floral displays that Namaqualand is famous for and which are important for the emerging ecotourism industry in the region (James *et al.*, 2007)

There are a number of vegetation types within the Namaqualand Sandveld bioregion. However, all the study sites (Figure 2.3 and Figure 2.4) occur in the Namaqualand Coastal Duneveld vegetation type (Mucina & Rutherford, 2006). The Namaqualand Coastal Duneveld occurs predominantly on the yellowish mobile sands (see Soils section below) adjacent to the coast, from north of Kleinsee to south of the Groen River. Shrub genera that are common in the Namaqualand Coastal Duneveld are *Pteronia*, *Tetragonia*, *Zygophyllum*, *Salvia*, *Lebekia*, *Eriocephalus*, *Othonna*, *Ruschia*, *Amphibolia* and *Stoebaria*. The spiny grass *Cladoraphus cyperoides* also occurs almost exclusively on the Namaqualand Coastal Duneveld where it can easily colonize the mobile sands, and often dominates large areas.

PLANT FUNCTIONAL GUILDS AND ECOLOGICAL STRATEGIES

Many attempts have been made to classify plants according to their functional or ecological traits (Grime, 1977; Grubb, 1998; Westoby *et al.*, 2002), and there is ongoing debate about the validity of these classifications. Previous studies in Namaqualand have either grouped species according to their longevity, i.e. annual or perennial species (Milton, 1995b), or succulence, i.e. succulent and non-succulent species (Simons & Allsopp, 2007), depending on the questions being asked (Cowling *et al.*, 1994). Others have delineated groups according to phylogeny, such as the Mesembryanthema (formerly the family Mesembryanthemaceae, but now part of the Aizoaceae) versus 'other' or non-Mesembryanthema (Yeaton & Esler, 1990). Such divisions may be less subjective, since taxonomy is well established and determined *a priori*, while succulence for example is more subjective since there is a continuum in the degree of succulence, as well as different types of succulence (e.g. leaf versus stem succulence). However, divisions based on phylogeny also incorporate ecological traits, since these are often inherent to groups of closely related species since they share a common ancestor. Here I have followed the latter grouping of Mesembryanthema and non-Mesembryanthema. This grouping is appropriate since the species that are used are all perennial species, and a classification based on the longevity of individuals is therefore not useful. Furthermore, the ecological traits that are of interest to this study are also well delineated by grouping species according to their respective phylogenies. Such traits include seed size, seed dispersal mechanism, photosynthetic pathway and rooting depth (Table 2.1).

The Mesembryanthema (hereafter 'Mesemb') species have relatively small seeds (<1 mm diameter) that are ejected from their hygrochastic capsules by the splash action of rain water falling on them (Parolin, 2006). While sheet flow of water over the soil surface is infrequent in Namaqualand, when it does occur it can disperse seeds further (Esler, 1999). Mesemb species utilize facultative crassulacean acid metabolism (CAM) photosynthetic pathways to varying degrees (Rundel *et al.*, 1999), which allows greater water-use efficiency and rapid water uptake when water is available (Midgley & van den Heyden, 1999). The use of CAM also renders them relatively slow growing. In addition, species in this guild have very shallow root systems (Carrick, 2003; Esler & Rundel, 1999; Midgley & van den Heyden, 1999), which allow them to use water from rainfall events as low as 6 mm. The perennial Mesemb species are generally woody-stemmed with evergreen succulent leaves.

The remaining woody perennial non-Mesembryanthema (hereafter 'non-Mesemb') species have relatively large seeds (c.2-6 mm diameter without seed covering or appendages). In most cases, seeds have large appendages, such as wings or pappi, which facilitate their movement by wind. A small proportion of species have fleshy fruits that are dispersed by birds and small mammals. The non-Mesemb species use C3 photosynthesis (Rundel *et al.*, 1999), which probably relates to the high maximum assimilation rates that are characteristic of non-succulent semi arid shrubs (Gibson, 1998). These 'non-Mesemb' species are typically woody, although some exhibit a degree of stem succulence (e.g. *Othonna*). They are characteristically deeper rooted than the Mesemb species (Carrick, 2003; Esler & Rundel, 1999; Midgley & van den Heyden, 1999). They mostly have non-succulent, drought-deciduous leaves, although these are also sometimes semi-succulent (e.g. *Zygophyllum* and *Othonna*) or evergreen (e.g. *Pteronia*).

SOILS

The surface soils (termed 'topsoil', see The Mining Process below) on the coastal plains of the Sandveld bioregion consist of a composite of windblown soils of both marine and terrestrial origins. There's little difference between the soils throughout the region. All are classified as sands since more than 90% of the soil fraction is comprised of sand. The calcareous, marine-derived sands just inland from the coastal strip are much younger at less than 100 000 years old (Desmet, 1996; Desmet, 2007), and can be recognized by their whitish color. The darker inland derived soils are finer-grained, weathered deposits of late Tertiary age, and about 2 million years old (Desmet, 2007). Within the older and more stable red and yellow soils, nutrient rich zoogenic mounds, called 'heuwelties' (Afrikaans for 'little hills'), are scattered throughout the landscape. These mounds are about 15-30 meters in diameter in the Sandveld, and were formed by termites over thousands of years (Milton & Dean, 1990), and have been enriched with nutrients to such an extent that they support a distinct assemblage of species (Midgley & Musil, 1990; Whitford & Kay, 1999). On an even smaller scale, the soil below perennial shrubs or clumps of shrubs, i.e. patches, is more nutrient rich than the soil in the open spaces between shrubs, i.e. inter-patches (Carrick, 2001; Desmet, 2007; Stock *et al.*, 1999). Soil samples from the undisturbed vegetation around the study sites indicated that carbon, nitrogen, potassium and phosphorus levels are all notably higher (in most cases double) in these resource rich patches, than in the soil of inter-patches (P.J. Carrick & R. Krüger, *unpublished data*). Thus, there is strong evidence for patch dynamics in Namaqualand.

About 2 to 5 meters below the relatively unstructured sandy topsoil layer is a hardpan of siliceous (dorbank) or calcareous (calcrete) deposits (Cowling *et al.*, 1999; Desmet, 2007; Francis *et al.*, 2007), although this can be shallower where wind erosion has scoured out the overlying soil (Desmet, 2007). This hardpan is a ubiquitous feature throughout the Sandveld, having formed over millennia from mineral deposits that were carried down through the upper soil layers as solutes in infiltrating rain water. When the water evaporates lower down the soil profile, the siliceous or calcareous deposits are left there, forming the hardpan. The soil below the hardpan is termed 'overburden' and exists as a sterile material with little or no mineral nutrients, while often containing high salt concentrations (see The Mining Process below). The soil properties of overburden soil differ greatly from those of topsoil. In overburden soil sodium concentrations are much higher than in topsoil, while carbon, nitrogen, and potassium levels are much lower than in topsoil (P.J. Carrick & R. Krüger, *unpublished data*). However, phosphorus concentrations are comparable between topsoil and overburden soils. The overburden soil layer is by far the thickest in the soil profile, and varies from a few meters to tens of meters deep. The substratum (termed 'bedrock') below the overburden layer consists of granite-gneiss metamorphic rock.

THE MINING PROCESS

During the long history of mining in the Namaqualand region, the processes by which valuable resources are extracted has continually evolved as new technologies have been developed. Although there are other types of mining in Namaqualand, diamond mining is the most extensive and the majority of the environmental degradation has occurred as a result of diamond mining. Historically, copper was mined inland of the coast, and currently mining for heavy minerals takes place in the southern part of Namaqualand as well as to the east in the Bushmanland region. The following is a general description of the current mining process as it occurs at the majority of alluvial diamond surface mines on the West Coast of Namaqualand.

The origins of diamonds in Namaqualand

The diamonds that are found in Namaqualand originate in kimberlite pipes in the interior of South Africa. These kimberlite pipes were formed by volcanic intrusions millions of years ago, and diamonds formed in them over thousands of years as the volcanic material cooled and hardened. The kimberlite pipes were then cut through by erosion of an

ancient river system (the precursor to the current Gariep River system), which entered the Atlantic ocean close to where the Buffels River mouth is today. Since diamonds are very hard, they resisted weathering while being washed hundreds of kilometers downstream. Some of the diamonds were deposited along the river banks, while others were washed out to sea. Here the predominant ocean current, the Benguela current which flows parallel to the West Coast from South to North, swept the diamonds northwards along the coast, depositing them onto marine terraces. Since then, the sea level has dropped considerably, and soil has been deposited on top of these marine terraces. Today these diamond rich marine terraces and paleo-river channels can be found a few meters from the soil surface (at the coast), to about 40 m below the soil surface a few kilometers inland.

Exploration

Before large scale mining can occur, mine operators have to locate deposits that are sufficiently rich and financially viable to mine. The first step in this process is to identify possible paleo-river channels and marine terraces from satellite imagery and aerial photography. Once these have been identified, surveyors need to ascertain whether there are indeed diamond deposits and whether the deposits are sufficiently rich. In the past, exploration for diamond deposits was a very destructive process, where large exploration trenches (100+ m long, by 20 m wide, up to 40 m deep) were excavated by earthmoving machinery in order to obtain samples of the diamondiferous deposits (see photos in Appendix). Today the exploration process is a lot less destructive in that relatively small, 2 m diameter cores of soil are drilled out, and these are brought to the surface and assessed. The drills are mounted on mobile cranes, which damage the vegetation, but do not disturb the soil as much as the exploration trenches. The vegetation usually recovers naturally since the soil is intact and the damaged areas are relatively small.

Removal of topsoil, subsoil and overburden

Since the diamondiferous deposits occur in the layer just above the bedrock, all the soil above this layer needs to be removed in order to gain direct access to the deposits. Firstly the topsoil is removed from the site by bulldozers that scrape the top 1-2 m of soil to the edges of the area to be mined, normally referred to as a mining block. These heaps of topsoil should not be higher than 1 m, since anoxic conditions in larger heaps will result in

the death of seeds and soil micro-organisms (Harris *et al.*, 1993; Strohmayer, 1999). Some mining operators make a distinction between topsoil and subsoil, where the former is described as the top few centimeters of the soil layer. However, the use of large earthmoving machinery makes the removal of a few centimeters of topsoil very difficult, and in practice the first layer of soil that is removed is between 30 and 50 cm deep. Subsoil is the layer of soil immediately underneath the topsoil, and in Namaqualand occurs up to the depth of the hardpan layer. The soil below this layer is known as overburden, and is generally sterile and lacks most of the nutrients that plants need to grow. The overburden layer is usually removed with bulldozers that load the soil onto dump trucks, which then transport the soil to a nearby location where it is either stored until mining is completed, or is ideally used to fill a previously mined block nearby.

Removal and processing of diamondiferous deposits

The layer of material immediately above the bedrock contains the diamonds, and once the overburden has been removed, this material is gathered and transported to a processing plant. Here the diamonds are removed by a series of processes that utilize the high density of diamonds to separate them from the lighter materials. During this process the materials are separated into fine and coarse particles, and these are dumped separately after the diamonds have been removed, resulting in coarse residue deposit (CRD) dumps and fine residue deposit (FRD) dams. The latter is dumped in a liquid slurry form, into large flat areas surrounded by a 'dam wall' to contain the slurry. The water then evaporates and leaves the fine sand, silt and salt deposits behind.

Backfilling

Once the diamondiferous deposits have been removed from the mining block, the soil should be returned to the block in the reverse order to which it was removed in a process termed 'backfilling'. While this is not yet standard practice amongst all mining operators in Namaqualand, it is recognized that this is the first vital step in the restoration process. Firstly, the overburden (which is by far the majority of the soil volume) is returned and compacted. The final slopes and landform of the backfilled block should be similar to the gentle slopes of the surrounding landscape in order to blend in visually and minimize water erosion on steep slopes (Day, 1997; Hancock, 2004).

Returning topsoil and subsoil

Once the mining block has been backfilled with overburden soil and profiled appropriately, the subsoil (if removed separately) is replaced evenly over the overburden. Lastly, the topsoil is spread over the area. The value of topsoil in restoration efforts has been known for some time (Howard & Samuel, 1979), although it has only been recognized by mining operators in Namaqualand recently. It has been determined that topsoil should not be stored for periods of more than one month, since longer storage periods results in the death of seedlings and soil-microorganisms, as well as possible leaching of soil nutrients (Schmidt, 2002; Strohmayer, 1999). However, this principle is not always adhered to in practice, due to a myriad of operational considerations that influence mining activities. Amongst these are poor planning, high staff turnover which results in poor continuity in management, fluctuating diamond prices and currency exchange rates.

Securing topsoil

The Namaqualand coastal plains experience severe wind conditions for the majority of the year (Figure 2.6). Combined with the sandy nature of topsoil in Namaqualand and the semi-arid climate, topsoil that is not secured by the roots and canopies of adult plants can be eroded away by strong winds very rapidly (Botha *et al.*, 2008). Besides the large financial loss that is represented by the removal of the topsoil, the dynamic soil movement on such an area greatly increases the difficulty of establishment for most plant species. An ingenious way of preventing this loss in topsoil has been developed. Rows of shade-cloth nets (hereafter called 'windbreaks') are erected perpendicular to the prevailing southerly or south-westerly winds in order to decrease the wind speed at ground level (see photos in Appendix). Wind physics determine that the optimal interval distance between the windbreaks is 6 m when using windbreaks that are 0.7 m high (Halbich, 2003).

RESEARCH APPROACH AND DESCRIPTION OF SITES

Five field experiments were conducted to test the key objectives and hypotheses outlined in Chapter 1. The experiments were set up in two different localities in Namaqualand (Figure 2.2) namely around the towns of Kleinsee and Hondeklipbaai, and were initiated in different years (2005, 2006 and 2007). The order of appearance of the experiments in this thesis is not chronological, and there is some overlap amongst the sites on which the

experiments were conducted (Table 2.2.). Three of the experiments were carried out on sites surrounding Kleinsee (Figure 2.3), while the other two experiments were carried out on sites surrounding Hondeklipbaai (Figure 2.4). A summary and brief description of the sites on which experiments were conducted is given in Table 2.3.

Due to the often haphazard nature of the mining process, it was not possible to find completely analogous site on which to replicate the experiments. The mining process is driven by many factors, as discussed above, and this leads to areas that are mined in a relatively patchy and unsystematic manner. It is therefore impossible to find any two sites in the same geographical area that had exactly the same history with respect to the age since it was mined, the exact methods that were used during mining, the period of time the topsoil was stored, how much topsoil was returned, and the thickness of the layer of topsoil that was returned. Another added complexity is that soil properties differ greatly within the area that is actively mined. The greatest variation occurs in overburden soils, since the physical and chemical properties vary greatly between different areas. Even the properties of topsoil varies substantially, ranging from whiter unstructured soils just inland from coastal dunes, to more yellow sands slightly inland, to the older reddish soils further inland that contain heuweltjies (see Soils above). While all topsoil sites used for the experiments had yellowish soils, these often had very different mining and rehabilitation[‡] histories.

The marked variation that existed between sites prohibited the use of traditional statistical methods (e.g. ANOVA, survival curves etc), and necessitated the use of statistical tools that could deal with greater complexity. The use of Generalized Linear Models (GLMs) has increased exponentially in ecology in recent years (Bolker *et al.*, 2009), due to the flexibility of such analyses and their increased robustness to unbalanced designs and assumptions of normality and homoscedacity (Crawley, 2007), which are required for most traditional statistical methods. More notably, GLMs can efficiently deal with complex arrangements of a high number of factors (Bolker *et al.*, 2009), as was necessitated by these experiments. The statistical approach used to analyze the results of each experiment is discussed separately in the two data chapters which follow.

[‡] The term 'rehabilitation' is used as opposed to 'restoration' (defined in Chapter 1) as it refers to interventions aimed at remediating disturbed areas to a degree, but without the ultimate goal of restoration (see Chapter 5). Here rehabilitation refers to mining blocks that were partially or fully backfilled, with topsoil with wind-breaks returned to some of them.

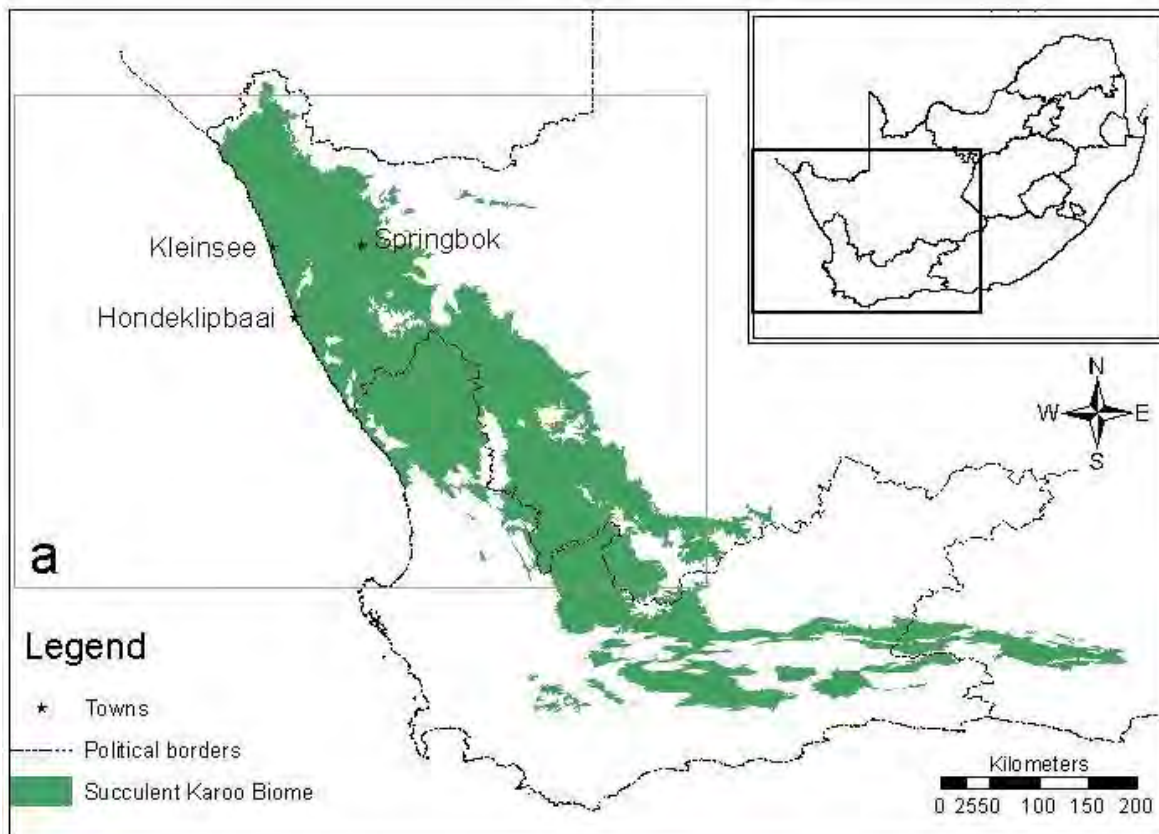


Figure 2.1 A map of the western part of South Africa, indicating the extent of the Succulent Karoo biome (Mucina & Rutherford, 2006), as well as the location of the two towns around which the experiments were conducted, Kleinsee and Hondeklipbaai. The grey box (a) indicates the borders of the map in Figure 2.2

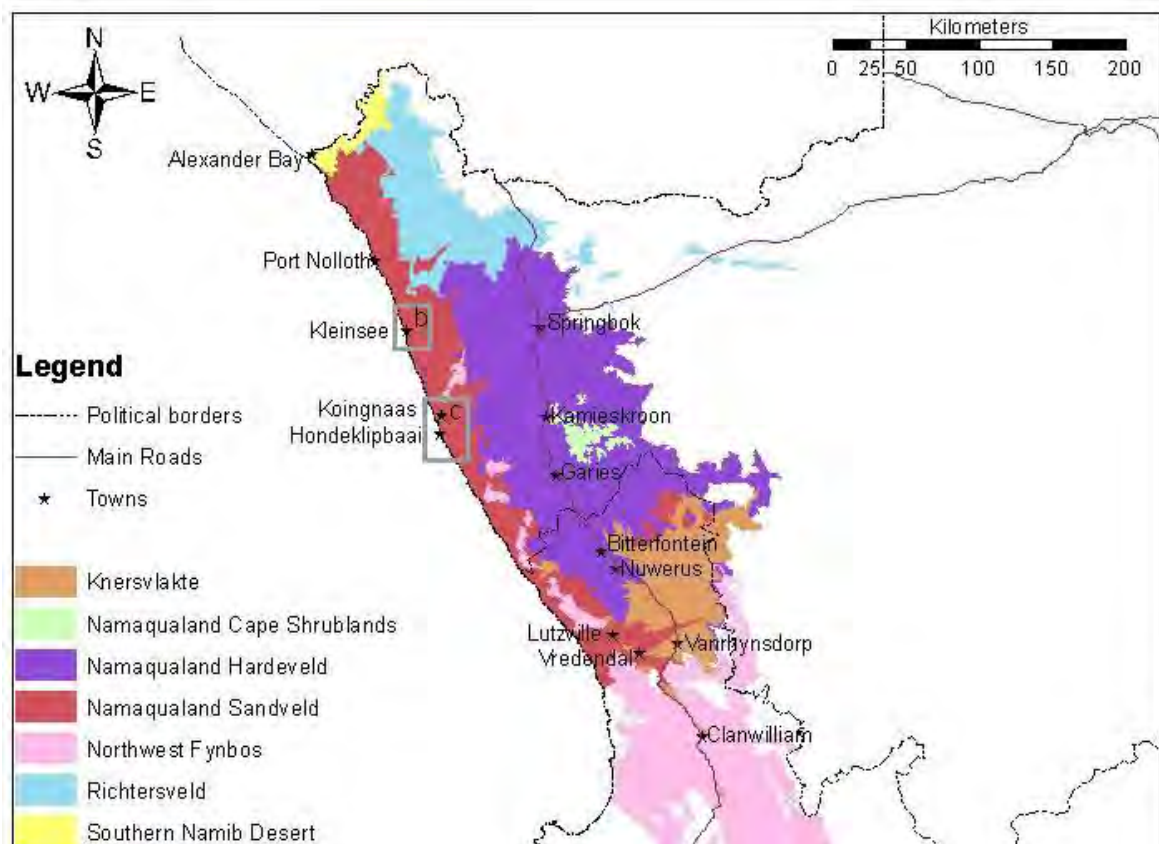


Figure 2.2 A Map indicating the bioregions of Namaqualand (Mucina & Rutherford, 2006). The study sites are all located within the Namaqualand Sandveld bioregion. The grey box (b) indicates the location of Figure 2.3, and (c) indicates the location of Figure 2.4.

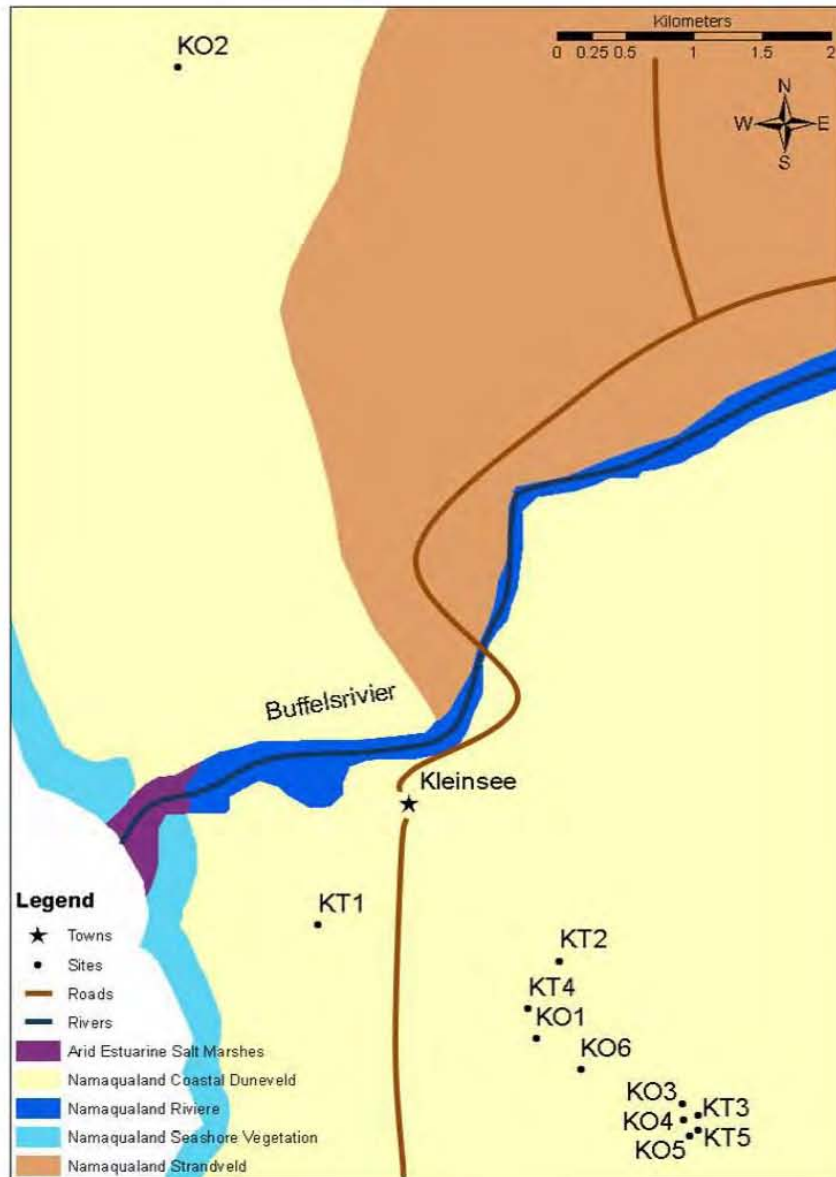


Figure 2.3 A map of the sites around Kleinsee where Experiments 1, 3 & 4 were conducted, indicating the vegetation types (Mucina & Rutherford, 2006). Sites with names that start with 'KT-' are topsoil sites, while sites that start with 'KO-' are overburden sites.

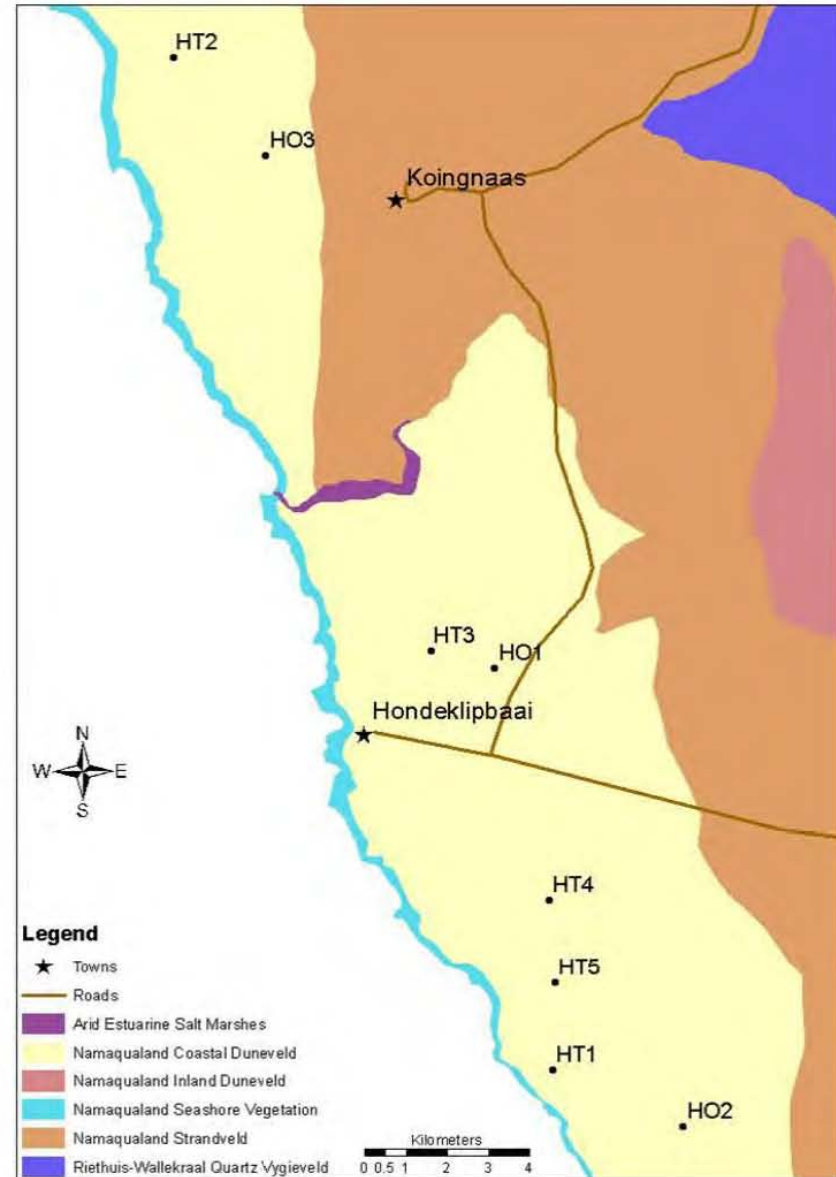


Figure 2.4 A map of the sites around Hondeklipbaai where Experiments 2 & 5 were conducted, indicating the vegetation types (Mucina & Rutherford, 2006). Sites with names that start with 'HT-' are topsoil sites, while sites that start with 'HO-' are overburden sites.

Table 2.1 The major ecological features that distinguish the Mesemb and non-Mesemb guilds from each other.

	Perennial species	
	Mesemb	Non-Mesemb
Seed size	Very small (<1mm)	Large (2-6mm)
Dispersal	Water	Mostly wind, some by insects, mammals and birds
Photosynthesis	Facultative CAM	C3
Relative growth rate	Slow	Slow to fast
Roots	Very shallow, reaches beyond canopy	Deeper rooted, mostly below canopy
Stems	Woody	Mostly woody, some slightly succulent
Leaves	Succulent, mostly evergreen	Mostly non-succulent and deciduous

Table 2.2 The localities and sites where experiments were conducted, as well as the year in which experiments were initiated. The chapter in which each experiment is described is also given.

Experiment	Chapter	Year initiated	Locality	Sites
Exp 1	3	2006	Kleinsee	KT1, KT2, KT3, KT4, KO1, KO2, KO3
Exp 2	3	2007	Hondeklipbaai	HT1, HT2, HT3, HT4, HT5, HO1, HO2, HO3
Exp 3	4	2005	Kleinsee	KT3, KT4, KT5, KO4, KO5, KO6
Exp 4	4	2006	Kleinsee	KT1, KT2, KT3, KT4
Exp 5	4	2007	Hondeklipbaai	HT1, HT2, HT3, HT4, HT5, HO1, HO2, HO3

Table 2.3 Details (co-ordinates, the mine block on which the site occurs, type of soil and vegetation cover, and the year in which the site was landformed) of the sites on which the experiments were conducted.

Site Name	Year site was landformed	Latitude (S)	Longitude (E)	Experiment	Description
KT1	2005	29.684627	17.064811	1 & 4	Soft yellow topsoil; medium vegetation cover; windbreaks
KT2	2002	29.687067	17.080664	1 & 4	Soft yellow topsoil; good vegetation cover
KT3	2002	29.697710	17.089811	1,3 & 4	Soft yellow topsoil with calcrete; good vegetation cover
KT4	2002	29.690369	17.078570	1,3 & 4	Soft yellow topsoil with calcrete; good vegetation cover
KT5	2002	29.698750	17.089797	3	Soft yellow topsoil with calcrete; good vegetation cover
KO1	2006	29.692434	17.079149	1	Hard white calcrete overburden; no vegetation
KO2	1985	29.625462	17.055518	1	Hard reddish overburden; little vegetation cover
KO3	2006	29.696965	17.088763	1	Hard white calcrete overburden; no vegetation
KO4	1995	29.697852	17.088701	3	Hard white calcrete overburden; no vegetation
KO5	1995	29.699147	17.089267	3	Hard white calcrete overburden; no vegetation
KO6	1995	29.694588	17.082096	3	Hard white calcrete overburden; no vegetation
HT1	2006	30.393680	17.320740	2 & 5	Soft yellow topsoil; no vegetation; windbreaks
HT2	2006	30.165370	17.238020	2 & 5	Soft whiter topsoil; good vegetation cover; windbreaks
HT3	2005	30.298960	17.294200	2 & 5	Soft yellow topsoil; good vegetation cover; windbreaks
HT4	2004	30.355240	17.319990	2 & 5	Soft whiter topsoil; good vegetation cover; windbreaks
HT5	2003	30.373970	17.321290	2 & 5	Soft yellow topsoil; very good vegetation cover; windbreaks
HO1	2005	30.303040	17.308130	2 & 5	Red overburden; little vegetation; windbreaks
HO2	2004	30.406300	17.349220	2 & 5	Soft white overburden; medium vegetation; windbreaks
HO3	2003	30.187250	17.258240	2 & 5	Hard white calcrete overburden; little vegetation cover; windbreaks

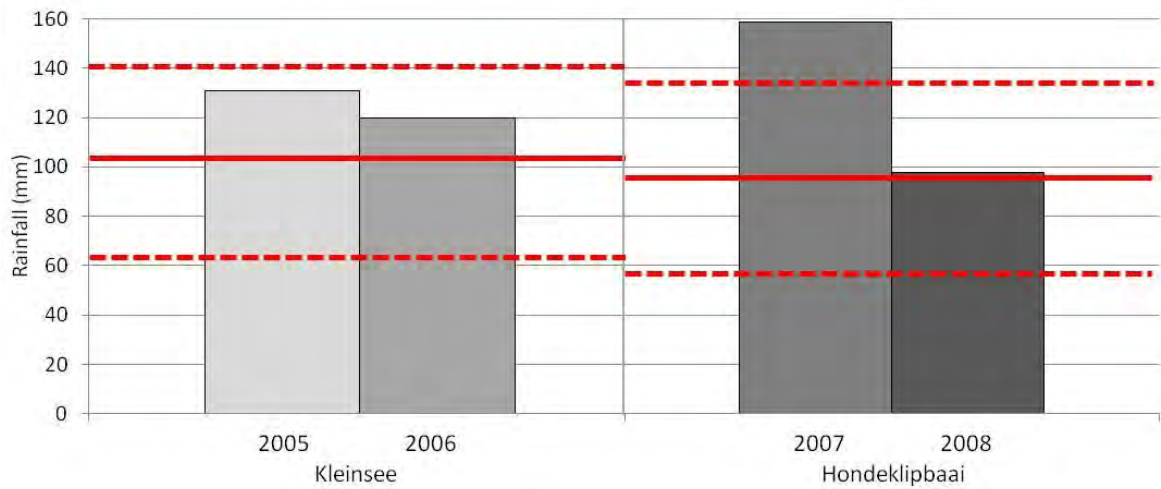


Figure 2.5 Annual rainfall (bars) relative to the long-term mean (solid red lines) and the coefficient of variation (dashed red lines) at Kleinsee (n=46) and Hondeklipbaai (n=39) for the years during which the experiments were monitored. Data was not available for 2007 at Kleinsee.

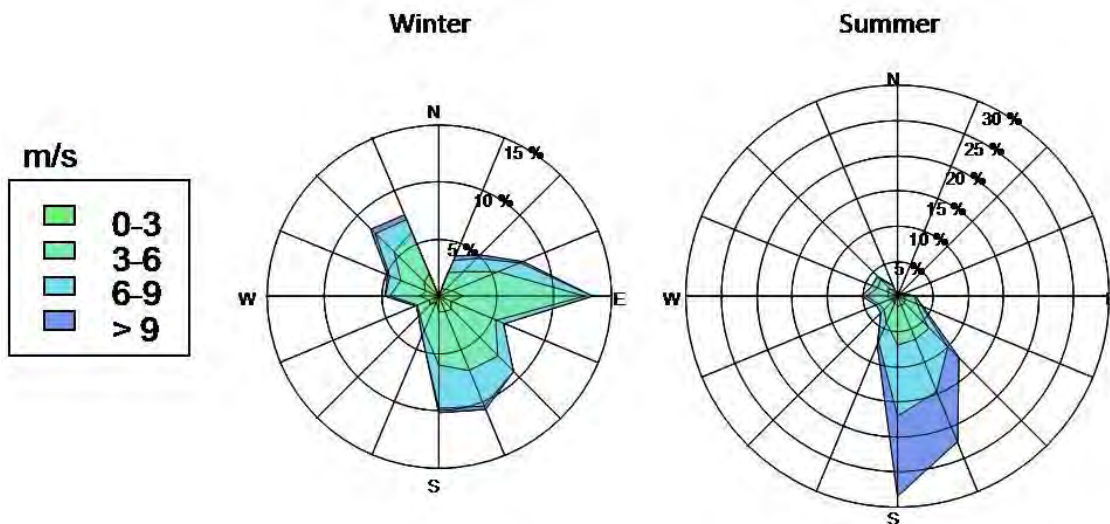


Figure 2.6 Wind roses for winter (June-August) and summer (December-February) data from Koingnaas, close to Hondeklipbaai (M.S. Botha, R. Krüger & P.J. Carrick, *in prep.*). The radiating 'spokes' of the rose indicate the direction from which the wind blows. Concentric circles indicate the frequency (in %) of winds from that direction, and the colors indicate the strength of the wind (in $m.s^{-1}$).

Chapter 3

LIVING THE SHELTERED LIFE: THE EFFECTS OF NURSE PLANTS AND ARTIFICIAL SHELTERS ON THE ESTABLISHMENT OF SEEDLINGS OF COMMON NAMAQUALAND SANDVELD SPECIES.

ABSTRACT

In semi-arid Namaqualand, multi-species clumps are maintained by functional guilds with different rooting niches, but the mechanisms by which they develop are poorly understood. Facilitation can occur by ameliorating non-resource environmental conditions through physical sheltering, such as when 'nurse' plants provide favorable micro-sites for seedlings to establish in. I tested whether seedling establishment is influenced by non-resource factors of micro-sites by sowing seeds of species from two functional guilds, Mesemb and non-Mesemb species, into unsheltered control plots and plots sheltered by transplanted adult shrubs, plastic tubes or square cardboard boxes.

Survival of Mesemb seedlings was unaffected by shelter of adult shrubs or plastic tubes in Year 0, 1 or 2. Mesemb seedlings were also unaffected by box shelters in Year 0, but in Year 1 and 2 box sheltered plots had significantly fewer seedlings, due to boxes collapsing onto seedlings. In a second experiment, the box methodology was improved so that they did not collapse, but seedling survival was still no different to unsheltered plots in Year 0. However, by Year 1 there were significantly more seedlings in box sheltered plots, although these were significantly smaller than those in unsheltered plots.

Significantly fewer non-Mesemb seedlings established under adult shrubs, while significantly more seedlings established in tube sheltered plots than in unsheltered ones in Year 0, 1 and 2. Box sheltered plots had significantly more non-Mesemb seedlings than unsheltered plots in Year 0 only, while in Year 1 and 2 they had significantly fewer

seedlings due to collapsing boxes. With the improved box methodology, box plots had significantly fewer non-Mesemb seedlings in both Year 0 and 1. However, these seedlings were significantly taller than in unsheltered plots in Year 1.

Potential nurse species used here do not facilitate seedling establishment of Mesemb or non-Mesemb seedlings, concurring with other findings in the Succulent Karoo. Higher survival rates of Mesemb seedlings and greater growth rates of non-Mesemb seedlings when sheltered adequately, indicate that there is some sheltering benefit, and can be applied to increase restoration success.

INTRODUCTION

Interactions between plants, whether negative (e.g. competition) or positive (e.g. facilitation) are largely responsible for the spatial distribution of plants in a landscape, and this is also true for semi-arid regions (Ward, 2009). In harsh environmental conditions, plants can ameliorate the effect of these conditions for other plants, thereby facilitating their mutual growth and survival (Callaway, 1995). In semi-arid regions, evidence for this often appears in the aggregated pattern of plants in the landscape (Ward, 2009).

In Namaqualand, the occurrence of multi-species clumps indicates that there is probably a high frequency of positive interactions between the perennial shrubs that dominate the vegetation (Eccles *et al.*, 1999). This raises several interesting questions. Firstly, what is the benefit to an individual plant of growing in a multi-species clump? Secondly, how do plants overcome the negative interactions that arise from being in close proximity to each other? Thirdly, what are the processes that have led to the formation of multi-species clumps?

It has been suggested that individuals growing within multi-species clumps in Namaqualand benefit due to mutual physical protection (Eccles *et al.*, 2001). Individual plants benefit by being sheltered from the effects of the frequent strong winds in the region, herbivory from both insects and mammals or from trampling by larger mammals (Carrick, 2001; Eccles *et al.*, 2001; Flores & Jurado, 2003). In semi-arid regions, the potential negative effects of occurring in such close proximity to other plants, such as competition for soil resources, is often avoided by spatial root segregation (Schenk *et al.*,

1999). In the Sandveld bioregion, evidence has been found that above ground clumping of shrubs is offset by horizontal root partitioning, where roots forage for nutrients and water in the gaps between clumps (Esler *et al.*, 2002). However, in the uplands of Namaqualand, in the Hardeveld bioregion, it is thought that vertical root partitioning allows different species to occur in close proximity to each other (Carrick, 2003). Since Mesemb roots are generally shallow and extend beyond their canopies, while non-Mesemb roots are deeper and occur mostly below their canopies (Carrick, 2003), it is probable that clumping is made possible through a combination of horizontal and vertical root partitioning. Shallow rooted Mesemb species access water from the top few centimeters of soil both beneath and beyond their canopies, while deeper rooted non-Mesemb species access water in the deeper soil layers mainly below their canopies. By adopting different growth strategies, these two guilds of plants can occupy the same above ground area while utilizing different below ground resources, or root niches (Cody, 1986). Mesemb species make use of frequent small rainfall events (< 6 mm) that occur in the region, by being able to quickly absorb water into their succulent leaves when it's available in the top soil layers (Carrick, 2001). Since the top layer of soil also dries out more quickly, the Mesemb species can use the water stored in their leaves once these upper soil layers have dried out. The non-Mesemb species have deeper roots and access water from larger rainfall events that infiltrate past the Mesemb roots into the deeper soil layers. The non-Mesemb species are generally non-succulent and can grow quickly, but only when water is available (Gibson, 1998). Since the deeper soil layers dry out more slowly, the non-Mesemb species have access to the water for longer periods than the Mesemb species.

The first two questions relate to the mechanisms by which multi-species clumps continue to exist. Although these questions have been reasonably well addressed by previous research (e.g. Carrick, 2001, 2003; Eccles *et al.*, 2001; Esler *et al.*, 2002) the processes by which clumps are formed are still largely speculative, mainly due to the relative dearth of research into the seedling ecology of Namaqualand species. Knowledge of seed dispersal and seedling establishment and growth are essential to understanding the processes whereby multi-species clumps arise (Boeken, 2008). Seed dispersal mechanisms can be inferred from the size, shape or structure of the seed and or seed appendages (Baskin & Baskin, 2001; Chambers *et al.*, 1991; Levin *et al.*, 2003; van Oudtshoorn & van Rooyen, 1999). In the Succulent Karoo, 98% of Mesemb species have hygrochastic capsules that

open when wet (Esler, 1999). The relatively small seeds (0.1 – 0.5 mm in length) are dislodged by rain droplets and can be propelled up to 1.65 meters in this way (Parolin, 2006), although secondary dispersal by sheet flow could probably increase this distance (Esler, 1999). Perennial non-Mesemb species have much larger seeds, and many have pappi or wing-like structures that aid in wind dispersal, while a few also have fleshy fruits that are most likely dispersed by birds (van Oudtshoorn & van Rooyen, 1999).

The contrasting dispersal mechanisms of these two functional guilds are useful in constructing hypotheses and predictions regarding seedling ecology, since they strongly influence the type of micro-site where seeds will collect, and later germinate (Gustafson & Gardner, 1996; Gutterman, 1993). It is likely that the seedlings will be suited to establishing in the conditions characteristic of micro-sites to which their seeds are dispersed. Water dispersed Mesemb seeds are more likely to collect in inter-patches (the open spaces between plants or clumps of plants) than in patches. Even though the seeds are dispersed short distances from the capsules, the meso-topography lends itself to sheet flow increasing these dispersal distances and collecting in inter-patches (Esler, 1999; Levin *et al.*, 2003). This is because most plants or clumps of plants in Namaqualand are located on small mounds, as a consequence of wind-blown sands being trapped by and deposited underneath their canopies (Boeken, 2008). This means that inter-patch spaces are lower than the surrounding patches, and thus sheet flow will transport the Mesemb seeds to these areas. From this, one can predict that Mesemb seedlings will establish and grow better in the absence of physical shelter provided by shrub canopies. In contrast, non-Mesemb seeds that are wind dispersed are likely to collect beneath shrub canopies (van Oudtshoorn & van Rooyen, 1999), since they are trapped in the branches of shrubs as the wind speed is reduced beneath the canopy. Similarly, seeds of fleshy, non-Mesemb fruits are dispersed by birds and are likely to be deposited in patches, as the birds defecate while perched in the shrubs (van Oudtshoorn & van Rooyen, 1999). In the Kalahari for example, seeds of fleshy fruits were found in 90% of plots under trees, while in only 8% of plots with no trees (Dean *et al.*, 1999). Thus one can predict that non-Mesemb seedlings will establish and grow better when sheltered by canopies of nurse plants than in open spaces, since this is where the seeds are likely to be dispersed to by wind or birds.

In this chapter, I explored the effects of non-resource factors of micro-sites on seedling establishment. I hypothesized that non-resource factors (such as wind, herbivory or trampling) of micro-sites will affect seedling establishment. I do not attempt to distinguish between different types of non-resource factors, such as the effects of wind versus herbivory versus trampling. Rather, I investigated the overall effect of different types of physical shelter on the establishment of seedlings of perennial Mesemb and non-Mesemb species, and compared it with establishment of seedlings in unsheltered micro-sites. The shelters included adult shrubs (nurse plants) as well as artificial shelters, such as cardboard boxes and plastic tubes. I predicted that the establishment of Mesemb seedlings would not be greater in unsheltered than in sheltered micro-sites, while non-Mesemb seedling establishment would be greater when sheltered.

METHODS

Two field experiments were set up to evaluate this hypothesis, one near Kleinsee and the other near Hondeklipbaai (Figure 2.2). The experiments were set up on a variety of previously mined sites, where seeds of the dominant perennial species were sown into 0.25 m² plots with various treatments. Experiment 1 tested the effect of three different types of sheltered micro-sites on the establishment of Mesemb and non-Mesemb seedlings, and compared it to unsheltered micro-sites. Experiment 2 tested the effect of one type of physical shelter on the establishment of Mesemb and non-Mesemb seedlings, compared to unsheltered micro-sites. In Experiment 1, both the unsheltered and sheltered treatments contained additional soil resources, imitating the higher resource levels found within patches in Namaqualand. In Experiment 2, neither the unsheltered or sheltered treatments contained additional soil resources, imitating the lower resource levels found in inter-patch soils. While the two experiments are not directly comparable due to different locations and starting times, the relative effects of the shelters with and without extra soil resources can be informative.

EXPERIMENT 1

EXPERIMENTAL DESIGN

Seeds of 8 Mesemb species, and 8 non-Mesemb species (Table 3.1) were sown into plots on 7 sites around Kleinsee that had been mined previously (Figure 2.3). On 4 of these sites topsoil had been replaced (Site KT1, Site KT2, Site KT3 and Site KT4), while on the

other 3 sites (Site KO1, Site KO2 and Site KO3) the topsoil had not been replaced, leaving the overburden soil exposed (Table 2.3). Seeds produced in the preceding winter or spring were collected from natural populations between the towns of Kleinsee and Hondeklipbaai (Figure 2.2). Varying seed numbers were used since the aim was to produce approximately the same number of seedlings per species in each plot. The seed numbers were calculated based on germination rates determined during preliminary experiments. However, due to differences in seed availability, it was not always possible to collect the desired amount of seeds. In such cases, seeds from species that were more abundant were collected so that the total number of seeds per functional guild was approximately similar.

Twenty replicate plots of each of the following treatments were set out on each site: control, transplant shelter, rectangular cardboard box shelter (hereafter box shelter) and plastic tube shelter (hereafter tube shelter). The control consisted of a 0.5 m x 0.5 m (0.25 m²) plot that was dug to a depth of about 0.2 m with a total soil volume of c. 0.05 m³. The removed soil was then returned to the hole, with the soil additives (a suite of macro and micro nutrients, water-absorbing polymer gel and leaf litter) being mixed evenly throughout the soil layer, and compacted. The plot was shaped into a slight depression (c.5 cm below the surrounding soil level at the centre of the plot), in order to increase the water input to the plot from rains. The edges of sand outside the plot were smoothed away to prevent the soil from collapsing onto the plot. All the other treatments followed a similar process (i.e. they all had nutrients, gel and leaf litter added to the soil). In addition, the transplant shelter plots had two small to medium sized shrubs, a Mesemb *Amphibolia rups-arcuatae* (Aizoaceae) and a non-Mesemb *Othonna sedifolia* (Asteraceae), planted in diagonally opposite corners of the plot. The box shelter treatment consisted of a plot where a cardboard box (0.53 m x 0.42 m) was placed inside the hole before the soil was returned. The top and bottom flaps of the cardboard box were removed prior to this, so that only the four sides of the box remained. The box was 0.44 m high, and the hole was deep enough for 0.2 m of the box sleeve to be placed into the hole, with the remaining c.0.24 m protruding above the surrounding soil surface (Figure 3.1). The soil was then returned to the hole (with soil additives). The soil in the plot was leveled slightly below the surrounding soil level (c.5 cm at the centre of the plot), and the edges of sand outside the box were smoothed away. The tube shelter treatment consisted of a round plastic tube with a diameter of c.0.5 m. The tubes were 0.5 m high,

and c.0.2 m of the height was placed into the hole before returning the soil and soil additives, resulting in an above ground height of c.0.3 m. The soil was compacted and leveled in the same way as the other treatments (see Appendix for photos).

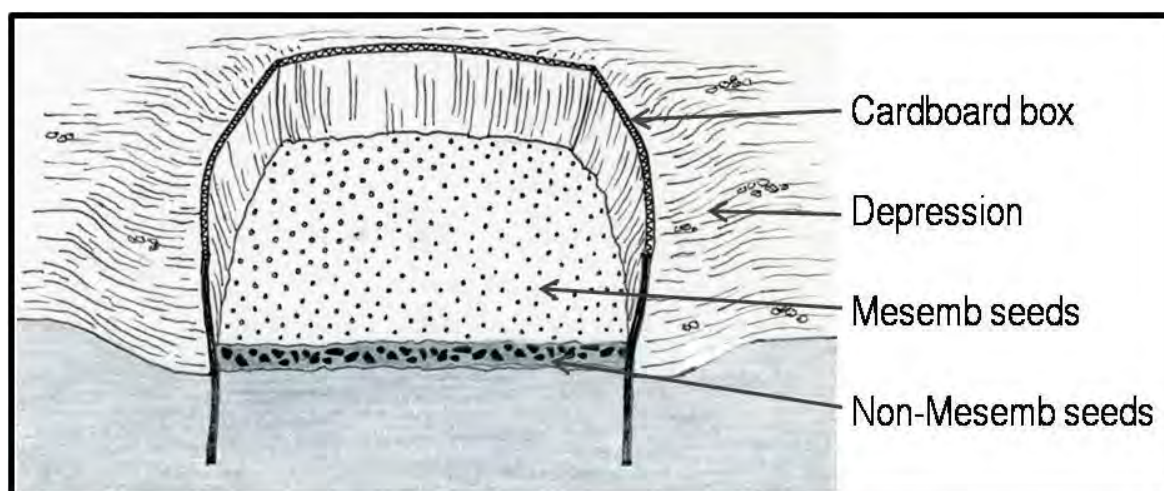


Figure 3.1 A plot with a cardboard box artificial shelter, showing the local depression in which the plot is situated. In Experiment 1 and 4, the soil level inside and outside the box was similar, leading to the boxes collapsing inward over time. In Experiment 2 and 5, the soil level inside the box was 2-5 cm higher than outside the box (shown here), thus preventing the box from collapsing inward, as well as the higher soil level inside the box than outside the box. Non-Mesemb seeds were sown c. 2cm beneath the soil, while Mesemb seedlings were sown on or just below the surface (Illustration by A. Roberts).

The gel that was added to the soil of all four treatments (control, transplant, box shelter and tube shelter), consisted of a water-absorbing polymer gel (“Stockosorb”), applied at the recommended rate of 700 g.m^{-3} (i.e. 35 g.plot^{-1}). The gel is thought to improve the absorption and retention of moisture in the soil after rain events, and is commonly used in horticulture and landscaping. The nutrients added to each of the four treatments (with the gel), consisted of an organic slow-release fertiliser which contained a complete suite of macro- and micronutrients (“Veg 6:3:4(15)SR VITA Organic Fertilizer” from Talborne Products), applied at a rate of 700 g.m^{-3} (i.e. 35 g.plot^{-1}). This rate is approximately the equivalent amount of nitrogen, phosphorus and potassium that occurs in undisturbed topsoil in patches under perennial shrubs in Namaqualand Strandveld (P.J. Carrick & R. Krüger, *unpublished data*). Four cups of leaf litter, collected from under shrubs in undisturbed veld, were added to each plot. Leaf litter adds organic content and microorganisms to the soil, thereby mimicking soil under the canopies of shrubs in undisturbed veld. Leaf litter benefits plants by increasing water infiltration, and decreasing water loss by evaporation from the soil (Went & Sheps, 1971; Went *et al.*, 1983).

Table 3.1 The species and number of seeds sown into each plot for Experiments 1 and 2. The family, primary seed dispersal mechanism and growth form of each species is included.

Family	Species	Number of seeds per plot		Primary dispersal mechanism	Growth form
		Ex 1	Exp 2		
Mesembrythemaceae	<i>Amphibolia laevis</i>	27		water	prostrate
	<i>Amphibolia rupis-arcuatae</i>	264	138	water	upright
	<i>Cephalophyllum spissum</i>		124	water	prostrate
	<i>Conicosia pugionoformis</i>	19		water	upright
	<i>Drosanthemum hispidum</i>	208	59	water	prostrate
	<i>Jordaaniella spongiosa</i>	124	138	water	prostrate
	<i>Psilocaulon spp</i>		15	water	prostrate
	<i>Ruschia extensa</i>		106	water	upright
	<i>Ruschia versicolor</i>	26	138	water	prostrate
	<i>Ruschia subpaniculata</i>	196	60	water	upright
	<i>Stoebaria utilis</i>	38		water	upright
	<i>Stoeberia beetzii</i>		138	water	upright
Mesemb sub-total		902	916		
Aizoaceae	<i>Tetragonia fruticosa</i>	64	78	wind	upright
Asteraceae	<i>Didelta carnososa carnososa</i>		17	wind	upright
	<i>Othonna cylindrica</i>		238	wind	upright
	<i>Pteronia paniculata</i>		85	wind	upright
	<i>Pteronia glabrata</i>	9		wind	upright
	<i>Pteronia incana</i>	11	85	wind	upright
	<i>Pteronia onobromoides</i>	91	37	wind	upright
Chenopodiaceae	<i>Atriplex semibaccata</i>	216	82	bird	prostrate
	<i>Atriplex vestita</i>		87	wind	upright
	<i>Manoclamys albicans</i>	107	123	bird	upright
Fabaceae	<i>Lebeckia sericea</i>	83		explosively dehiscent	upright
Molluginaceae	<i>Pharnaceum sp</i>		85	passive	upright
Zygophyllaceae	<i>Zygophyllum morgsana</i>	44	84	wind	upright
Non-Mesemb sub-total		625	1001		
All seeds Total		1527	1917		

The Mesemb and non-Mesemb seeds were sown as evenly as possible throughout the plots, in two separate layers. First the larger non-Mesemb seeds were sown, covered with c.2 cm of soil and patted down, after which the small Mesemb seeds were sown, covered with a few millimetres of soil, and then patted down.

The plots were set out over a two week period during June 2006, and site replicates were stratified over that time (i.e. approximately half of the replicates on each site were done in the one week, and half in the second week). The start date of the experiment was the week of 26 June 2006. The emergence and survival of seedlings from each functional guild (i.e. Mesemb seedlings and non-Mesemb seedlings) were monitored for each plot (seedlings.plot⁻¹) over a period of 115 weeks (at 6, 13, 24, 53, 67 and 115 weeks after the initiation of the experiment).

STATISTICAL ANALYSES

The Mesemb and non-Mesemb data were analysed separately. Data from three time periods (Weeks 13, 67 and 115) were used in the analysis, corresponding to the same month / season (September / Spring) in each year (Year 0, Year 1 and Year 2) of the experiment, in order to avoid noise in the data caused by senescence during the hot summer months.

Data was analysed using Generalized Linear Models (GLMs) in the programme R (R Development Core Team, 2009), with the 'glm' function in the 'base' package. The count data had a Poisson distribution, therefore a Poisson distribution with a logarithmic link, denoted by "Poisson (link=log)" in the 'glm' command, was selected in the GLM (Bolker *et al.*, 2009). The following factors (and levels) were fitted to the response variable (counts):

- Treatment (control, transplant shelter, box shelter, tube shelter),
- Year (0, 1 and 2) and
- Site (KT1, KT2, KT3, KT4, KO1, KO2 and KO3).

Typically, site and year factors are modelled as random factors using Generalized Linear Mixed Models (GLMMs), but in this case both were modelled as fixed factors since random factors require many levels (>20) in order to be useful in a mixed model (D. Bates, *pers. comm.*), and in this case there were only 7 levels for 'Site', and 3 for 'Year'. These factors were included in the analyses mainly as co-variates to the main effects of

treatment, in order to account for the differences between sites and years. However, taking the results of the co-variates into account can provide greater depth and understanding of the treatment results, in particular when interaction effects are tested for.

The Treatment factor was crossed with the Year factor (Treatment*Year), as the effect of the Treatments over time were of interest to the study. The optimal model, which fits the data best, was found by an iterative process, whereby the maximal model (with all available main effects and interaction terms included) was reduced in a stepwise manner until the optimal model was reached (where only significant terms are retained). This model reduction was done by removing a factor from the analysis if all the terms that include that factor were non-significant (starting with those with the highest p-value), and then refitting the model. This was repeated until only factors with significant terms remained. The process was started with the interaction terms between factors, after which the main effects factors were eliminated if not significant. Where interaction terms were significant, the higher order main effects factors that were included in those interactions were retained even if they were not significant (Bolker *et al.*, 2009; Crawley, 2007). Due to the data being overdispersed (where the variance was greater than the mean for each parameter estimate, or where the variance increases as the mean for the parameter estimate increased), the standard errors (SE) were corrected using a quasi-GLM model where the corrected variance was

$$s^2 = \mu \times \phi$$

where μ denotes the mean and ϕ is the overdispersion parameter (Zuur *et al.*, 2009). The Laplace approximation of the likelihood was chosen for its greater accuracy and efficiency than the more traditional penalized quasilielihood (PQL) method of estimation (Bolker *et al.*, 2009; Crawley, 2007). The results of the GLM estimated the mean magnitude and direction of all the terms using the Poisson distribution. The coefficient (model estimate) for each term was back transformed to calculate the magnitude of the effect (factor), by

$$factor = e^{\Lambda(\text{coefficient})}$$

where e is the base of the natural log, and then converted to percentage. The 95% Confidence Interval range (95% CI range) around the estimated effect was calculated by

$$95\% CI_{lower} = e^{\Lambda(\text{coefficient} - 2 * \text{Standard Error})}$$

$$95\% CI_{upper} = e^{\Lambda(\text{coefficient} + 2 * \text{Standard Error})}$$

EXPERIMENT 2

EXPERIMENTAL DESIGN

Seeds of 9 Mesemb species and 11 non-Mesemb species (Table 3.1) were sown into plots on 8 sites around Hondeklipbaai that had been previously mined (Figure 2.4). Seeds produced in the preceding winter or spring were collected from natural populations between the towns of Kleinsee and Hondeklipbaai (Figure 2.2). Five of the sites were covered with topsoil (Site HT1, Site HT2, Site HT3, Site HT4 and Site HT5), while the other three did not have topsoil replaced on top of the overburden (Site HO1, Site HO2 and Site HO3). The ages of the sites at the start of the experiment varied from 1 to 4 years (Table 2.3). All 8 sites had shade cloth nets erected to act as windbreaks to prevent wind erosion of the soil.

Fifteen replicate plots of each of the following treatments were set out on each site: control and cardboard box shelter. The plots were made in the same manner as those in Experiment 1, except that the soil level inside the cardboard box treatment plots was c.2-5 cm higher than the soil level outside the plot, in order to prevent the cardboard boxes from collapsing inward over time (Figure 3.1).

The Mesemb and non-Mesemb seeds were sown in two separate layers, as outlined in Experiment 1. The only difference was that the Mesemb seeds were not covered with any soil after being sown, but were just patted down into the soil. The reason for this change in methods was that very few Mesemb seedlings emerged in Experiment 1, and it was thought that the seeds may have been sown too deep.

The plots were set out over a 2 week period during May 2007, with the start date in the week of 14 May 2007. The emergence and survival of seedlings from each functional guild (i.e. Mesemb seedlings and non-Mesemb seedlings) were monitored for each plot (seedlings.plot⁻¹) over a period of 62 weeks (at 11, 27 and 62 weeks after the start of the experiment), and the height (mean height of seedlings.plot⁻¹) of seedlings was recorded at week 62 only.

STATISTICAL ANALYSES

The Mesemb and non-Mesemb data was analysed separately. Data from two time periods (Weeks 11 and 62) was used in the analysis, and these corresponded to the same month / season (July / Winter) in each year (Year 0 and 1) of the experiment.

The data was analysed using GLMs, following similar procedures to those described for Experiment 1. The count and height data for both Mesemb and non-Mesemb seedlings had Poisson distributions. The following factors (and levels) were fitted to the response variable for the count data:

- Treatment (control and box shelter),
- Year (0 and 1) and
- Site (HT1, HT2, HT3, HT4, HT5, HO1, HO2, HO3).

The Treatment*Year interactions were included in the analysis. The height data was only recorded for Year 1, so only the Treatment and Site factors were included in this analysis. All factors were included as fixed factors, for the same reasons described in Experiment 1, and the same model selection process was followed. The estimated effect (%) and 95% CI range were calculated as in Experiment 1.

RESULTS

EXPERIMENT 1

In this experiment, the number of Mesemb seedlings.plot⁻¹ (Figure 3.2.A-G) were much lower than the number of non-Mesemb seedlings.plot⁻¹ (Figure 3.2.H-N), by a factor of more than 10 in all cases, and up to a factor of about 20 in some cases. The effect of Year was consistent amongst Sites for the non-Mesemb seedlings, where there were high seedling numbers in Year 0, after which the numbers dropped off substantially. There was no consistent effect of Year for the Mesemb seedlings.

MESEMB SEEDLINGS

Year & Treatment effects

At 5 out of 7 Sites there were fewer than 1 seedling.plot⁻¹ in Year 0 and Year 2, and at 5 out of 7 sites there were fewer than 2 seedlings.plot⁻¹ in Year 1 (Figure 3.2.A-G). The model estimates a significant increase of 194% (64-426%; 95% CI range, and so

throughout this chapter unless stated otherwise) in the number of seedlings.plot⁻¹ from Year 0 to Year 1 ($t=3.706$, $p=0.00022$; Table 3.2.A). A significant increase of 111% (15-288%) is estimated from Year 0 to Year 2 ($t=2.447$, $p=0.01450$), which translates to a decrease of 43% from Year 1 to Year 2, also evident in the graphs.

There were fewer seedlings.plot⁻¹ in the transplant plots than in the control plots on all 7 sites at all three time periods (although only marginally fewer at some Sites / Years; Figure 3.2.A-G). However, neither the transplant nor the transplant*Year terms were significant (Table 3.2.A).

The box shelter treatment effect did not contribute significantly to the model, however the box*Year 1 and box*Year 2 interaction terms were significant in the model, indicating that the effect of the box shelters changed over time. This implies that there is no significant effect of box shelters in Year 0, but the model estimates that in Year 1, the box treatment has 84% (54-94%) fewer seedlings.plot⁻¹ than the control treatment ($t=-3.545$, $p=0.00040$; Table 3.2), and in Year 2 there were 91% (66-98)% fewer seedlings.plot⁻¹ than the control treatment ($t=-3.596$, $p=0.00033$). These estimates are reflected in the graphs, where the box treatment had almost no seedlings left by Year 2 (Figure 3.2.A-G).

The graphs show that tube treatment plots had lower seedling numbers.plot⁻¹ than the control treatment (Figure 3.2.A-G), except at Site KT2 (old topsoil) and Site KO3 (overburden). Neither the tube nor the tube*Year terms were significant in the model (Table 3.2.A).

Site effects

The model indicates that Site KO3 (overburden) and Site KT4 (old topsoil) had the fewest Mesemb seedlings.plot⁻¹ of all the Sites, regardless of Treatment (Table 3.2.A). Site KO2 (overburden) had the most seedlings.plot⁻¹ of all the Sites, while Sites KT1 (new topsoil), KT2 and KT3 (old topsoil) as well as KO1 (overburden) had an intermediate number of seedlings.plot⁻¹.

NON-MESEMB SEEDLINGS

Year & Treatment effects

The overall trend for the non-Mesemb seedlings was that there were relatively large numbers of seedlings.plot⁻¹ in Year 0, with a large drop in seedling numbers between Year 0 and Year 1 (Figure 3.2.H-N). There was a much smaller decrease in numbers between Year 1 and Year 2 for most of the Treatments at each Site. This was reflected by the model, where Year 1 and Year 2 effects contributed significantly to the model. The model estimates a 66% (58-73%) decrease in the number of seedlings.plot⁻¹ between Year 0 and Year 1 ($t=-9.703$, $p<0.0001$; Table 3.2.B), and an 81% (75-86%) decrease from Year 0 to Year 2 ($t=-11.809$, $p<0.0001$), or a 23% decrease from Year 1 to Year 2.

Transplant plots had lower seedling numbers than the control plots at all Sites and all Years (Figure 3.2.H-N). The model estimates a significant effect of transplants ($t=-2.575$, $p=0.01012$; Table 3.2.B), with 19% (5-32%) fewer seedlings.plot⁻¹ in the transplant plots than in the control plots, across all Years and Sites. The transplant*Year 1 and transplant*Year 2 terms were, however, not significant in the model, indicating that there was no change in the effect of transplants over time.

The graphs indicate that the box shelter plots had more seedlings.plot⁻¹ in Year 0 than the control treatments at 6 of the 7 sites (Figure 3.2.H-N), with Site KT1 (new topsoil) being the exception. By Year 1, this difference at the 6 sites had diminished, with the box shelter plots having very similar seedling numbers to the control treatment plots. This pattern was also apparent at Year 2. The box*Year 1 and box*Year 2 interaction terms were significant in the model, confirming that the effect of the box treatment changed over time. In Year 0, the box treatment had a significantly positive effect on seedling numbers, with an estimated 78% (55-105%) more seedlings.plot⁻¹ than the control plots ($t=8.233$, $p<0.0001$; Table 3.2.B). By Year 1, box plots had an estimated 67% (53-76%) fewer seedlings.plot⁻¹ than the control treatment ($t=-6.329$, $p<0.0001$), and by Year 2 there were an estimated 57% (34-71%) fewer seedlings.plot⁻¹ than the control plots ($t=-4.006$, $p<0.0001$).

Tube shelter plots had more seedlings.plot⁻¹ than the control plots in Year 0 at 6 out of the 7 Sites (Figure 3.2.H-N). At Year 1, tube shelter plots had more seedlings.plot⁻¹ than the control plots at only 3 of the 7 sites, Site KT1 (new topsoil), Site KO3 and Site KO1

(both overburden). The tube shelter plots also had more seedlings than the control treatment at 6 of the 7 sites in Year 2, the exception being Site KT2. The effect of tube shelters was significant in the model, which estimates that plots with tube shelters had 78% (54-104%) more seedlings.plot⁻¹ than the control plots($t=8,169$, $p<0.0001$; Table 3.2.B), across all years and sites.

Site effects

The patterns on the various sites were quite similar, with the only notable exception being that there were more non-Mesemb seedlings (between c.5 and c.15 seedlings.plot⁻¹) in the Plastic shelter treatments on the overburden Sites (Sites KO1, KO2, KO3) by Year 2 than at any of the topsoil sites (all $<c.5$ seedlings.plot⁻¹).

The model estimates that Site KO3 (overburden), Site KT2 and Site KT4 (both old topsoil) had the lowest seedling numbers of all the sites across treatments, while Site KO2 (overburden) had the most seedlings (Table F). Site KT3 (old topsoil), Site KT1 (new topsoil) and Site KO1 (overburden) had an intermediate number of seedlings.plot⁻¹.

EXPERIMENT 2

There were far fewer Mesemb seedlings.plot⁻¹ than non-Mesemb seedlings.plot⁻¹ at all the Sites (Figure 3.3). In Year 0, the mean number of seedlings.plot⁻¹ for Mesemb seedlings at all Sites and Treatments ranged between c.0 and c.12 seedlings.plot⁻¹, while in Year 1 the means ranged from c.0 to c.10 seedlings.plot⁻¹. In Year 0, the mean number of non-Mesemb seedlings at all Sites and Treatments ranged from c.2 to c.55 seedlings.plot⁻¹, while in Year 1 the range of means was reduced to c.5 to c.30 seedlings.plot⁻¹. The number of non-Mesemb seedlings.plot⁻¹ diminished between Year 0 to Year 1 in most cases (at 14 of the 16 Site/Treatments combinations), while the number of Mesemb seedlings.plot⁻¹ frequently increased from Year 0 to Year 1 (at 8 of the 16 Site / Treatment combinations).

MESEMB SEEDLINGS

Treatment & Year effects

At 4 of the 8 Sites, the control treatment seedling numbers decreased from Year 0 to Year 1, while at 6 of the 8 Sites the box treatment seedling numbers increased over the same period (Figure 3.3.A-H). There were few differences between Treatments and Sites in Year

0, with 12 out of 16 of the Treatments / Sites having between 1 and 4 seedlings.plot⁻¹. The overall trend of seedling numbers is reflected in the model where seedling numbers in control plots decrease with Year and seedling numbers in box plots increase with Year. Neither the Year or box effects contributed significantly to the model, although the interaction term box*Year 1 was significant (t=3.154, p<0.0017; Table 3.2.C). The model estimates that the box treatment in Year 1 would have 109% (31-233%) more seedlings.plot⁻¹ than the control treatment.

In contrast to the trends in the number of seedlings.plot⁻¹, the trends for mean heights.plot⁻¹ (Figure 3.4.A) indicated that Mesemb seedlings were shorter in Year 1 in the box shelter treatment plots than in the control treatment plots at 6 of the 8 Sites. The exceptions to this trend were Site HT1 and Site HT2 which are both new topsoil sites with no seedlings recorded in the control plots at the first site. This difference in height was small in most cases except at Site HO1 (overburden), where the mean seedling heights in the box shelter plots were about half of those in the control plots (c.1.25 cm versus c.2.25 cm). The box effect was significant in the model (t=-3.340, p=0.0011; Table 3.2.D), with the model estimating that the Mesemb seedlings would be 20% (9-30%) shorter in the box treatment than the control treatment in Year 1, across all sites

Site effects

At the three overburden sites (Site HO1, Site HO2 and Site HO3), the box shelter plots had more Mesemb seedlings.plot⁻¹ than the respective control plots in both Year 0 and Year 1, and there was not much change with respect to seedling numbers between the two years (only Site HO1 showed an increase of seedlings in both control and box shelter plots; Figure 3.3.A-H). On the topsoil sites, Site HT3 and Site HT5 (old topsoil) had markedly greater seedling numbers in the control plots than in the box shelter plots in Year 0, although this difference was either reduced (Site HT3) or reversed (Site HT5) by Year 1. For the other 3 topsoil sites, there was little difference between the control and box shelter plots in Year 0, but by Year 1 the box treatments had far greater seedling numbers than the control treatments at all the sites except Site HT2 (new topsoil) and Site HT3 (old topsoil), where the two treatments had very similar seedling numbers. Site HO1 had the tallest seedlings of all the Sites, while Site HO2 (overburden), Site HT5 and Site HT4 (both old topsoil) had the shortest seedlings according to the model (Table 3.2.D) and the graphs (Figure 3.4.A).

NON-MESEMB SEEDLINGS

Treatment & Year effects

There were large differences in the numbers of seedlings.plot⁻¹ between the Sites in Year 0 (Figure 3.3.I-P), ranging from c.2 to c.55 seedlings.plot⁻¹ (i.e. range of c.53 seedlings.plot⁻¹). The range halved by Year 1, with c.5 to c.30 seedlings.plot⁻¹ (i.e. range of c.25 seedlings.plot⁻¹) among all sites and treatments. The Year effect was significant in the model ($t=-12.186$, $p<0.0001$; Table 3.2.E), which estimated that there would be 49% (43-55%) fewer seedlings.plot⁻¹ in Year 1 than in Year 0.

At 5 of the 8 Sites, the control treatment plots had more seedlings.plot⁻¹ than the box treatment plots in Year 0 (Figure 3.3.I-P). By Year 1, most of the Sites showed very little difference between the control and box treatment plots in terms of seedlings.plot⁻¹. In the model, neither the box effect or the box*Year 1 effect was significant with regard to seedling numbers (Table 3.2.E).

The box shelter plots had taller seedlings than the control plots on 5 of the 8 sites in Year 1 (Figure 3.4.B). On the other three sites (overburden Site HO2, old topsoil Site HT3 and old topsoil Site HT4) the seedlings in the control and box shelter plots were approximately the same height, with these three sites also displaying the shortest seedlings amongst all the sites. The box effect was significant in the model ($t=6.184$, $p<0.0001$, Table 3.2.F), which estimated that non-Mesemb seedlings would be approximately 39% (25-54%) taller in the box treatment plots than in the control treatment plots in Year 1.

Site effects

On the overburden sites (Site HO1, Site HO2 and Site HO3; Figure 3.3.N-P) the control plots had more seedlings.plot⁻¹ in Year 0 than their respective box shelter plots, but by Year 1 this trend had reversed in two of the sites (Site HO1 and Site HO2), with approximately equal seedlings number in the two treatments at Site HO3. For 4 of the 5 topsoil sites, the box shelter plots had greater number of seedlings than the control plots in Year 0. The exception was Site HT5 (the oldest topsoil site) where the control plot had approximately double the number of seedlings than the box shelter plots (c. 15 versus 30 seedlings.plot⁻¹). By Year 1, only Site HT3 (old topsoil) had more seedlings.plot⁻¹ in the box shelter than the control plots, while the other 4 topsoil sites had either similar seedlings numbers in the two treatments (Site HT1 and Site HT2, both new topsoil), or marginally

fewer seedlings in the box shelter treatments than in the control treatments (Site HT4 and Site HT5, both old topsoil sites).

The heights of non-Mesemb seedlings varied greatly between sites (Figure 3.4.B), with the two young topsoil sites (Site HT1 and Site HT2) producing the tallest seedlings by far. The older topsoil sites (Site HT3, Site HT4 and Site HT5) had shorter seedlings than two of the overburden sites (Site HO1 and Site HO3).

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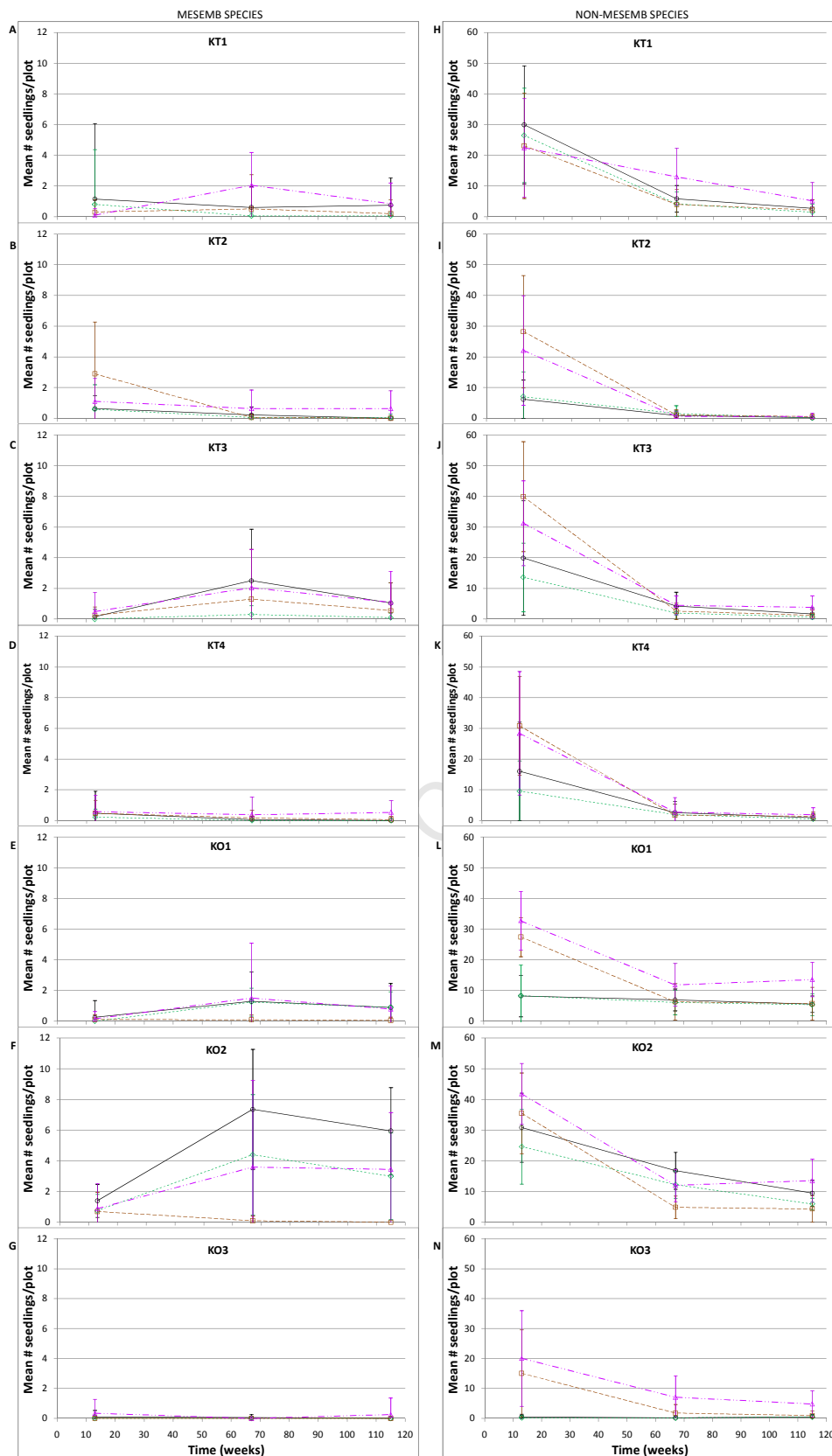


Figure 3.2 Graphs indicating the mean (and standard error; whiskers) number of seedlings.plot⁻¹ for Treatments in Experiment 1. Time is given in the number of Weeks since the start of the experiment, with Week 13 representing Year 0, Week 67 representing Year 1 and Week 115 representing Year 2. The Control (black circle, solid line), Transplant (green triangle, short dashed line), cardboard Box (brown square, long dashed line) and Plastic shelter (magenta triangle, dashed-dotted line) are shown for the Mesembs (A-G) and non-Mesembs (H-N) at the 7 sites.

Table 3.2 Results from the analysis of Experiment 1 and 2, using Generalized Linear Models. The effect of Treatments (transplant shelter = T, cardboard box shelter = B, plastic tube shelter = P), Years and Sites on the number (and heights for Experiment 2, Year 1 only) of Mesemb and Non-Mesemb seedlings are tested. The estimated size effect (positive or negative) and the corresponding 95% Confidence Interval is expressed in percentage (%). Significance is indicated by the following codes: 0 < * < 0.001 < ** < 0.01 < * < 0.05.**

Experiment, plant group, data type & number of observations		Term	Coefficient	Estimated size effect (%)	95% CI _{lower}	95% CI _{upper}	t value	Pr(> t)			Experiment, plant group, data type & number of observations	Term	Coefficient	Estimated size effect (%)	95% CI _{lower}	95% CI _{upper}	t value	Pr(> t)		
A	Ex1	(Intercept)	-0.49				-1.688	0.0917		C	Ex2	(Intercept)	0.79				3.486	0.0005	***	
	Mesemb	T	-0.58	-44	-76	30	-1.379	0.1680			Mesemb	B	-0.07	-7	-34	32	-0.391	0.6959		
	Counts	B	0.10	11	-44	122	0.301	0.7638			Counts	Year 1	-0.13	-13	-38	24	-0.765	0.4448		
	n=1656	P	-0.13	-12	-58	83	-0.354	0.7235			n=464	B*Year 1	0.74	109	31	233	3.154	0.0017	**	
		Year 1	1.08	194	64	426	3.706	0.0002	***			HT1	-0.89	-59	-82	-6	-2.139	0.0330	*	
		Year 2	0.75	111	15	288	2.447	0.0145	*			HT2	-0.38	-32	-63	28	-1.209	0.2272		
		T*Year 1	-0.11	-10	-66	138	-0.226	0.8209				HT3	1.22	238	115	433	5.358	0.0000	***	
		T*Year 2	-0.17	-16	-70	138	-0.325	0.7452				HT4	0.42	52	-9	154	1.619	0.1062		
		B*Year 1	-1.80	-84	-94	-54	-3.545	0.0004	***			HT5	0.82	126	40	265	3.401	0.0007	***	
		B*Year 2	-2.42	-91	-98	-66	-3.596	0.0003	***			HO1	0.36	43	-15	141	1.372	0.1708		
		P*Year 1	-0.04	-4	-59	125	-0.097	0.9225				HO2	0.68	97	21	222	2.771	0.0058	**	
		P*Year 2	-0.01	-1	-59	143	-0.013	0.9894			D	Ex2	(Intercept)	0.45				4.443	0.0000	***
		KT1	-0.29	-25	-54	23	-1.155	0.2481			Mesemb	B	-0.23	-20	-30	-9	-3.340	0.0011	**	
		KT2	-0.36	-31	-58	16	-1.417	0.1566			Heights	HT1	0.06	6	-36	78	0.238	0.8120		
		KT4	-1.22	-71	-85	-41	-3.529	0.0004	***		n=155	HT2	0.13	14	-15	51	0.890	0.3750		
	KO1	-0.30	-26	-55	22	-1.206	0.2281			HT3	-0.05	-5	-26	21	-0.445	0.6567				
	KO2	1.17	221	121	365	6.278	0.0000	***		HT4	-0.23	-20	-39	3	-1.747	0.0828				
	KO3	-2.58	-92	-98	-74	-4.225	0.0000	***		HT5	-0.16	-15	-34	11	-1.222	0.2238				
B	Ex1	(Intercept)	2.82				37.887	0.0000	***		HO1	0.24	27	-0	61	1.986	0.0489	*		
	Non-Mesemb	T	-0.22	-19	-32	-5	-2.575	0.0101	*		HO2	-0.21	-19	-38	6	-1.564	0.1200			
	Counts	B	0.58	78	55	105	8.233	0.0000	***	E	Ex2	(Intercept)	3.89				59.146	0.0000	***	
	n=1656	P	0.57	78	54	104	8.169	0.0000	***	Non-Mesemb	Year 1	-0.68	-49	-55	-43	-12.186	0.0000	***		
		Year 1	-1.09	-66	-73	-58	-9.703	0.0000	***	Counts	HT1	-0.61	-45	-57	-31	-5.143	0.0000	***		
		Year 2	-1.67	-81	-86	-75	-11.809	0.0000	***	n=464	HT2	-0.20	-18	-32	-1	-2.121	0.0345	*		
		T*Year 1	-0.07	-7	-34	31	-0.432	0.6659			HT3	-0.34	-29	-42	-14	-3.518	0.0005	***		
		T*Year 2	-0.15	-14	-45	33	-0.695	0.4874			HT4	-0.69	-50	-60	-38	-6.318	0.0000	***		
		B*Year 1	-1.10	-67	-76	-53	-6.329	0.0000	***		HT5	-0.73	-52	-61	-40	-6.613	0.0000	***		
		B*Year 2	-0.83	-57	-71	-34	-4.006	0.0001	***		HO1	0.09	9	-9	30	0.976	0.3296			
		P*Year 1	-0.25	-22	-42	4	-1.721	0.0855			HO2	-0.36	-30	-42	-15	-3.630	0.0003	***		
		P*Year 2	0.16	17	-17	65	0.899	0.3685		F	Ex2	(Intercept)	1.48				17.284	0.0000	***	
		KT1	0.11	12	-3	30	1.576	0.1152		Non-Mesemb	B	0.33	39	25	54	6.184	0.0000	***		
		KT2	-0.59	-45	-54	-34	-6.586	0.0000	***	Heights	HT1	1.51	353	278	444	16.607	0.0000	***		
		KT4	-0.24	-22	-33	-8	-3.007	0.0027	**	n=232	HT2	0.62	86	53	127	6.270	0.0000	***		
	KO1	0.10	10	-5	28	1.359	0.1744			HT3	-0.81	-55	-67	-41	-5.620	0.0000	***			
	KO2	0.53	69	48	94	7.912	0.0000	***		HT4	-0.87	-58	-69	-44	-5.907	0.0000	***			
	KO3	-0.88	-59	-66	-50	-9.052	0.0000	***		HT5	-0.50	-39	-53	-22	-3.865	0.0001	***			
										HO1	0.24	27	2	57	2.221	0.0264	*			
										HO2	-0.85	-57	-68	-43	-5.835	0.0000	***			

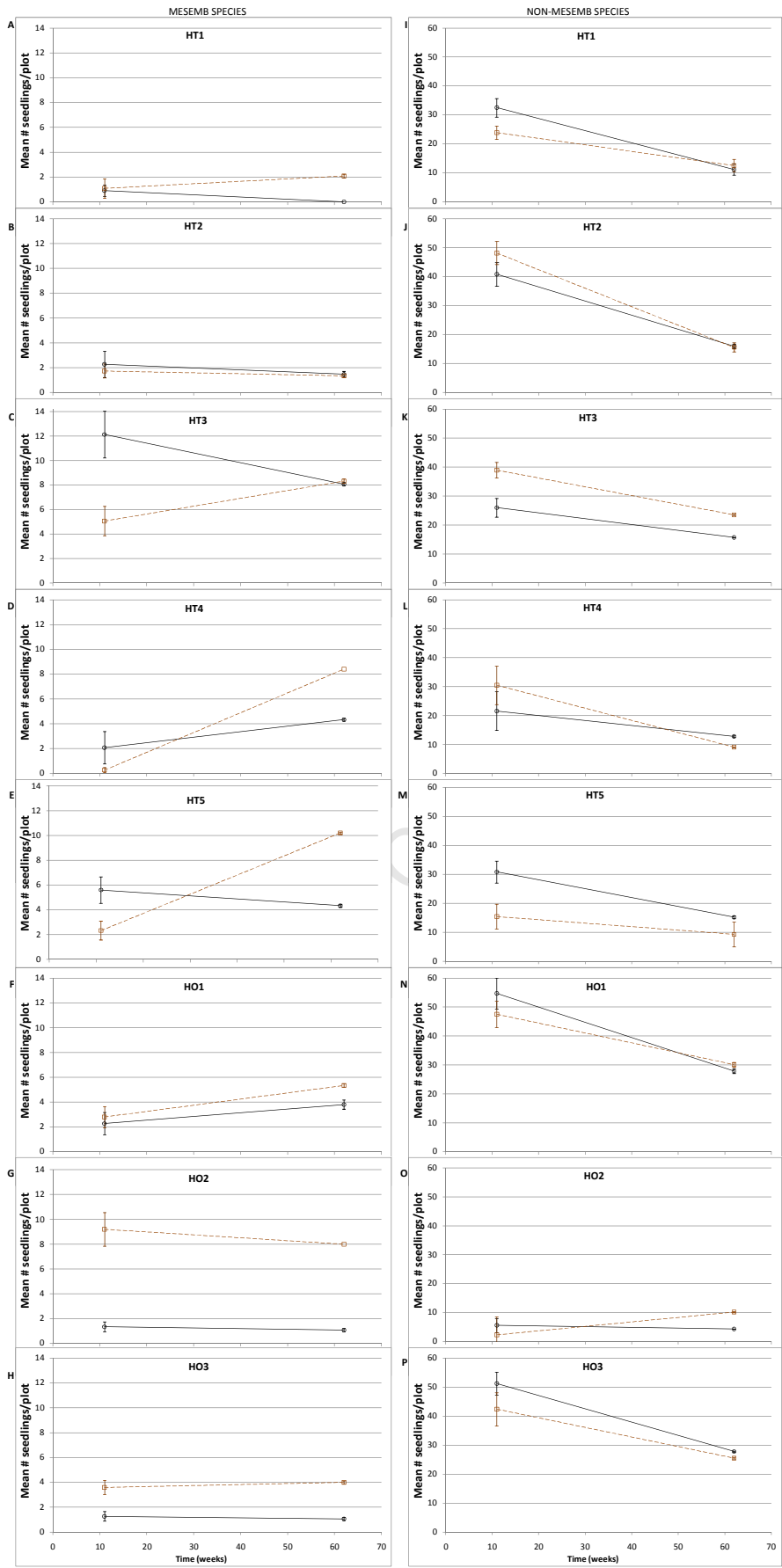


Figure 3.3 The mean number of seedlings.plot⁻¹ for the Control (black circle, solid line) and cardboard Box shelter (brown squares, long-dashed line) treatments (with standard error bars) on the 8 Sites for Mesembs (A-H) and non-Mesembs (I-P) in Experiment 2. The time periods at which data was collected corresponds to Year 0 for Week 11 and Year 1 for Week 62.

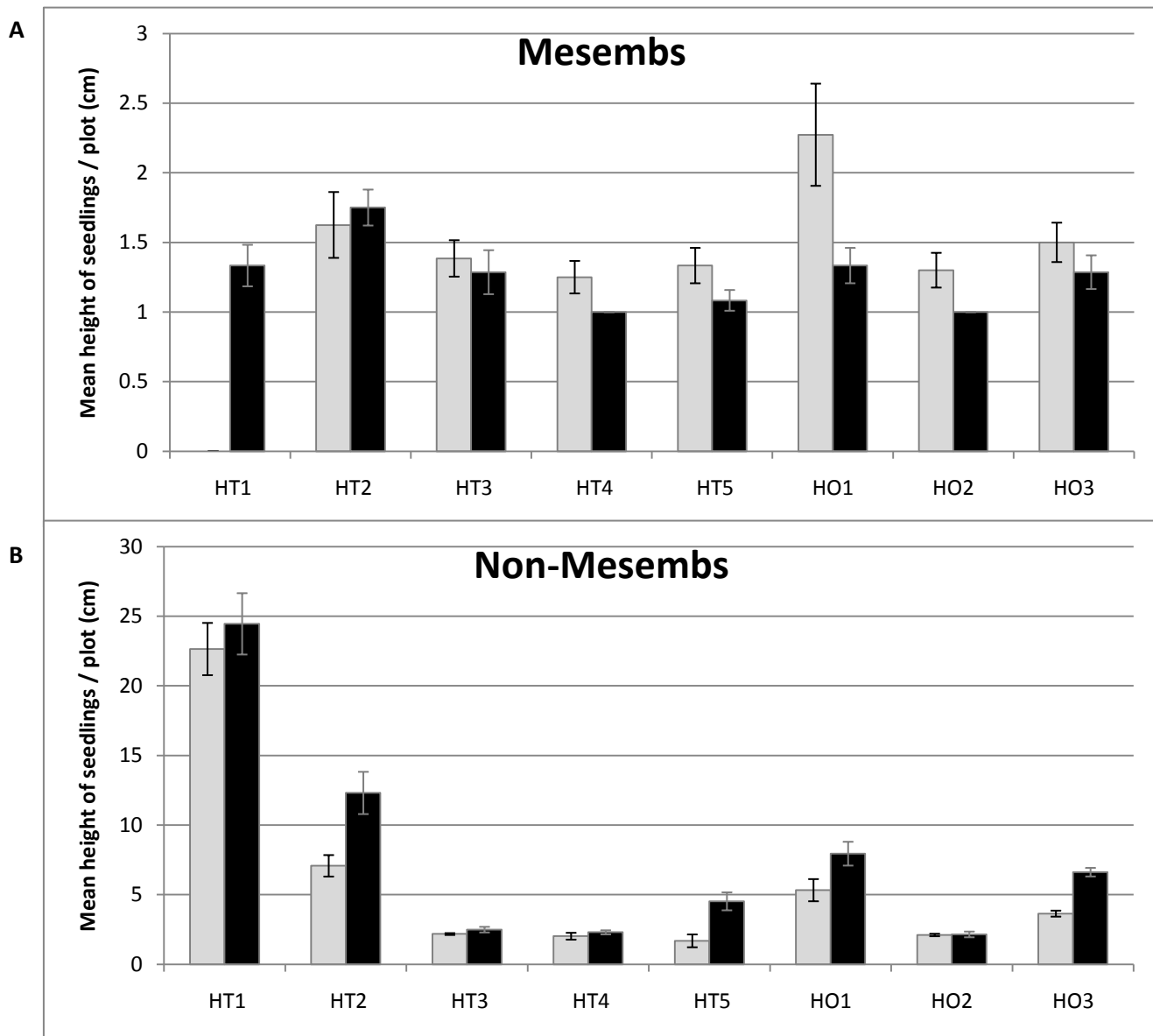


Figure 3.4 The mean (and standard error) seedling heights per plot for the Control (grey) and cardboard Box (black) treatments in Year 1 of Experiment 2 for Mesemb (A) and non-Mesemb (B) seedlings at the 8 sites.

DISCUSSION

FUNCTIONAL GUILDS AND ECOLOGICAL STRATEGIES

Mesemb and non-Mesemb seedlings displayed different survival and growth patterns over time. There were always far fewer Mesemb than non-Mesemb seedlings, despite being sown in similar quantities (Table 3.1). However, Mesemb seedlings displayed much greater resilience once they had emerged than non-Mesemb seedlings, which is most likely attributable to their succulent leaves. Non-Mesemb seedlings displayed greater growth rates than Mesemb seedlings, which could be attributable to their larger seed size (Coomes & Grubb, 2003), which results in larger leaf surface area and potential rates of photosynthesis.

In Experiment 1 and Experiment 2, the frequent increase in Mesemb seedlings over the course of the experiments indicated a degree of delayed germination or dormancy in their seeds. This is contrary to findings of seed bank studies, where Mesemb seeds were uncommon in the soil seedbank (de Villiers *et al.*, 2003). In a study comparing the composition of the standing vegetation with that of the soil seedbank in the Strandveld, only 2 of the 11 perennial Mesemb species in the standing vegetation were represented in the soil seedbank (de Villiers *et al.*, 2003), which would indicate low levels of dormancy. In a laboratory germination study, a Mesemb (*Ruschia robusta*) achieved maximal germination far quicker than two perennial non-Mesemb species (*Tripteris sinuata* and *Hipicium alienatum*, both Asteraceae), as well as achieving a higher total germination rate (Carrick, 2004). Physiologically, small seeds tend to germinate quickly since they require less water before they are fully imbibed and thus have lower levels of dormancy (Baskin & Baskin, 2001).

These results may, however, also be an artifact of the methods, experimental design and data collection. The Mesemb seeds may have been sown too deeply in this experiment, thus preventing them from pushing through to the soil surface after germination. Furthermore, young Mesemb seedlings are very small and only become easily visible once they have developed past the cotyledon stage. During the cotyledon stage, the two cotyledons that emerge from seeds of most Mesemb species lie flat against the ground, and are only a few millimeters in diameter, and are thus difficult to see, especially amongst the much larger non-Mesemb seedlings that were growing in the same plots.

The cotyledon stage of a Mesemb seedlings can last a few months (pers. obs.), especially in low nutrient conditions, and thus the higher Mesemb seedling number in the years after sowing could simply be because they became more visible with time. In addition the non-Mesemb seedling number decreased over time, which would make it easier to identify the Mesemb seedlings. However, despite these observations, Mesemb seedlings seem to be much more resilient to summer drought than non-Mesemb seedlings, which corresponds to the findings of other studies in the Succulent Karoo (Carrick, 2001; Esler & Phillips, 1994; Hoffman *et al.*, 2009; Lechmere-Oertel & Cowling, 2001).

THE EFFECT OF SHELTERS

MESEMB SEEDLINGS

Mesemb seedlings did not survive better in sheltered or unsheltered micro-sites in terms of initial germination of seeds or subsequent survival and growth in Year 0 (i.e. the first growing season). None of the various sheltered plots, transplanted nurse plants (Experiment 1), boxes (Experiment 1 and 2) or tube shelters (Experiment 1) had significantly different seedling numbers to unsheltered plots in Year 0.

However, in the subsequent growth seasons, there were significant effects of cardboard boxes. At first glance, the results from the two experiments seem to be at odds with one another. In Experiment 1, relative to the unsheltered plots, the box shelters had a negative effect on Mesemb seedling numbers over time, while in Experiment 2 the box shelters had a positive effect on seedling numbers over time. This confounding result can be attributed to the slight difference in methodology between the two experiments. In Experiment 1, the soil inside the box was slightly lower (c.2-5 cm) than the soil on the outside (see Methods in this chapter). This resulted in the sides of the boxes collapsing inward over time since structural strength of the box was lost when the boxes became wet during rain events. This allowed the soil outside the box to push the sides of the box inwards. These inward collapsing boxes would eventually almost completely cover the plot, resulting in the death of seedlings that were in the plot. In Experiment 2, the methodology was changed as a result of the observations from Experiment 1. The soil level inside the box was raised so that it was c.2-5 cm higher than the soil outside the box. This resulted in the soil pushing the box outward rather than inward when the soil and box were wetted, thus not flattening the seedlings. One can therefore discount the results of box shelters in Experiment 1 for Year 1 and Year 2, since the boxes were no

longer providing shelter, but were in fact collapsing onto the seedlings which resulted in higher mortality. The results from Experiment 2 can be viewed as more accurate, since these boxes were still providing shelter to the seedlings in the second growing season, resulting in significantly greater seedling numbers than in the open plots. However, despite the increase of Mesemb seedlings in the box treatment over time in Experiment 2, the seedlings were significantly shorter in the box than the control treatment in the second growing season. This is probably due to the high number of non-Mesemb seedlings in the sheltered plots, which grow much larger than the Mesemb seedlings, shading them in the process.

From these results, there is no evidence that supports the hypothesis that Mesemb seedlings are affected by the non-resource factors of micro-sites in their first season of establishment. This can probably be interpreted in light of the low seed dormancy of this guild, since being sheltered from wind and animals will have little effect on how many seeds germinate, but could be more consequential to survival and establishment. In subsequent years however, there is support for the hypothesis that non-resource factors of micro-sites affect Mesemb seedling establishment, where shelter is adequate and competition with adults is absent. It is difficult to interpret the results in terms of whether there is an overall positive or negative effect of shelter, since the box shelter plots had more Mesemb seedlings, but they were shorter than in unsheltered plots. I postulate that the Mesemb seedlings in sheltered plots have a greater chance of becoming adult plants. Although the average seedling heights in the unsheltered plots were taller than those in sheltered plots, the tallest individual Mesemb seedlings were most frequently in the box shelter plots. Furthermore, due to the larger non-Mesemb seedlings in the box sheltered plots (see below), especially in Year 0, the much smaller Mesemb seedlings would initially be limited by light. Two factors would decrease this light limitation over time: 1) non-Mesemb seedlings die off over time, and 2) as non-Mesemb seedlings grow taller, their stems close to the ground have fewer leaves, which allows the oblique sun rays to penetrate to the ground level where the Mesemb seedlings can capture the light. Furthermore, the Mesemb seedlings that establish will have the benefit of being sheltered not only by the cardboard box, but also by the non-Mesemb seedlings here.

In the adjacent Nama Karoo it was found that three times more seeds accumulate under shrub canopies than in open micro-sites (Jones & Esler, 2004), although the plant

categories used are too broad to be aligned with the ones in this thesis. However, seed presence does not necessarily result in successful seedling emergence or establishment (Nathan & Muller-Landau, 2000). Milton (1995b) found that 93% of the seedlings that emerged on bare soil (i.e. unsheltered micro-sites) were small seeded species elsewhere in the Succulent Karoo. While the grouping of species is not the same as used in this thesis, the Mesemb species all have small seeds (compared to non-Mesemb species) and are likely to have made up the majority of these 'small seeded' species. Yeaton & Esler (1990) also found that twice as many Mesemb seedlings emerged in open (i.e. unsheltered) micro-sites than in any other micro-site. This means that a third of the seedlings still emerged in micro-sites with some type of shelter, indicating that although more seedling survive in open micro-sites, a large proportion survive in the sheltered ones too. The results of the experiments in this chapter concur with the findings of these studies in that Mesemb seedlings can establish in unsheltered micro-sites.

NON-MESEMB SEEDLINGS

There were significantly fewer non-Mesemb seedlings in the plots with transplanted nurse plants than in the unsheltered plots. This negative effect of nurse plants was consistent amongst all sites. It was also evident from the first growing season, and the effect remained throughout the duration of the experiment. This indicates that despite possible positive effects of seedlings being sheltered by adult plants, there is a net negative effect on their survival and establishment. It's unlikely that shading is one of these negative effects, since the canopies of the transplanted nurse plants were not extremely dense, and in the case of *Amphibolia rupis-arcuatae* they don't have a very broad canopy. It is more likely that competition for soil resources contributed to this result, although based on these results it is not possible to say whether it was competition for water, nutrients or both.

Another factor to consider is that the two transplanted nurse plants do not necessarily mimic natural conditions accurately. For a start, a post-mining landscape has very different conditions to an undisturbed landscape. The latter has a high proportion of vegetation cover of adult shrubs that breaks the wind speed and prevents excessive soil movement on a landscape level. Occasional adult shrubs interspersed between large areas of bare soil may not provide meaningful shelter for the seedlings that grow under them. Elsewhere in Namaqualand, Schmidt (2002) found that more seeds germinated

under clumps of three nurse plants than under isolated nurse plants that were transplanted onto previously mined sites. This supports the notion that there is a cumulative effect of adult plants in a landscape, and that nurse plants can only be effective in conjunction with other adult plants.

The non-Mesemb seedlings were also not immune to the inward collapsing boxes of Experiment 1, despite the larger size and faster growth rates in comparison with Mesemb seedlings. However, the positive effect of the box shelters was evident in the first growing season for the non-Mesemb seedlings, with box sheltered plots having significantly greater seedling numbers than the unsheltered plots in Year 0. By Year 1 the collapsing boxes resulted in significantly fewer seedling numbers than the unsheltered plots, and this effect was carried through to Year 2. The changes in methodology in Experiment 2 did not result in any significant differences between box and control plots in terms of seedling numbers, but seedlings in boxes were significantly taller than those in control plots by the second growing season.

There is a correlation between the size of a seedling and its ability to survive (Coomes & Grubb, 2003). A parallel study (not part of this thesis) showed that the initial size of seedlings (of Mesemb and non-Mesemb functional guilds) was positively correlated to their ability to survive through to the second growing season (R. Krüger & P.J. Carrick, *unpublished data*). In view of the importance of size in the survival of a seedling, the fact that box sheltered plots yielded larger seedlings than the unsheltered plots, indicates that the sheltered non-Mesemb seedlings were more likely to survive. Perhaps one of the reasons why there was no significant difference in seedling numbers between boxes and control plots was that self-thinning due to root competition occurred to the same extent in both treatments (in Experiment 2).

These results provide support for the hypothesis that the establishment of non-Mesemb seedlings is affected by non-resource factors. While there is no support for the nurse plant effect, the evidence suggests that where shelter is sufficient and root competition with adult plants is minimized, non-Mesemb seedlings grow much faster. This is likely to mean that they will ultimately be more successful at becoming adult plants where they are sheltered from non-resource factors such as wind, herbivory and trampling by animals.

Other studies in the Succulent Karoo concur with these findings. Elsewhere in the Sandveld, it was found that most seedlings have do not have variable survival between unsheltered micro-sites and those sheltered by non-Mesemb shrubs (de Villiers *et al.*, 2001a). While this study did not group seedlings according to functional guilds, almost all the perennial species that were recorded were non-Mesemb species. This is in agreement with the findings of in this chapter that the non-Mesemb shrubs do not facilitate establishment of non-Mesemb seedlings, probably due to the increased competition for soil resources since their roots occupy the same region in the soil profile. Other studies have confirmed that when competition is reduced, non-Mesemb seedling establishment is facilitated by micro-sites sheltered by shrubs. This occurs when the shrub is a Mesemb species since they have very shallow root systems. Yeaton & Esler (1990) found that seedlings of their 'woody shrub guild' (comparable to the non-Mesemb guild in this thesis) occurred far more frequently in micro-sites with shelter of some kind (Mesemb shrub skeletons, live Mesemb shrubs, rocks or mounds) than in unsheltered micro-sites. Another study found that seedlings of two non-Mesemb species (*Tripteris sinuatum* and *Hirpicium alienatum*) established beneath various Mesemb shrubs (Carrick, 2004). These findings concur with the findings in this chapter that non-Mesemb seedlings establish better in micro-sites that are sheltered than unsheltered micro-sites.

CONCLUSIONS

These results do not support the notion that nurse plants facilitate the establishment of either Mesemb or non-Mesemb seedlings in Namaqualand. Since only two potential 'nurse' species (one Mesemb and one non-Mesemb species) were tested, it is possible that there are other species nurse seedlings successfully. Furthermore, the two species were tested together, which may have masked any possible benefit by one of the species. It would have been more prudent to test the nursing potential of these functional types separately. Indeed, others have noted that Mesemb species may be better nurse plants since they have shallow root systems (Carrick, 2004; Yeaton & Esler, 1990).

The results also provide evidence that non-Mesemb seedling establishment is higher if sufficient shelter is provided. The artificial shelters do not compete with the seedlings for resources, so whether this evidence points towards the possibility of facilitation in natural vegetation is debatable. However, it is an exciting result for restoration purposes. The potential shown by the artificial shelters, in particular the cardboard boxes, to markedly

improve the rate of seedling establishment from sown seeds, means that restoration practitioners can improve the efficiency and reduce the cost of restoration endeavors.

Evidence for fine-scale processes that influence seedling ecology can help us to understand landscape patterns (Peters *et al.*, 2006) and metapopulation dynamics (Levin *et al.*, 2003). The evidence that seedlings of non-Mesemb species benefit from being sheltered can go some way in explaining the development of multi-species clumps in Namaqualand (Eccles *et al.*, 2001; Eccles *et al.*, 1999). This, combined with evidence that Mesemb seedlings can establish in unsheltered micro-sites, can explain the co-existence of these two functional guilds (Levin *et al.*, 2003; Tilman, 1994; Yeaton & Esler, 1990).

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THE EFFECTS OF NUTRIENTS AND WATER ON THE ESTABLISHMENT OF SEEDLINGS OF COMMON NAMAQUALAND SANDVELD SPECIES

ABSTRACT

In semi-arid regions, long-lived plants can form resource-rich patches by accumulating and retaining resources beneath their canopies. These patches may provide more favorable conditions for seedlings to establish in. I tested whether seedling establishment of two functional guilds, Mesemb and non-Mesemb species, is affected by increasing the available micro-site resources (nutrients and water) compared to untreated control plots. Seedlings of both guilds were cultivated in a greenhouse and transplanted into field plots where nutrients (N, P and K) were added to the soil at ecologically relevant quantities. In a further two experiments, seeds of species of both guilds were sown into plots. In the one, nutrients (suite of macro and micro nutrients) and a water-absorbing polymer gel were added as soil treatments to unsheltered plots. In the other experiment, the soil treatments were nutrients, gravel and kelp fragments and all the plots were sheltered.

Mesemb seedling establishment (survival and growth) was unaffected by nutrients in all three experiments. Increasing water availability by adding gel had no effect on survival of Mesemb seedlings, while kelp and gravel treatments had significantly negative effects on seedling survival. However, the kelp treatment yielded significantly taller Mesemb seedlings. Non-Mesemb seedling survival was significantly increased by nutrients in two experiments and also yielded significantly taller seedlings in one of them. Increasing water availability by adding gel or kelp had no significant effect on non-Mesemb survival, but adding gravel increased seedling survival significantly. The kelp treatment yielded significantly taller non-Mesemb seedlings in Year 1.

Mesemb seedlings are unaffected by soil resources, and may establish better in the low-resource open spaces between patches. Non-Mesemb seedlings benefit from additional soil resources, such as occur in patches in undisturbed vegetation, especially when the micro-site is also physically sheltered. The results support the notion that seed dispersal mechanisms and seedling ecology are linked, and can inform restoration practices.

INTRODUCTION

There is considerable overlap between two of the major ecological concepts that are widespread in semi-arid systems, namely patch dynamics and facilitation. Patch dynamics is the process whereby mobile resources (mainly associated with soil) are concentrated in patches below plant canopies, with a concomitant depletion of these resources in inter-patches between plants or clumps of plants (Aguiar & Sala, 1999). The resulting heterogeneous distribution of these resources, such as nutrients, organic matter and sometimes water, can impact seedling establishment (Guterman, 1993). The nurse effect, a subset of the more general facilitation between any two or more plants, occurs when seedling establishment is facilitated under 'nurse plants' (Niering *et al.*, 1963). The mechanisms by which this occurs vary from amelioration of non-resource environmental factors (such as wind, herbivory, trampling), to increasing the availability of resources in the soil (Callaway, 1995; Flores & Jurado, 2003; Maestre *et al.*, 2009). The overlap between the two concepts is apparent where seedling establishment is facilitated by nurse plants due to higher resource availability beneath their canopies, and these plant interactions affect population dynamics in semi-arid regions (Armas & Pugnaire, 2005) .

In this chapter I explore the effects of resource factors on the establishment (survival and growth) of seedlings of the dominant species in the semi-arid Namaqualand Sandveld bioregion (Figure 2.2) of the Succulent Karoo (Figure 2.1) in South Africa. More specifically, I investigated the effect of water and nutrient availability on seedling establishment, since these are potentially limiting resources to plants in semi-arid regions (Grubb, 1992). Two experiments consider these resources independently, while a third experiment tests the effects of water and nutrients as well as the interaction effects between them.

WATER AVAILABILITY IN PATCHES

Water is often concentrated under the canopies of adult plants in semi-arid regions. Rain drops that fall on the canopy trickle down towards the main stem, resulting in greater water input around the base of the plant (Mauchamp & Janeau, 1996; Whitford, 1999). This so-called 'stem-flow' usually results in a greater infiltration depth in patches than in inter-patches, especially during small rainfall events (Pugnaire & Luque, 2001; Tewskbury & Lloyd, 2001) as occur frequently in Namaqualand (Carrick, 2001). Deeper infiltration results in slower evaporation rates since water is further away from the top layer of soil from where water evaporates readily (Poesen & Lavee, 1994). Fog or mist is often associated with many desert regions that are geographically close to the ocean, due to large fluctuations in temperatures and humidity, and is a common feature in Namaqualand (Desmet, 2007; Desmet & Cowling, 1999a). This moisture in the air can condense on plant canopies (Babu & Went, 1978) and drip onto the soil below or trickle down towards the main stem and enter the soil around the base of the plant. The higher humidity from transpiring leaves, shade (Franco & Nobel, 1989) and leaf litter mulch beneath canopies also results in less evaporation of water from the soil below plants, resulting in less water stress for the plants or seedlings establishing beneath them (Milton, 1995b; Went & Sheps, 1971). Despite all these potentially positive impacts of adult plants on soil moisture, there is the obvious fact that the adult plants themselves absorb water via their roots, thus competing with seedlings that attempt to establish beneath them (Callaway, 1995).

The net effect between facilitation mediated by additional water availability and competition for the same water, will determine whether it is beneficial for seedlings to establish in patches or under nurse plants (Callaway, 1995). In Mexico for example, field trials on cactus seedlings that establish under nurse plants report significant increases in growth rates where soil moisture was increased experimentally (Martínez-Berdeja & Valverde, 2008). In this chapter I explored the effect of increasing water availability on the establishment (survival and growth) of Mesemb and non-Mesemb seedlings, in order to determine whether this feature of patches benefits seedlings sufficiently to increase establishment. In light of the restoration goals of these studies and the lack of abundant fresh water in the region where the experiments were conducted, water availability was not increased by adding water to the soil. Rather, the water dynamics of the soil were altered in such a way to increase the length of time water would be available to seedlings

after a rain event, thereby mimicking more closely the conditions that are likely to benefit seedlings in patches in natural vegetation. The water holding capacity of the soil was increased firstly, by adding water-absorbing materials. A polymer gel that absorbs about 190 times its own mass in water, was used in one experiment, and dry kelp (*Laminaria digitata*) that absorbs about 6.7 times its own mass in water (P.J. Carrick, *unpublished data*), was used in another experiment. Both these materials, however, have the potential adverse effect of withholding water from plant roots, and thus having the opposite effect to which was intended. Secondly, water availability was increased by altering the soil properties in order to increase infiltration. Adding coarse impermeable rock material to the soil increases infiltration depth of water from a rain event and also decreases the potential evaporation of water from near the soil surface (Agassi & Levy, 1991; Poesen & Lavee, 1994; Poesen *et al.*, 1994).

NUTRIENT LEVELS IN PATCHES

There are a number of mechanisms that can account for nutrient accumulation in patches beneath plant canopies in semi-arid or arid regions (Aguiar & Sala, 1999). These processes can be summarised as follows: plant canopies 'trap' nutrient-rich windborne particles (Camargo-Ricalde & Dhillion, 2003; El-Bana *et al.*, 2003), they create 'focal points' for animal activity that increases nutrients input (Aguilera *et al.*, 1999; Dean *et al.*, 1999) and the roots of plants 'draw in' nutrients through their roots from the soil beyond their canopies and return it to the soil via decomposition of leaf litter (Zaady *et al.*, 1996). However, nutrients are also depleted simultaneously by other processes such as uptake by plant roots and leaching by rainwater (Johnson *et al.*, 2009). For nutrients to accumulate in patches in the soil beneath plants, the rate of accumulation has to be greater than the rate of depletion or loss of nutrients from the patches. Low rainfall areas are particularly well primed for low rates of nutrient loss from patches for a number of reasons. Firstly, the low rainfall is less likely to leach away the nutrients in patches. Secondly, while nutrients tend to accumulate all year round, plants can only take up nutrients below their canopies when water is available in the days after a rain event (Grubb, 1992). Thus, nutrient accumulation can occur all year round, while depletion can only occur in the rainy season (through nutrient uptake and possibly leaching).

There also needs to be sufficient time for nutrients to accumulate in patches beneath plants. Even if the rate of nutrient accumulation is greater than the rate of depletion, it is

likely that the disparity will be small. It therefore requires substantial time for nutrients to accumulate to levels that are significantly different to those in inter-patch soils. The lifespan of a plant is therefore related to its potential for creating nutrient patches. In Namaqualand, it has been shown that longer lived species accumulate greater nutrient levels relative to the surrounding soil than shorter lived species (Stock *et al.*, 1999). It follows from this that patches can be stable and long-lived features in the landscape. Furthermore, if patches are indeed more favourable for seedling establishment, they may outlive single plants and become quasi-permanent features in the landscape over time as they are successively colonised by new plants. While positive feedback mechanisms can promote conspecific recruitment (Catovsky & Bazzaz, 2000), it would be intriguing to investigate community-level mechanisms of this nature.

In the Succulent Karoo evidence for higher nutrient levels in the soils under shrubs in patches than in inter-patch soils have been found in Namaqualand (Carrick, 2001; Stock *et al.*, 1999) and elsewhere (Jones & Esler, 2004). Furthermore, preliminary analysis of soil samples from undisturbed vegetation in the region surrounding the study sites in this thesis indicated that the levels of the macronutrients nitrogen (N), phosphorus (P) and potassium (K) in patches (under shrubs) were approximately twice that of soils from inter-patches (R. Krüger & P.J. Carrick, *unpublished data*). In this chapter, I also investigated whether higher nutrient availability, affects seedling establishment (survival and growth) of common perennial species in the Namaqualand Sandveld bioregion. In order to do this, macronutrients (N, P and K) were added to the soil in plots at a rate similar to the difference between the concentrations in patches and inter-patches, in order to mimic the higher nutrient levels in patch micro-sites. Seedling survival and growth in these plots were compared to control plots with no additional nutrients.

METHODS

Three field experiments were set up to evaluate the hypotheses in the Namaqualand Sandveld bioregion (Figure 2.2) within the semi-arid Succulent Karoo Biome in South Africa (Figure 2.1). Two of the experiments were set up around Kleinsee and the other one around Hondeklipbaai. The experiments were set up on a variety of previously mined sites. Experiment 3 tested the effect of nutrients on the survival of seedlings of a Mesemb and a non-Mesemb species that were grown in a greenhouse and then planted in 0.5 m² plots in the field. Experiment 4 and 5 tested the effects of increasing the water and

nutrient availability on the establishment of these and other Mesemb and non-Mesemb seedlings in 0.25 m² plots. In Experiment 3 and 4, all the treatment plots were unsheltered treatments with additional soil resources, which thus imitated conditions in the unsheltered micro-sites between patches. In Experiment 5, all the treatment plots were sheltered, imitating the sheltered effect of micro-sites within patches. While the three experiments are not directly comparable due to different locations and starting times, the relative effects of the extra soil resources with and without shelters can be informative.

EXPERIMENT 3

EXPERIMENTAL DESIGN

Species

Seedlings of two common perennial species from the Namaqualand Sandveld bioregion (Figure 2.2) were grown in a greenhouse and transplanted into field sites in the winter of 2005, where the survival of individuals was monitored over a period of 154 weeks (3 growth seasons). The species were representative of two functional guilds in Namaqualand: a Mesemb, *Jordaaniella spongiosa* (Mesembryanthemaceae) and a non-Mesemb, *Zygophyllum morgsana* (Zygophyllaceae).

Seed collection & preparation

Seeds used in the experiment were obtained from natural populations on the West Coast of South Africa. Seeds were removed from their capsules (*J. spongiosa*) or dehiscent fruit (*Z. morgsana*). Seeds of both species were soaked in a half-strength (1 ml concentrate per 100 ml solution) germination stimulant (Super Smoke Plus – Cape Seed Primer[§], supplied by the South African National Biodiversity Institute at Kirstenbosch Botanical Gardens) for 24 hours directly prior to sowing. This is known to stimulate germination, even in non-fire prone species, and was shown to significantly increase germination in almost half the Mesemb species that were tested (Brown *et al.*, 2003).

[§] *Super Smoke Plus – Cape Seed Primer* is a commercial product developed by N.A.C. Brown at Kirstenbosch Botanical Gardens, and hence the exact contents are unknown. What is known, however, is that the product contains solutes of smoke generated by the incineration of fynbos plant material as well as gibberillic acid, which is known to enhance germination.

Sowing and growth in glasshouse

Seeds of the two species were sown into plastic punnets (200 mm x 250 mm x 150 mm), with a growth medium consisting of an equal mixture of acid-washed sand and field sand, and were placed in a glasshouse at the University of Cape Town. The punnets were evenly watered to saturation immediately after sowing. Thereafter they were watered to saturation every second day until the rate of seedlings emergence started slowing. The seedlings were then watered twice a week initially, and once a week for the two weeks prior to the first field transplanting in order to prepare and 'harden' the seedlings for field conditions.

Localities & sites

Plots were set up on previously mined sites with topsoil or overburden soil around the mining town of Kleinsee (Figure 2.3). Three topsoil sites (Site KT3, Site KT4 and Site KT5) were used, and for each of these an overburden site was located in the nearest area with overburden soil (Site KO4, Site KO5 and Site KO6; Table 2.3). The soil at the overburden site (Site KO6) was re-profiled by bulldozing subsequent to the start of experiment. This resulted in the loss of the experimental plots and this incomplete data set was therefore excluded from the analysis.

Field transplanting

At each site, two 0.5 m² plots were set up, one control plot and one nutrient addition plot (described below). In each plot, seedlings of the two species were transplanted in a non-random grid arrangement, so that each species had equal exposure to other inter- and intraspecific seedlings as well as to the edge of the plot, and could be identified during data collection. Between 10 and 20 *J. spongiosa* seedlings were transplanted into each plot, and between 8 and 10 *Z. morganiana* seedlings were transplanted into the same plots. More seedlings of *J. spongiosa* were planted because these seedlings are much smaller than those of *Z. morganiana*, and thus they were expected to have greater mortality due to 'transplant shock'.

Due to seedling mortality associated with the stress of transplanting glasshouse seedlings into the field, seedlings that had died after the 1st transplanting were replaced with new seedlings after 3 and 5 weeks of the 1st transplanting. The 1st field transplanting took place in the week of 15 August 2005. The 1st treatment application (W0) was done in the

week of 19 September (at the 3rd transplanting), which allowed most of the seedlings to acclimatize to field conditions prior to receiving the soil treatments. Plots into which seedlings were transplanted were watered prior to transplanting (5 L/0.5 m²) and after transplanting (5 L/0.5 m²), thus receiving a total of 10 L/0.5 m² which is approximately equivalent to a 20 mm rainfall event. Plots were protected from mammalian and avian herbivores by 25 mm chicken wire exclusion cages that covered the plots on the top and on the sides. In order to remove root competition from surrounding vegetation, the roots were severed with a spade to a depth of c.30 cm around the perimeter of each plot. This was done at the 1st planting, as well as at the each subsequent treatment application.

Treatments

At each site, the control plot received just water (10 L), while the nutrient addition plot received nutrients in solution (10 L). The macro-nutrients Nitrogen (in the form of ammonium nitrate, NH₄NO₃), Phosphorus (in the form of sodium dihydrogen orthophosphate dehydrate, NaH₂PO₄.2H₂O and potassium dihydrogen orthophosphate, KH₂PO₄) and Potassium (in the form of potassium dihydrogen orthophosphate, KH₂PO₄) were added in two applications 6 weeks apart at the start of each growing season (at W0 and W7 for Year 0, W46 and W52 for Year 1, and W92 and W98 for Year 2). Each application consisted of 2.5 g.m⁻² of each of the nutrients (N, P and K), resulting in a total of 5 g.m⁻² per growing season.

Monitoring, data collection and watering

Each individual seedling of both species was monitored and recorded as 'alive' or 'dead' at 0, 2, 4, 7, 10, 15, 21, 31, 46, 52, 62, 106 and 154 Weeks after the commencement of the experiment at W0. Each plot received 10L of water (equivalent to c.20 mm rainfall event) at each of the three plantings and two treatment applications (W0, W7) and 5 L (equivalent to a 10 mm rainfall event) at each monitoring time interval up to W15. In addition to these waterings, plots received 5 L each at W1, W3, W4, W5 and W8. Since seedlings took longer to establish than initially planned, the start of the experiment (W0) was later in the rainy season than anticipated, and thus the additional waterings compensated for the lack of rainfall going into the autumn and early summer months.

STATISTICAL ANALYSES AND GRAPHS

The survival data was analysed using Cox Proportional Hazards models (Crawley, 2007) in the programme R (R Development Core Team, 2009), with the 'coxph' function in the 'Survival' package (Therneau & Lumley, 2009). The two species were analysed separately, and the factors (with levels), and their interaction terms, incorporated into the maximal models were as follows:

- Treatment (nutrients and control) and
- Site (Site KT5, Site KT3, Site KT4, Site KO4 and KO5).

Model simplification was not necessary for either of the species, and hence the results from the maximal models are presented. The coefficient (model estimate) for each term was back transformed to calculate the magnitude of the effect (factor), by

$$factor = e^{\wedge}(coefficient)$$

where e is the base of the natural log, and was then converted to percentage. The 95% Confidence Interval range (95%CI range), which is a measure of confidence in the estimated effect, was calculated by

$$95\% CI_{lower} = e^{\wedge}(coefficient - 2 * Standard Error)$$

$$95\% CI_{upper} = e^{\wedge}(coefficient + 2 * Standard Error)$$

The data was graphed by plotting the proportion of seedlings that were alive ("Survivorship") for each treatment at each site with time (number of weeks since the start of the experiment). The standard error bars generated by the model were calculated using the variance for each treatment and time period at all the sites.

EXPERIMENT 4

EXPERIMENTAL DESIGN

Seeds of 8 Mesemb species, and 8 non-Mesemb species (Table 4.1) were sown into plots on four topsoil sites (Site KT1, Site KT2, Site KT3 and Site KT4) around Kleinsee that had been mined previously (Figure 2.3; Table 2.3). Seeds produced in the preceding winter or spring were collected from natural populations between the towns of Kleinsee and Hondeklipbaai (Figure 2.2)

Table 4.1 The species and number of seeds sown into each plot for Experiments 4 and 5. The family, primary seed dispersal mechanism and growth form of each species is included.

Family	Species	Number of seeds per plot		Primary dispersal mechanism	Growth form
		Ex 4	Exp 5		
Mesembrythemaceae	<i>Amphibolia laevis</i>	27		water	prostrate
	<i>Amphibolia rupis-arcuatae</i>	264	138	water	upright
	<i>Cephalophyllum spissum</i>		124	water	prostrate
	<i>Conicosia pugioniformis</i>	19		water	upright
	<i>Drosanthemum hispidum</i>	208	59	water	prostrate
	<i>Jordaaniella spongiosa</i>	124	138	water	prostrate
	<i>Psilocaulon spp</i>		15	water	prostrate
	<i>Ruschia extensa</i>		106	water	upright
	<i>Ruschia versicolor</i>	26	138	water	prostrate
	<i>Ruschia subpaniculata</i>	196	60	water	upright
	<i>Stoebaria utilis</i>	38		water	upright
	<i>Stoeberia beetzii</i>		138	water	upright
Mesemb sub-total		902	916		
Aizoaceae	<i>Tetragonia fruticosa</i>	64	78	wind	upright
Asteraceae	<i>Didelta carnosus carnosus</i>		17	wind	upright
	<i>Othonna cylindrica</i>		238	wind	upright
	<i>Pteronia paniculata</i>		85	wind	upright
	<i>Pteronia glabrata</i>	9		wind	upright
	<i>Pteronia incana</i>	11	85	wind	upright
	<i>Pteronia onobromoides</i>	91	37	wind	upright
Chenopodiaceae	<i>Atriplex semibaccata</i>	216	82	bird	prostrate
	<i>Atriplex vestita</i>		87	wind	upright
	<i>Manoclamys albicans</i>	107	123	bird	upright
Fabaceae	<i>Lebeckia sericea</i>	83		explosively dehiscent	upright
Molluginaceae	<i>Pharnaceum sp</i>		85	passive	upright
Zygophyllaceae	<i>Zygophyllum morgsana</i>	44	84	wind	upright
Non-Mesemb sub-total		625	1001		
All seeds Total		1527	1917		

Twenty replicate plots of each of the following treatments were set out on each site: control (C), gel (Ge), nutrients (N) and gel*nutrients (Ge*N). The same methods as those described in Experiment 1 (Chapter 3) were followed, however, the soil additives were the treatments, and no physical shelters were used. The polymer gel was added at a rate of 35 g.m², and the nutrients were added at a rate of 9.9 g.m² of nitrogen, 4.9 g.m² of Phosphorus and 6.4 g.m² of potassium.

STATISTICAL ANALYSES

The Mesemb and non-Mesemb data was analysed separately, and three time periods (Weeks 13, 67 and 115) were used, corresponding to the same month / season (September / spring) in each year (Year 0, Year 1 and Year 2) of the experiment. Data was analysed using Generalized Linear Models (GLMs) in the programme R (R Development Core Team, 2009), with the 'glm' function in the 'base' package, as described in Experiment 1 (Chapter 3). The following factors (and levels) were fitted to the response variable (counts):

- Treatment (control, gel, nutrients and nutrients*gel),
- Year (0, 1 and 2) and
- Site (KT1, KT2, KT3 and KT4).

The 'treatment' factor was crossed with the 'year' factor, as the effects of the treatments over time were of interest to the study. All factors were included as fixed factors, for the same reasons described in Experiment 1, and the same model selection process was followed. The estimated effect (%) and 95% CI range were calculated as per Experiment 1.

EXPERIMENT 5

EXPERIMENTAL DESIGN

Seeds of 9 Mesemb species and 11 non-Mesemb species (Table 4.1) were sown into plots on 8 sites around Hondeklipbaai that had previously been mined (Figure 2.4). Seeds produced in the preceding winter or spring were collected from natural populations between the towns of Kleinsee and Hondeklipbaai (Figure 2.2). Five of the sites were covered with topsoil (Site HT1, Site HT2, Site HT3, Site HT4 and Site HT5), while the other three had overburden soil without topsoil (Site HO1, Site HO2 and Site HO3). The ages of

the sites at the start of the experiment varied from 1 to 4 years (Table 2.3). All 8 sites had shade-cloth nets erected to act as windbreaks in order to reduce wind erosion of the soil.

Fifteen replicate plots of each of the following treatments were set out on each site: control, gravel, kelp and nutrients. All four treatments were sheltered with cardboard boxes (as described in Experiment 2, Chapter 3), with the methodology adjusted to prevent the boxes from collapsing inwards. The control treatment contained no soil additives, while gravel, kelp and nutrient treatments contained the relevant soil additives.

All the soil treatments were mixed evenly in the soil layer within the box (c 0.2 m). The gravel treatment consisted of 8 spades of small stones (c.5 mm – 20 mm diameter). The kelp treatment consisted of 6 cups (1800 ml) per plot of dried kelp (*Laminaria digitata*) that had been broken into small pieces (<10 mm) by a hammer mill. The nutrient treatment consisted of the same organic slow-release fertiliser described in Experiment 1, applied at the same rate of 700 g.m⁻³ (i.e. 35 g.plot⁻¹), which is equivalent to a rate of 9.9 g.m² of nitrogen, 4.9 g.m² of phosphorus and 6.4 g.m² of potassium.

The Mesemb and non-Mesemb seeds were sown in two separate layers as described in Experiment 2, where non-Mesemb seeds were covered by c.2 cm of soil and the Mesemb seeds were not covered with any soil, but just patted down into the soil. The plots were set out over a 2 week period during May 2007, and data collection was carried out as described in Experiment 2 (Chapter 3).

STATISTICAL ANALYSES

The response of Mesemb and non-Mesemb seedlings was analysed separately. Data from two time periods (Weeks 11 and 62) was used in the analysis, and these corresponded to the same month / season (July / Winter) in each year (Year 0 and 1) of the experiment. The data was analysed using GLMs, following similar procedures to those described for Experiment 1. The count and height data for both Mesemb and non-Mesemb seedlings had Poisson distributions. The following factors (and levels) were fitted to the response variable for the count data:

- Treatment (control, gravel, kelp and nutrients),
- Year (0 and 1) and
- Site (HT1, HT2, HT3, HT4, HT5, HO1, HO2, HO3),

with the Treatment*Year interactions being included in the analysis. The height data was only recorded for Year 1, so only the treatment and site factors were included for this analysis. All factors were included as fixed factors, for the same reasons described in Experiment 1, and the same model selection procedure was followed. The estimated effect (%) and 95% CI range were calculated as per Experiment 1.

RESULTS

EXPERIMENT 3

The survival curves of the Mesemb seedlings (*J. spongiosa*) were very different from those of the non-Mesemb seedlings (*Z. morganiana*). At 4 of the 5 Sites, most of the Mesemb seedlings had died by W31 (Figure 4.1.A-E), while the non-Mesemb seedlings survived much longer at 4 of the 5 Sites (Figure 4.1.F-J), with more than 30% of the seedlings still being alive at W31. Both Mesemb and non-Mesemb seedlings responded to the nutrient treatment with a lower rate of mortality compared to the control treatment, although the magnitude of the response differed between Mesemb seedlings and non-Mesemb seedlings and between sites.

MESEMB SEEDLINGS

There was a very steep drop in seedling survival at the beginning of the experiment, with most of the Mesemb seedlings dying by W31 of the experiment (Figure 4.1.A-E). The seedlings at Site KT4 (old topsoil) survived much longer than seedlings at any of the other sites, with more than 30% still being alive at W106. In the first few weeks (before W 15) of the experiment there was little difference between the control and nutrient treatment plots at all 5 Sites. At three of the four sites where most of the seedlings had died by W31, the seedlings in the nutrient treatment plots survived longer. Only at Site KT4 (old topsoil) was there a noticeable difference in survivorship between the Treatments, where at the end of the experiment (W154) c.65% of the seedlings in the nutrient treatment were still alive, compared to 0% in the control treatment.

The overall effect of the nutrient treatment was not significant ($z=-1.517$, $p=0.1292$; Table 4.2.A) in the model, which is to be expected given the small differences between the treatments at 4 of the 5 sites. Site KT4 was significantly different to the other sites ($z=-$

5.258, $p < 0.0001$), and there was a significantly, although rather weak, negative effect of nutrients at Site KT3 ($z = 2.028$, $p = 0.0425$).

NON-MESEMB SEEDLINGS

There was a steep decline in the number of seedlings in the first few weeks (up to about W21) at most of the sites, subsequent to which a far slower rate of mortality occurred until the end of the experiment (Figure 4.1.F-J). All the seedlings in the control plots had died by W21 at 3 of the 5 Sites, while at 4 of the 5 Sites there were still seedlings alive in the nutrient treatment plots at W106. At all 5 sites, the nutrient treatment plots had greater survivorship than the control treatment plots at all time periods from W15 onwards. Only 3 sites had any seedlings surviving by W154, with all of these in the nutrient treatment plots. The model indicated that there was an overall significant effect of the Nutrient treatment on seedlings survival ($z = -3.434$, $p = 0.0006$; Table 4.2.B), with 85% (56-95%) greater survivorship in the nutrient treatment plots than in the control treatment plots. The magnitude of the effect of nutrients was significantly greater on Site KO5 (overburden), with 90% (41-98%) greater survivorship in the nutrient treatment plots than the control plots at this Site ($z = -2.551$, $p = 0.0107$), compared to the other sites.

EXPERIMENT 4

In this experiment, the number of Mesemb seedlings which emerged in each plot 13 weeks after sowing (Figure 4.2.A-D) was much lower than the number of non-Mesemb seedlings.plot⁻¹ (Figure 4.2.E-F). The effect of year was consistent amongst sites for the non-Mesemb seedlings, where there were high seedling numbers in Year 0, after which the numbers dropped off sharply. There was no consistent effect of year on Mesemb seedlings amongst any of the sites.

MESEMB SEEDLINGS

Year & Treatment effects

There was no consistent pattern for the effect of year on the survival of the Mesemb seedlings. At Site KT3 there were many more seedlings.plot⁻¹ in Year 1 than in Year 0 (Figure 4.2.B), while at Site KT2 there were many more seedlings.plot⁻¹ in Year 0 than in Year 1 or Year 2 (Figure 4.2.D). The model does however estimate 40% (8-61%) fewer seedlings.plot⁻¹ in Year 2 than the other two time periods ($t = -2.359$, $p = 0.0185$; Table 4.3.A), regardless of site and treatment.

There were no consistent treatment effects on the number of seedlings.plot⁻¹ between years or sites for the Mesemb seedlings. This is reflected by the model, where neither the gel, nutrient, nor the interaction between the two treatments was significant.

Site effects

The Mesemb seedlings responded differently at each of the sites (Figure 4.2.A-D), which is also reflected in the model where the sites were significantly different to each other (Table 4.3.A). There was very little pattern between the years at Site KT1, although the gel*nutrient treatment had the most seedlings.plot⁻¹ at all three time periods. The patterns at Site KT3 were unique amongst the four sites, with very low seedling numbers in Year 0, followed by a large increase in number from Year 0 to Year 1 (>400% increase in all treatments except control), and then halving again between Year 2 and Year 3.

NON-MESEMB SEEDLINGS

Year & Treatment effects

In contrast to the Mesemb seedlings, there was a consistent pattern for the effect of year among all four sites (Figure 4.2.E-H). All four sites had the highest number of seedlings in Year 0, but there was a marked decrease in numbers from Year 0 to Year 1. There was a small further decrease in seedling numbers from Year 1 to Year 2. The year effects were significant in the model, with the model estimating that there would be an 83% (80-86%) decrease in the number of seedlings.plot⁻¹ from Year 0 to Year 1 ($t=-21.433$, $p<0.0001$; Table 4.3) and a 94% (92-95%) decrease from Year 0 to Year 2 ($t=-21.244$, $p<0.0001$), or a 13% decrease from Year 1 to Year 2.

The differences between the treatments were largest in Year 0, although there were few consistent patterns among sites. By Year 1 and Year 2, there were very few distinguishable differences between the Treatments at all the Sites. Neither the gel, nutrient, nor gel*nutrient terms were significant in the model (Table 4.3.B), and there were no interaction effects between any of the soil additives and time.

Site effects

The sites produced quite different number of seedlings.plot⁻¹, with Site KT1 producing about 30 seedlings.plot⁻¹ in Year 0, and Site KT2 about 10 seedlings.plot⁻¹ in Year 0. By

Year 2, all sites had fewer than 5 seedlings.plot⁻¹, regardless of treatment. The model indicates that there were significant differences amongst the Sites (Table 4.3).

EXPERIMENT 5

In this experiment, there were far fewer Mesemb (Figure 4.3.A-H) than non-Mesemb (Figure 4.3.I-P) seedlings.plot⁻¹ at all the sites. In Year 0, the mean number of seedlings.plot⁻¹ for Mesemb seedlings at all sites and treatments ranged between 0 and 7 seedlings.plot⁻¹, while in Year 1 the means ranged from 0 to 13 seedlings.plot⁻¹. In Year 0, the mean number of non-Mesemb seedlings at all sites and treatments ranged from 15 to 53 seedlings.plot⁻¹, while in Year 1 the mean was reduced to between 10 and 30 seedlings.plot⁻¹. The number of Mesemb seedlings.plot⁻¹ increased from Year 0 to Year 1 at 25 of the 32 site / treatment combinations, while the number of non-Mesemb seedlings.plot⁻¹ decreased from Year 0 to Year 1 in all site / treatments combinations.

MESEMB SEEDLINGS

Year & Treatment effects

The general trend amongst all eight sites was for the number of seedlings.plot⁻¹ to either have increased from Year 0 to Year 1, or to have remained relatively similar (Figure 4.3.A-H). This pattern was most evident at the three old topsoil Sites (Site HT3, Site HT4 and HT5). The model indicates that year had a significant effect on seedling number.plot⁻¹ ($t=7.690$, $p<0.0001$; Table 4.3.C), indicating that there would be approximately 95% (64-132%) more seedlings.plot⁻¹ in Year 1 than in Year 0, regardless of site or treatment.

The gravel treatment had fewer seedlings.plot⁻¹ than the control treatment at 10 of the 16 year / site combinations (Figure 4.3.A-H). There was an overall significant negative effect of gravel in the model ($t=-3.311$, $p=0.0010$; Table 4.3.C), with the model estimating that there would be 32% (14-46%) fewer seedlings.plot⁻¹ in the gravel treatment plots than in the control treatment plots, regardless of year or site. There was no significant effect of gravel on the height of Mesemb seedlings (Table 4.3.D)

The kelp treatment also had fewer seedlings.plot⁻¹ than the control treatment plots at 15 of the 16 Year / Site combinations (Figure 4.3.A-H). The effect of kelp was significant in the model ($t=-6.319$, $p<0.0001$; Table 4.3.C), estimating that there would be 57% (44-67%) fewer seedlings.plot⁻¹ in the kelp treatment than in the control treatment. At 6

of the 8 sites, the kelp treatment plots had taller seedlings than any of the other treatments in Year 1 (Figure 4.4.A). The exceptions to this were the new topsoil site (Site HT1; Control plots had the tallest seedlings) and the old topsoil site (Site HT4; gravel plots had the tallest seedlings). The model indicates that kelp had a significant effect on the heights of seedlings ($t=5.907$, $p<0.0001$; Table 4.3.D), estimating that seedlings in the kelp treatment plots would be 112% (65-174%) taller than those in the control plots.

There was no consistent (Figure 4.3.A-H) or significant (Table 4.3.C) effect of the nutrient treatment on the number of seedlings.plot⁻¹. Seedlings in the nutrient plots were taller than those in the control plots on the three overburden Sites (Site HO1, Site HO2 and Site HO3), while there was little difference between these treatments on the topsoil sites (new and old).

Site effects

The three old topsoil sites displayed the greatest increase in the number of seedlings.plot⁻¹ from Year 0 to Year 1 of all the sites (Figure 4.3.C, D and E). At these three sites, the nutrient treatment had more seedlings.plot⁻¹ than the Control plots, most notably in Year 1.

NON-MESEMB SEEDLINGS

Year & Treatment effects

There was a marked decrease in non-Mesemb seedling numbers between Year 0 and Year 1 for most of the treatments and sites (Figure 4.3.I-P), but in contrast with Experiment 4, where there was more than a 70% decline at all sites, most of the sites and treatments in Experiment 5 showed less than 50% decline in seedling numbers. The model indicated that there was a significant effect of year ($t=-16.712$, $p<0.0001$; Table 4.3.E), estimating that there would be 46% (42-50%) fewer seedlings.plot⁻¹ in Year 1 than in Year 0, regardless of site or treatment.

The gravel treatment had more seedlings.plot⁻¹ at 13 of the 16 site / year combinations (Figure 4.3.I-P). The effect of gravel was significant in the model ($t=3.028$, $p=0.0025$; Table 4.3.E), which estimates that there would be 17% (5-29%) more seedlings.plot⁻¹ in the gravel treatment plots than in the control treatment plots, regardless of site or year.

There was however no significant effect of gravel on the height of seedlings (Table 4.3.F; Figure 4.4.B).

There was no consistent effect of kelp on the number of seedlings.plot⁻¹, and there were frequently many more or many fewer seedlings.plot⁻¹ in the Kelp treatment plots than in the control treatment plots (Figure 4.3.I-P). The Kelp treatment was not significant in the model (Table 4.3.E). The Kelp treatment plots had the tallest seedlings at 7 of the 8 sites in Year 1 (Figure 4.4.B). The model indicated that the effect of kelp ($t=8.209$, $p<0.0001$; Table 4.3.F) was significant on the heights of non-Mesemb seedlings, and that they would be 107% (74-148%) taller than those in the control treatment plots.

The nutrient treatment plots had more seedlings.plot⁻¹ than the control plots at 8 of the 16 site / year combinations (Figure 4.3.I-P), with these occurring most frequently on the old topsoil sites. The effect of nutrients was significant in the model ($t=2.357$, $p=0.0186$; Table 4.3.E), which estimates that there would be 13% (2-25%) more seedlings.plot⁻¹ in the Nutrient treatment plots than in the control treatment plots. The nutrient treatment plots had the second tallest seedlings at 7 of the 8 sites in Year 1 (Figure 4.4.B). The model indicated that the effect of nutrients ($t=2.725$, $p=0.0067$; Table 4.3.F) was significant on the heights of non-Mesemb seedlings, estimating that seedlings in the Nutrient treatment plots would be 30% (7-57%) taller than the control treatment plots.

Site effects

The seedling numbers were quite similar amongst the 8 sites, and there were no distinguishable patterns of treatment effect between the sites in terms of seedling numbers. The differences between the heights of seedlings in the kelp and nutrient plots (tall) and the gravel and control plots (short) were more marked on the old topsoil sites (Site HT3, Site HT4 and Site HT5) as well as the overburden sites (Site HO1, Site HO2 and Site HO3; Figure 4.4.B). The new topsoil site (Site HT1) had the tallest seedlings, regardless of treatment.

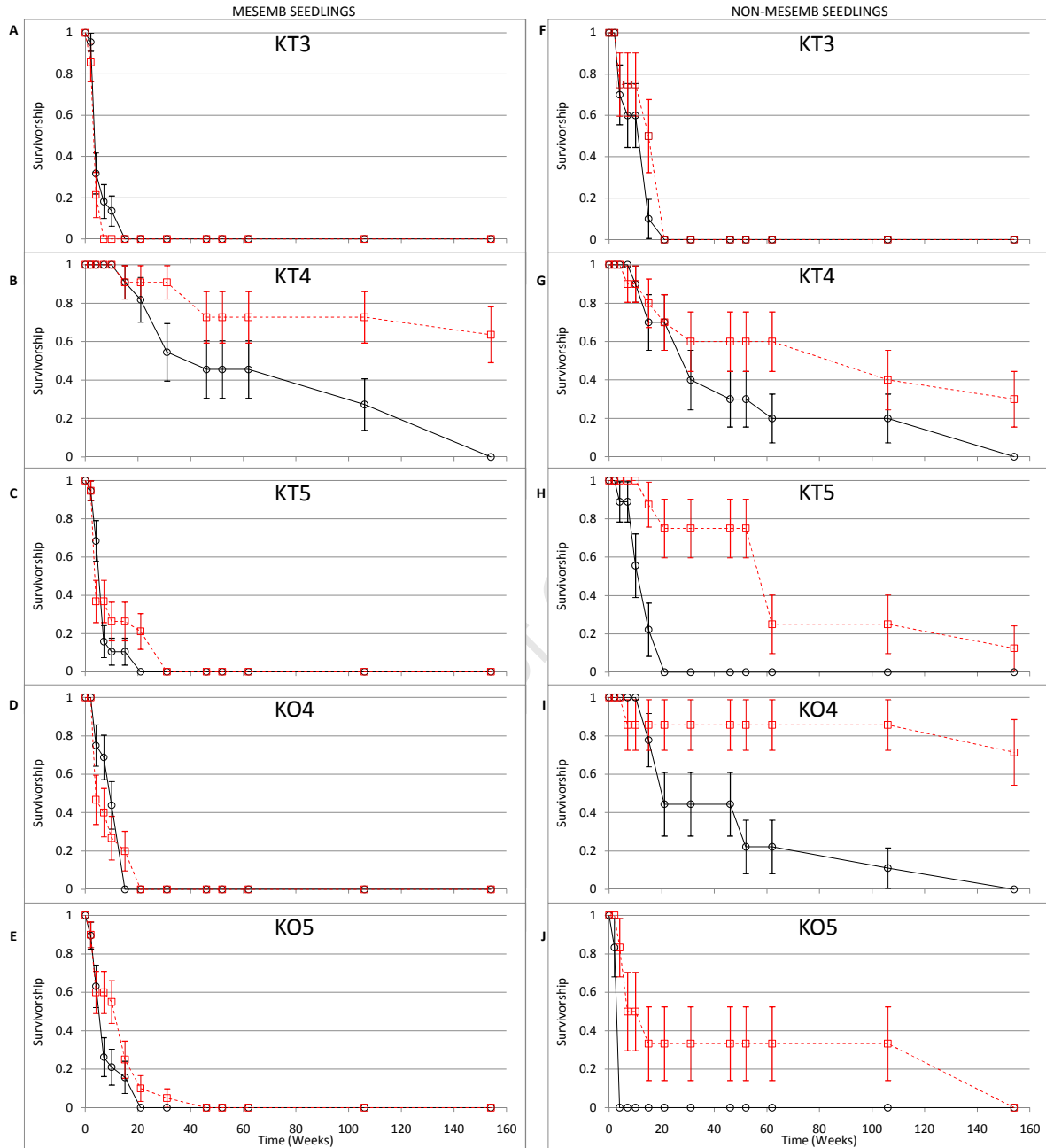


Figure 4.1 The proportion (with standard error bars) of surviving seedlings ('survivorship') in Experiment 3 at each time period (in weeks) in the Control (black circles, solid lines) and Nutrient (red squares, dashed lines) treatments at 5 Sites for Mesemb seedlings *Jordaaniella spongiosa* (A-E) and non-Mesemb seedlings *Zygophyllum morganiana* (F-J).

Table 4.2 Results from the analysis of Experiment 3, using the Cox Proportional Hazards models. The effect of nutrients (N) on the survival of Mesemb seedlings *Jordaaniella spongiosa* (A) and non-Mesemb seedlings *Zygophyllum morgsana* (B) on various Sites is tested. The estimated size effect and the corresponding 95% Confidence Interval is expressed in percentage (%). Significance is indicated by the following code: 0 < * < 0.001 < ** < 0.01 < * < 0.05.**

Plant group and number of observations	Term	Coefficient	Estimated size effect (%)	95% CI _{lower}	95% CI _{upper}	z-value	P-value	
A Mesemb Counts n=166	N	-0.52	-40	-69	16	-1.517	0.1292	
	KT3	0.37	45	-22	168	1.173	0.2406	
	KT4	-2.52	-92	-97	-79	-5.258	0.0000	***
	KO4	-0.32	-27	-63	42	-0.937	0.3490	
	KO5	-0.12	-12	-53	67	-0.382	0.7025	
	KT3*N	0.99	170	3	603	2.028	0.0425	*
	KT4*N	-0.53	-41	-85	135	-0.746	0.4559	
	KO4*N	0.64	90	-28	400	1.299	0.1938	
KO5*N	-0.12	-11	-64	120	-0.254	0.7994		
B Non-Mesemb Counts n=83	N	-1.89	-85	-95	-56	-3.434	0.0006	***
	KT3	0.24	27	-48	214	0.522	0.6019	
	KT4	-1.43	-76	-91	-37	-2.876	0.0040	**
	KO4	-1.50	-78	-92	-38	-2.895	0.0038	**
	KO5	2.43	1 032	218	3 932	3.745	0.0002	***
	KT3*N	1.32	276	-8	1 441	1.84	0.0657	.
	KT4*N	1.11	205	-27	1 172	1.53	0.1261	
	KO4*N	-0.08	-7	-86	499	-0.079	0.9372	
KO5*N	-2.30	-90	-98	-41	-2.551	0.0107	*	

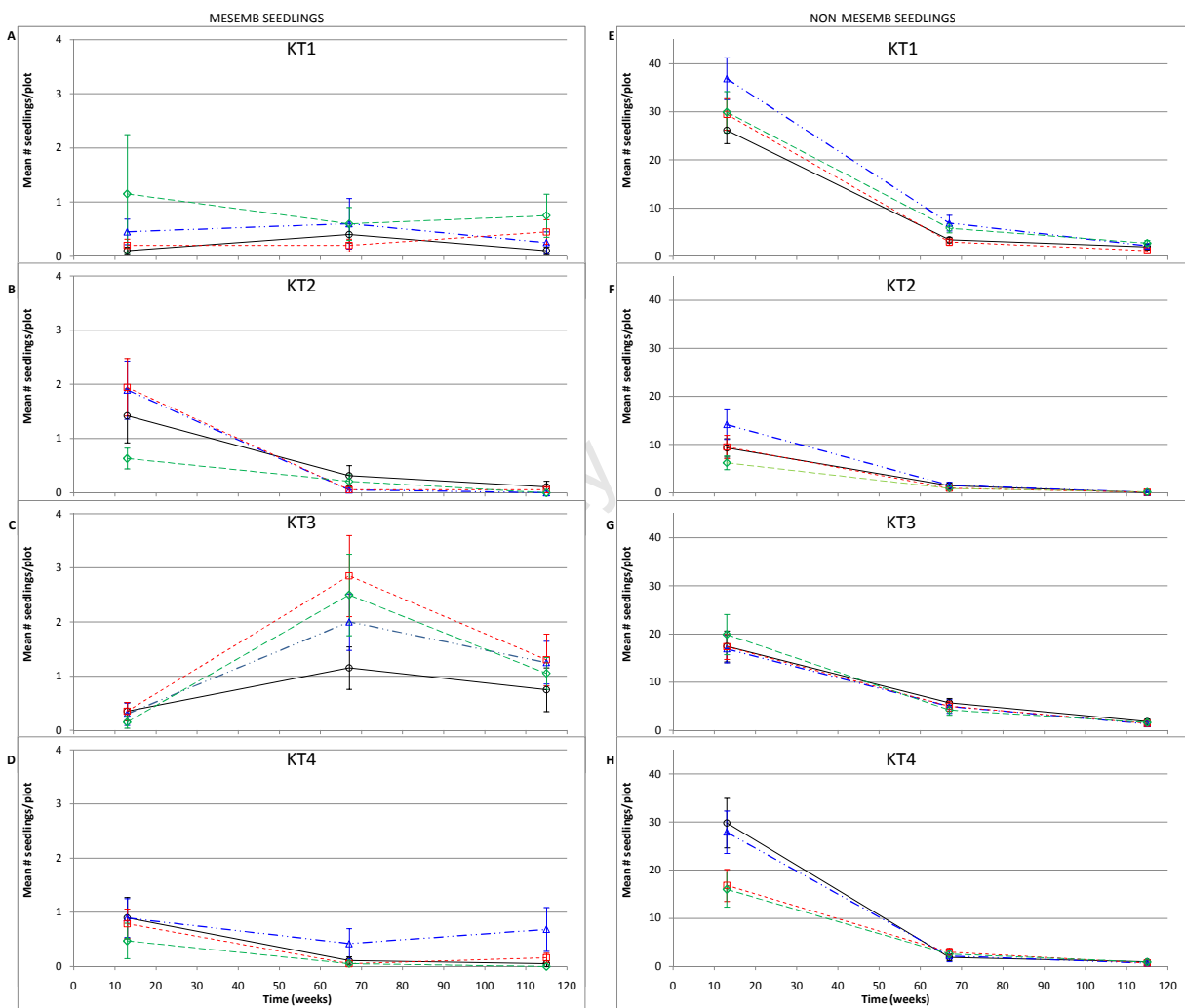


Figure 4.2 The mean number of seedlings.plot⁻¹ in Experiment 4 for the Control (black circle, solid line), Gel (blue triangle, dotted line), Nutrient (red square, short dashed line) and Gel-Nutrient (green diamond, long dashed line) treatments on the four Sites for Mesembs (A-D) and non-Mesembs (E-H). The time periods (in Weeks) for which data was collected corresponds to Year 0 for W13, Year 1 for W67 and Year 2 for W115.

Table 4.3 Results from the analysis of Experiment 4 and 5, using Generalized Linear Models. The effect of Treatments (gel = Ge, nutrients = N, gravel = Gr, kelp = K), Years and Sites on the number of seedlings (and heights of seedlings for Experiment 5, Year 1 only) are tested for Mesemb and non-Mesemb. The estimated size effect and the corresponding 95% Confidence Interval is expressed in percentage (%). Significance is indicated by the following code: 0 < * < 0.001 < ** < 0.01 < * < 0.05.**

Experiment, plant group, data type &	Term	Coefficient	Estimated size effect (%)	95% CI _{lower}	95% CI _{upper}	t value	Pr(> t)
A Ex4 Mesemb Counts n=936	(Intercept)	0.01				0.040	0.9680
	Ge	0.43	54	-6	151	1.741	0.0820 .
	N	0.39	47	-10	142	1.559	0.1192
	Ge*N	0.29	34	-19	122	1.153	0.2493
	Year 1	-0.00	-0	-32	45	-0.023	0.9817
	Year 2	-0.52	-40	-61	-8	-2.359	0.0185 *
	KT1	-0.98	-62	-76	-40	-4.224	0.0000 ***
	KT2	-0.74	-52	-69	-26	-3.405	0.0007 ***
B Ex4 Non-Mesemb Counts n=936	(Intercept)	2.95				37.869	< 2e-16 ***
	Ge	0.15	16	-1	36	1.881	0.0602 .
	N	0.07	7	-9	25	0.812	0.4172
	Ge*N	-0.09	-8	-22	8	-1.028	0.3043
	Year 1	-1.77	-83	-86	-80	-21.433	< 2e-16 ***
	Year 2	-2.81	-94	-95	-92	-21.244	< 2e-16 ***
	KT1	0.54	71	48	98	7.363	0.0000 ***
	KT2	-0.79	-55	-63	-44	-7.474	0.0000 ***
C Exp5 Mesemb Counts n=928	(Intercept)	0.67				3.990	0.0001 ***
	Gr	-0.38	-32	-46	-14	-3.311	0.0010 ***
	K	-0.84	-57	-67	-44	-6.319	0.0000 ***
	N	0.05	5	-15	29	0.454	0.6500
	Year 1	0.67	95	64	132	7.690	0.0000 ***
	HT1	0.05	5	-33	64	0.221	0.8255
	HT2	-0.67	-49	-69	-16	-2.671	0.0077 **
	HT3	0.97	163	86	270	5.624	0.0000 ***
	HT4	0.36	43	-2	110	1.894	0.0586 .
	HT5	0.89	143	71	244	5.104	0.0000 ***
	HO1	0.33	39	-5	104	1.720	0.0858 .
	HO2	0.90	146	74	248	5.201	0.0000 ***
D Exp5 Mesemb Heights n=286	(Intercept)	0.34				2.386	0.0177 *
	Gr	-0.04	-4	-27	26	-0.317	0.7517
	K	0.75	112	65	174	5.907	0.0000 ***
	N	0.13	14	-13	50	0.990	0.3229
	HT1	-0.48	-38	-62	2	-1.912	0.0570 .
	HT2	0.31	36	-8	101	1.561	0.1197
	HT3	-0.22	-19	-42	12	-1.323	0.1869
	HT4	-0.45	-36	-56	-6	-2.347	0.0196 *
	HT5	-0.11	-10	-36	25	-0.641	0.5220
	HO1	-0.19	-17	-43	20	-1.023	0.3070
	HO2	-0.15	-14	-38	20	-0.899	0.3696
	E Exp5 Non-Mesemb Counts n=928	(Intercept)	3.58				58.450
Gr		0.15	17	5	29	3.028	0.0025 **
K		0.08	8	-3	20	1.498	0.1345
N		0.12	13	2	25	2.357	0.0186 *
Year 1		-0.62	-46	-50	-42	-16.712	< 2e-16 ***
HT1		-0.19	-17	-29	-3	-2.419	0.0158 *
HT2		-0.01	-1	-13	14	-0.087	0.9308
HT3		-0.03	-3	-15	11	-0.428	0.6685
HT4		0.02	2	-11	16	0.256	0.7980
HT5		-0.26	-23	-33	-11	-3.581	0.0004 ***
HO1		0.10	11	-3	26	1.539	0.1243
HO2		-0.10	-10	-21	4	-1.466	0.1431
F Exp5 Non-Mesemb Heights n=464	(Intercept)	2.40				24.333	< 2e-16 ***
	Gr	-0.11	-11	-28	10	-1.075	0.2831
	K	0.73	107	74	148	8.209	0.0000 ***
	N	0.26	30	7	57	2.725	0.0067 **
	HT1	-0.27	-24	-40	-3	-2.228	0.0264 *
	HT2	-0.53	-41	-54	-25	-4.408	0.0000 ***
	HT3	-1.01	-64	-73	-52	-7.209	0.0000 ***
	HT4	-0.09	-9	-26	13	-0.887	0.3757
	HT5	-0.65	-48	-59	-33	-5.219	0.0000 ***
	HO1	-0.55	-42	-54	-26	-4.553	0.0000 ***
	HO2	-0.48	-38	-51	-21	-4.036	0.0001 ***

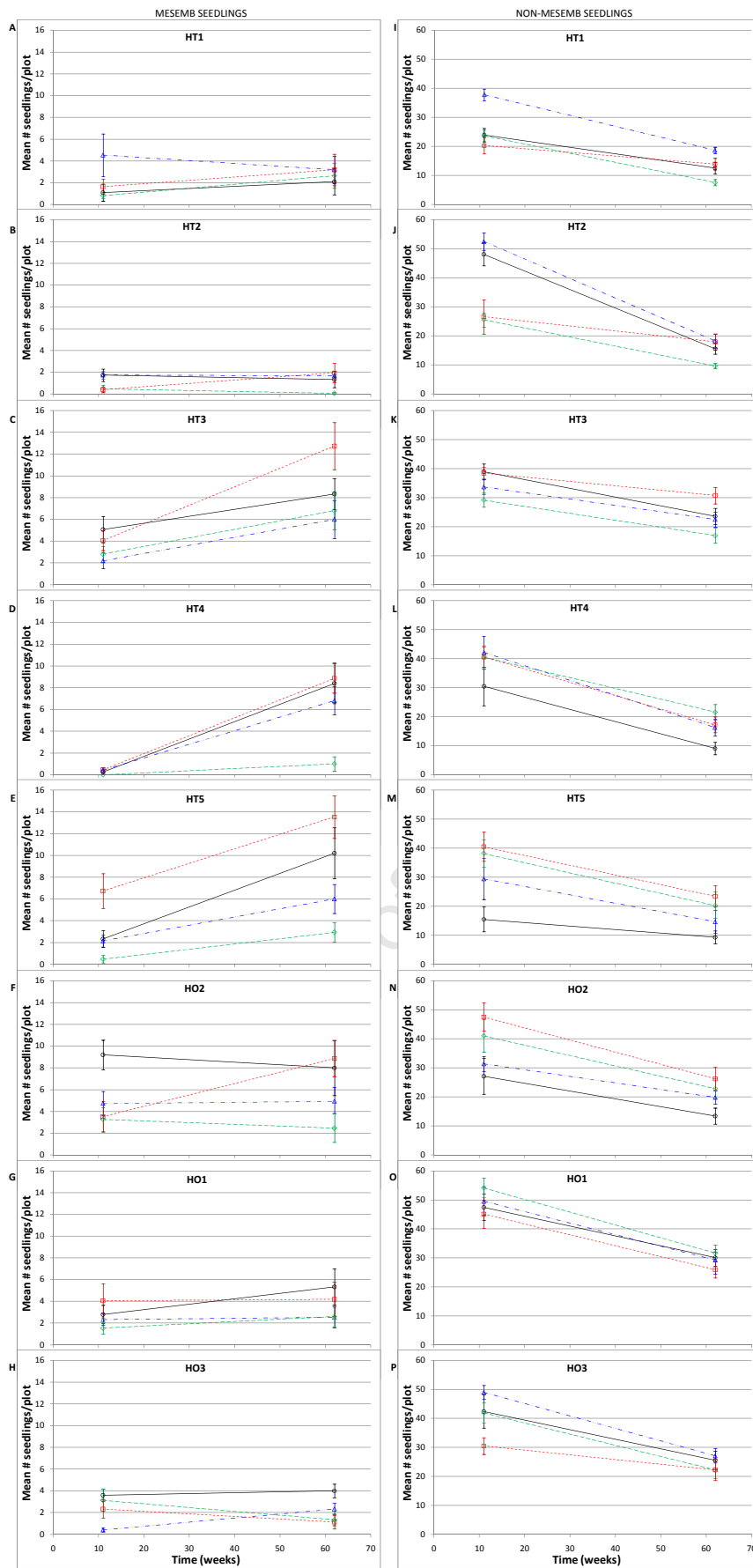


Figure 4.3 The mean number of seedlings.plot⁻¹ in Experiment 5 for the Control (black circle, solid line), Gravel (blue triangle, dotted line), Nutrient (red square, short dashed line) and Kelp (green diamond, long dashed line) treatments (with standard error whiskers) on the 8 Sites for Mesembs (A-H) and non-Mesembs (I-P). The time periods at which data was collected corresponds to Year 0 for W11 and Year 1 for W62.

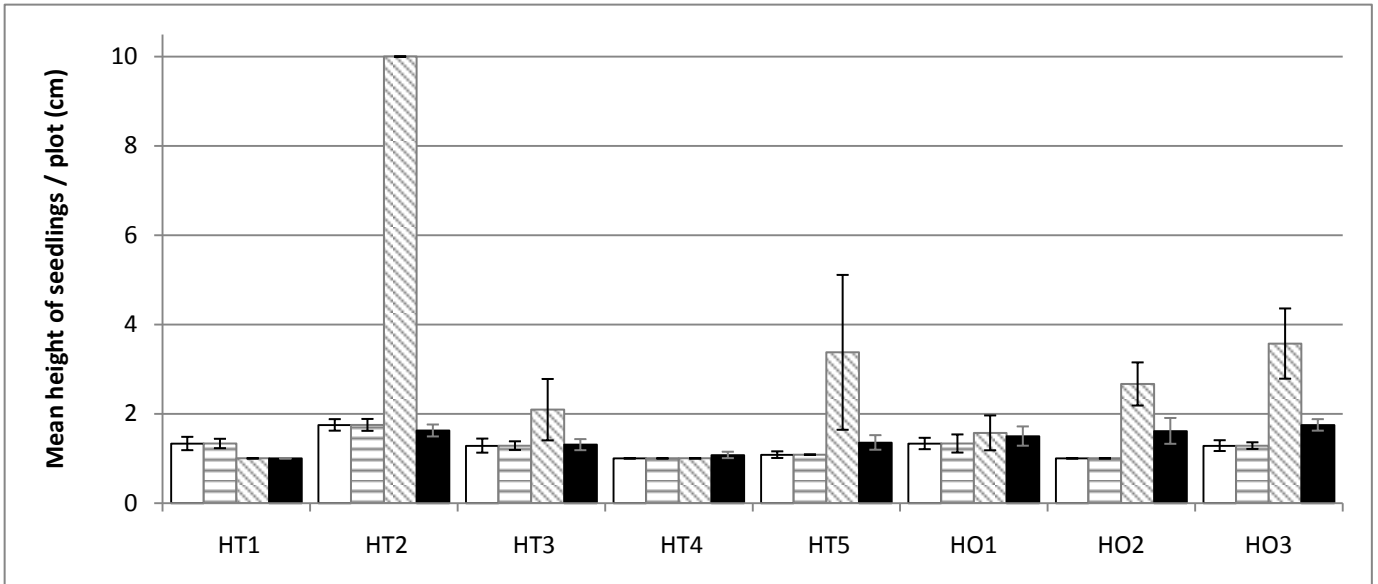
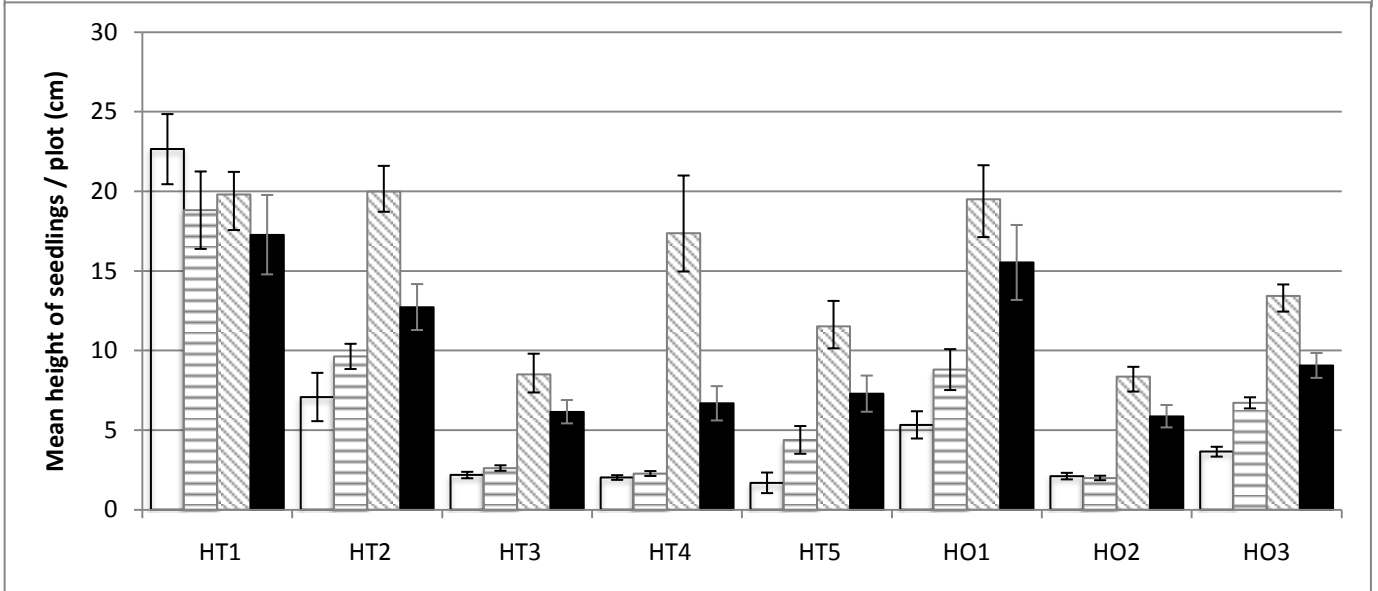
A**B**

Figure 4.4 The mean heights of Mesemb (A) and non-Mesemb (B) seedlings per plot on the 8 Sites in Year 1 of Experiment 5, in the Control (white), Gravel (horizontal hatch), Kelp (diagonal hatch) and Nutrient (black) treatments (with standard error bars).

DISCUSSION

FUNCTIONAL GUILDS AND ECOLOGICAL STRATEGIES

The survival and growth of Mesemb and non-Mesemb seedlings were markedly different. In Experiment 3, the survival rates of Mesemb seedlings were much poorer than that of non-Mesemb seedlings (Figure 4.1). The sharp decline in Mesemb seedling numbers at 4 of the 5 sites may be attributable to a single, relatively high rainfall event that occurred at that time. Approximately 40 mm of rain fell within 24 hours, which most likely washed out the meagerly-rooted Mesemb seedlings from the sandy soil. Indeed, while monitoring the seedling survival around this time, it was frequently noted that the Mesemb seedlings had not desiccated, but had completely disappeared. Further evidence for this is that Mesemb seedlings were occasionally found washed out in a different location to which they had been planted. It was an unfortunate event, which most likely influenced the non-significant result obtained for the effect of nutrients on the Mesemb seedlings in the model. However, it is indicative of how much more vulnerable Mesemb seedlings are than non-Mesemb seedlings to events such as these, due to their relatively diminutive size and rooting depth as seedlings.

In the two experiments where seeds were sown into the plots, the Mesemb seedling numbers were also far lower than that of non-Mesemb seedlings (Figure 4.2 and Figure 4.3), despite being sown in approximately similar quantities (Table 4.1). The low initial germination of the Mesemb seedlings seems to be a result of their bet-hedging strategy of germinating seeds over a number of years, since there was frequently an increase in Mesemb numbers after Year 0 in both these experiments. In Experiment 4, there was no effect of the soil treatments for Mesemb seedlings, and at 3 of the 4 sites they persisted well once they had emerged.

Despite their germination in greater numbers in Year 0, non-Mesemb seedlings were not as persistent as Mesemb seedlings. Pot experiments by several other also found that Mesemb seedlings are far more drought tolerant than non-Mesemb seedlings (Carrick, 2001; Esler & Phillips, 1994; Lechmere-Oertel & Cowling, 2001). Although there were no significant treatment effects among non-Mesemb seedlings in Experiment 4, it would appear that the lack of physical shelter was an overriding factor in the initial sharp decline in survival, precluding them from competing for the additional soil resources over time. In

Experiment 5, non-Mesemb seedling numbers decreased over time as competition between them resulted in self-thinning.

THE EFFECT OF GREATER WATER AVAILABILITY

The gel treatment had no effect on the survival of Mesemb seedlings where plots were unsheltered, where the plots were sheltered, there was a negative effect of both gravel and kelp treatments. For the non-Mesembs, there were also no effects of gel in Experiment 4, while in Experiment 5, kelp increased seedling establishment and survival while gravel had no effect. This indicates that in unsheltered micro-sites, greater water availability on its own is not sufficient to promote greater seedling establishment for either Mesemb or non-Mesemb seedlings. However, in sheltered micro-sites, non-Mesemb seedlings appeared to have benefited from increased water availability and exhibited lower mortality. However, the lower Mesemb seedling numbers in the gravel and kelp treatments in Experiment 5 may be directly attributable to the success of the non-Mesemb seedlings in these treatments, since the much larger size of non-Mesemb seedlings means that the Mesemb seedlings are shaded (and therefore grow more slowly), and are hard to see (and thus count during data collection).

Non-Mesemb seedling establishment appears to be positively affected by increased water availability in the soil, but only when seedlings are sheltered. In the absence of shelter, additional water availability is not sufficient to increase survival. While Mesemb seedlings also grow more quickly when water availability is increased, the non-Mesemb seedlings are able to benefit to a greater extent. However, results from Experiment 5 suggest that Mesemb seedlings are not killed by the larger, shading non-Mesemb seedlings. Mesemb seedling numbers generally increased over time regardless of treatment, which suggests that they can persist in the shade, and emerge when non-Mesemb seedlings die. It therefore appears as though Mesemb seedlings are shade tolerant as well as being tolerant to low levels of nutrients and water. This is contrary to the general perception that Mesemb species are sun loving (Esler, 1999), although shade tolerance and sun loving are not necessarily mutually exclusive characteristics. Mesemb seedlings can therefore survive where non-Mesemb seedlings flourish under high nutrient levels, suggesting that Mesemb seedlings are not exclusive inter-patch colonizers as is generally thought to be the case (Yeaton & Esler, 1990). Indications are that they can colonize

patches too, despite the superior non-Mesemb competitors there, but whether they can mature to reproductive age still needs to be demonstrated.

Another study in Namaqualand found no evidence that increased water availability increases seedling establishment of succulent or non-succulent perennial species (Simons & Allsopp, 2007), although studies across the Succulent Karoo indicate that succulent seedlings appear to be far more drought resistant than non-succulent seedlings (Hoffman *et al.*, 2009). Since seedlings were grouped according to slightly different functional guilds in these studies, the results cannot be compared directly to the results in this chapter. However, Milton (1995b) found that many more seedlings established in areas where plant litter had accumulated, which could be associated with greater water availability, due to shading effect on the soil. The majority of these seedlings were non-Mesemb species, since not many Mesemb species were recorded in this study (Milton, 1995b). While these findings are at odds with each other, the results from the experiments in this chapter indicated that non-Mesemb seedlings benefit from increased water availability, such as occurs in patches under shrubs, while there was no benefit for Mesemb seedlings. Thus the increased water availability in patches under shrubs can benefit seedlings that establish here, as has been shown in other semi-arid regions (Martínez-Berdeja & Valverde, 2008; Villarreal-Barajas & Martorell, 2009).

The different rooting layers that are utilized by Mesemb and non-Mesemb adults (Carrick, 2003) may also be applicable to Mesemb and non-Mesemb seedlings, thereby providing a mechanism for them to grow in close proximity without competing with each other for water (Cody, 1986; Yeaton & Cody, 1976). During the set-up phase of Experiment 3, where seedlings were grown in a greenhouse and then transplanted into field plots, it was noted that Mesemb seedlings had much smaller roots (by a factor of greater than 10) compared to non-Mesemb seedlings of a similar age (<10 mm for Mesemb seedlings and >100 mm for non-Mesemb seedlings at about 2 months since germination).

THE EFFECT OF GREATER NUTRIENT AVAILABILITY

The survival of Mesemb seedlings was not improved by increased nutrient availability in any of the three experiments, regardless of whether the seedlings were sheltered or not. In contrast, non-Mesemb seedlings had higher survival rates when additional nutrients were available in both unsheltered and sheltered micro-sites, as well as higher growth

rates in sheltered micro-sites. The fact that non-Mesemb seedlings in Experiment 4 did not respond to additional nutrients was surprising. I suspect that this result is due to a combination of lack of physical shelter, as well as a large rainfall gap in the middle of the rainy period, which may have caused the majority of the mortality in seedlings in all the treatments. This points toward a finely poised balance between different factors and where nutrients only have a positive effect when other factors such as shelter or sufficient water are present (Grubb, 1992). This means that in a low rainfall year, non-Mesemb seedlings can only establish in patches with high nutrients where the shrubs provide sufficient shelter. In high rainfall years, on the other hand, non-Mesemb seedlings could establish in patches with high nutrients even if the shrubs there do not provide good quality shelter.

Although Mesemb seedlings respond by growing larger in the presence of additional nutrients, non-Mesemb seedlings can utilize additional nutrients to greater effect by growing faster. In terms of survival, the Mesemb seedlings showed that they can persist in the absence of additional nutrients, even though growth was slower. It appears that Mesemb seedlings are unaffected by additional nutrients, whether in sheltered or open micro-sites. There is, therefore, minimal evidence that Mesemb seedlings are obligate inter-patch colonizers. Rather, it seems they can colonize both patches and inter-patches, but there is a greater survival in inter-patches since competition with non-Mesemb seedlings and adult plants is avoided here.

CONCLUSIONS

The results of these experiments do not support the hypothesis that resource factors influence the establishment of Mesemb seedlings in Namaqualand. The Mesemb seedlings were unaffected or negatively affected by the higher resources in the experimental plots in all cases except one. It must be added though that the experimental design, where the Mesemb and non-Mesemb seeds were sown in the same plots, could have contributed to this. The relative success of the non-Mesemb seedlings when additional soil resources were available could have directly contributed to the lack of success for the Mesemb seedlings, for example by shading them. The non-Mesemb seedlings responded to the additional soil resources by exhibiting faster growth rates and better survival rates than when they did not receive additional soil resources. Furthermore, the results provide evidence that non-Mesemb seedlings can be re-

established on degraded areas with greater success if they are provided with additional soil resources.

Mesemb species tend to disperse seeds to both patches and inter-patches, and appear able to establish equally successfully in either of these micro-sites. The seeds of non-Mesemb species on the other hand disperse predominantly to patch micro-sites, and this is reflected by their greater establishment success in micro-sites with higher soil resources. The evidence that seedlings of non-Mesemb species benefit from additional soil resources in patches provides a possible mechanism for the development of multi-species clumps in Namaqualand (Eccles *et al.*, 2001; Eccles *et al.*, 1999). The differing dispersal mechanisms and seedling ecological strategies of Mesemb and non-Mesemb species can explain the dynamic co-existence of these two functional guilds in undisturbed vegetation (Levin *et al.*, 2003; Tilman, 1994; Verdu *et al.*, 2009; Yeaton & Esler, 1990) as well as spatial patterns in these semi-arid landscapes (Pueyo *et al.*, 2008).

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LINKING THEORY AND PRACTICE – FIRST STEPS TOWARD RESTORING ECOSYSTEM FUNCTION IN A SEMI-DESERT

INTRODUCTION

Restoration ecology is a relatively young discipline. It emerged from the realization that in order to successfully restore ecosystems, a thorough understanding is required, not only of the individual species that constitute those ecosystems, but also of the processes that maintain and drive them. The most widely accepted definition of ecological restoration is “to repair ecosystems with respect to their health, integrity, and self-sustainability” (Society for Ecological Restoration International Science and Policy Working Guild, 2004). ‘Rehabilitation’ and ‘reclamation’ are frequently misused as synonyms for ecological restoration. In ecological restoration, the goal is to reproduce a system founded on the ecological principles that were present prior to degradation (Higgs, 2005), whereas rehabilitation and reclamation refer to a ‘stabilization’ or ‘improvement’ of the degraded area to an alternative state that does not necessarily represent the pre-existing one, in terms of its community composition or ecological function. To illustrate this difference one can use the example of degradation due to strip-mining. An open mine block could be rehabilitated or reclaimed to any one of the following alternative states: it could be refilled with overburden and capped with topsoil, and covered with exotic vegetation or one or two pioneer species, or if the water table seeps into the hole it could be used as a lake for recreational activities or for the production of abalone or mussels. While none of these states resembles the ecosystem that was present before the mining took place, they are more stable or useful than if no remediating intervention had taken place.

Traditionally, ecological restoration aimed, through a range of manipulative interventions, to return the historical abiotic conditions and disturbance regimes at a site and then to rely on successional change over time, to complete the recovery process (Suding *et al.*, 2004). The abiotic factors that can usually be manipulated most easily are edaphic factors such as the chemical and physical properties of the soil or the slope of the site. In the example of strip mining mentioned above, this would involve returning the soil to the

mine block in order to conform to the surrounding landscape, and capping it with a layer of topsoil as outlined in the section on The Mining Process (see Chapter 2). However, in many instances this type of intervention is not sufficient to promote succession and a complete return to the pre-disturbed state of the system (Carrick & Krüger, 2007). In Namaqualand, for example, due to the long delay between initial removal of the topsoil, and replacement of it on a filled mine hole, the quality of the topsoil has deteriorated significantly by the time it is used for restoration (le Roux & Odendaal, 1992; Mahood, 2003; Schmidt, 2002). This decline in topsoil quality is linked to the anoxic conditions that are present in large heaps of stored topsoil and which kills soil micro-organisms (Harris *et al.*, 1993; Strohmayer, 1999) that are essential for nutrient cycling. Furthermore, seeds in the topsoil often germinate or become unviable during the storage period and are thus lost to restoration efforts (Bellairs & Bell, 1993; Koch *et al.*, 1996). A further challenge in Namaqualand is that only about 50% of the perennial species in natural vegetation is represented in the soil seedbank (de Villiers *et al.*, 2001b), at least partly because most Mesemb species have canopy stored seeds (Esler, 1999) and very little dormancy. Thus, even if topsoil is only stored for a short amount of time, the species composition on a site which has been restored using this topsoil is unlikely to be representative of the pre-disturbance vegetation (de Villiers *et al.*, 2001b).

More recently, it has been recognized that strong feedback loops between biotic and abiotic elements can improve the effectiveness of restoration interventions (McIver & Starr, 2001; Pueyo *et al.*, 2009; Suding *et al.*, 2004). In semi-arid regions, like Namaqualand plants create resource rich patches (Carrick, 2001; Stock *et al.*, 1999) and provide shelter to each other from non-resource factors such as wind, trampling and herbivory (Eccles *et al.*, 2001). These feedback loops, which usually include key ecological processes, could be utilized to improve restoration success by setting the restoration area on a trajectory towards its historical state (Didham *et al.*, 2005; Suding *et al.*, 2004). The accuracy of this trajectory will be determined by how closely the abiotic conditions resemble the historical conditions, and by how closely the feedback loops represent the historical ecological processes that maintained the system. In a sense, restoration ecology is an acid-test for ecological understanding (Bradshaw, 1983). Some restoration studies have shown that initial intervention can set a system on a succession trajectory towards a historical state. For example in Kwa-Zulu Natal, South Africa, where a forest system has been degraded by strip mining, medium term results indicate that the system is slowly

progressing towards its previous state after an initial manipulation of the biotic environment (Lubke *et al.*, 1996). Similar examples of successful biotic intervention exist elsewhere in South Africa in the Cape Floristic Region (Holmes, 2001), and also in Australia (Bellairs & Bell, 1993), Asia (Gao *et al.*, 1998) and South America (Parrotta & Knowles, 2001).

The “health, integrity and self-sustainability” (Society for Ecological Restoration International Science and Policy Working Guild, 2004) of a restored ecosystem is implicitly targeted when restoration focuses on the initiation or recreation of key ecological processes. For a system to be ‘self-sustainable’, it implies that it should not require further human intervention, but should be maintained solely by natural, ecological processes. This can be achieved if key ecological processes are initiated during restoration are demonstrated to be self-perpetuating. A ‘healthy’ ecosystem is one that is resilient to disturbance, including natural disturbances, such as droughts. Although debated, a system’s resilience to disturbance has been linked to increased complexity of ecosystem processes, higher biological diversity (Steiner *et al.*, 2006) and greater functional diversity (Funk *et al.*, 2008; Suding & Hobbs, 2008). Therefore, restoration should aim to re-instate as many key ecosystem processes as possible, along with the biodiversity associated with such processes. The ‘integrity’ or wholeness of an ecosystem refers to how closely it resembles the historical system that was degraded.

Restoration interventions often focus on promoting establishment of vascular plants that are representative of the community that previously existed in that area, both in terms of biological and functional diversity. Ultimately, the goal is for other components of the ecosystem to return too, such as invertebrates and vertebrates. The assumption that underlies this focus is that a particular vegetation community will ultimately support and encourage the return of other ecosystem components. There are cases where this has been demonstrated, for example, for butterflies (Holl, 1995), ants (Andersen, 1993) and soil micro-organisms (Korb *et al.*, 2003). In fact, due to the mobility of invertebrates, they have often been touted as indicators of restoration success, with soil micro-organisms (Harris, 2003; Mummey *et al.*, 2002) and ants (Hoffmann & Andersen, 2003) being commonly used bioindicators. In the Namaqualand Sandveld bioregion, strong evidence exists that the invertebrate community recovers concomitantly with the vascular plant community, and has potential to be used as an indicator of restoration success (Lyons,

2009). Preliminary studies in Namaqualand indicate that the recovery of most other ecosystem components, such as small mammals (A.G. Ellis & P.J. Carrick, *unpublished data*), reptiles (A. Channing & P.J. Carrick, *unpublished data*), birds (W.R.J. Dean & P.J. Carrick, *unpublished data*), biological crusts (R. Krüger & P.J. Carrick, *unpublished data*) and soil nematodes (J. Rossouw & P.J. Carrick, *unpublished data*), are strongly correlated with the recovery of vascular plants on previously degraded sites.

In this chapter I explore the links between ecology and restoration of perennial vascular plants in Namaqualand. I do this by way of summarizing the main findings of this thesis and extrapolating applied principles for restoration, under a number of themes that are raised in this thesis. Future research ideas are suggested where relevant.

FACILITATING ECOLOGICAL RESTORATION – ‘NATURAL’ OR ‘ARTIFICIAL’ INTERVENTION?

In addition to merely ameliorating the abiotic and edaphic conditions, nurse plants have been proposed as a restoration intervention in semi-arid regions because they initiate positive feedback loops and promote ecological processes such as patch dynamics (Pueyo *et al.*, 2009). However, nurse plants are not a ubiquitous feature of semi-arid regions (Valladares & Gianoli, 2007) and might not, therefore, be a useful intervention in all cases. The results of the experiments presented in this thesis support this view and suggest that in Namaqualand, seedlings do not benefit from being sheltered by shrubs, even though there is strong evidence for facilitation among adult plants (Carrick, 2001; Eccles *et al.*, 1999). From Experiment 1 it appears that there is no overall benefit to either Mesemb or non-Mesemb seedlings of emerging and establishing below the canopies of the two adult plant species (one Mesemb and one non-Mesemb) used as nurse plants in this experiment. In fact, non-Mesemb seedlings are distinctly disadvantaged by these ‘nurse’ plants, probably due to competition for soil resources such as water and nutrients (Philips, 1981). In undisturbed systems in Namaqualand, the non-Mesemb seeds are however more likely to be dispersed to patches or individual adult plants, due to the large proportion of them being wind dispersed (Chapter 2). Thus one might expect that non-Mesemb seedlings establish better under nurse plants. However, despite the potential benefit provided by the addition of soil resources (nutrients, water and plant material), in order to lessen the effect of competition for soil resources in Experiment 1, the physical

shelter provided by the nurse plants was insufficient to significantly increase the establishment success of seedlings used in this study. However, this result should be considered in the light of the lack of overall site stability (i.e. high wind and mobile sand particles) due to the low plant cover on the experimental sites. It is possible that at sites with higher vegetation cover and greater site stability, one would have a better chance of observing the possible effects of nurse plants on the establishment of seedlings under adult shrubs. Furthermore, to gain insight into the general facilitative effects in Namaqualand, I propose that experiments in undisturbed vegetation be done on seedling establishment under adult shrubs. These studies would also prove useful for restoration ecology, as they may show that nurse plants can be effective in the context of overall landscape stability.

The combined use of Mesemb and non-Mesemb transplanted nurse plants seemed reasonable before the experiment, since many multi-species clumps in undisturbed vegetation contain species of both guilds. However, it is possible that non-Mesemb seedlings in particular would be more successful if the nurse plant was a Mesemb species (Yeaton & Esler, 1990). Mesemb species are shallow rooted and non-Mesemb seeds are large and may provide enough resources for the seedling roots to grow beyond the Mesemb adult's roots (Carrick, 2001), thus avoiding competition for soil resources. Future experiments done in undisturbed vegetation could shed more light on this if Mesemb and non-Mesemb plants can be isolated in order to determine their nursing potential.

The results indicate, however, that nurse plants are not effective as a restoration intervention aimed at facilitating seedling establishment on areas where the degradation is so severe that it affects the soil stability at a landscape level. Schmidt (2002) found that more seedlings established under clumps of three nurse plants than under isolated nurse plants that were transplanted onto previously mined sites elsewhere in Namaqualand. Given that in natural vegetation plant clumps often consist of many individual plants (van Rooyen, 2001), it would be interesting to experiment with greater clump sizes for restoration purposes. However, in the south of Namaqualand, it was found that seedling densities were significantly higher in unsheltered micro-sites than under shrubs, but there was no significant difference in seedling survival between these two micro-sites (de Villiers *et al.*, 2001a). Thus it may be a moot point whether nurse plants should be used at all in a restoration context.

The higher Mesemb seedling numbers in the cardboard box shelters over time (when they do not collapse onto seedlings, such as in Experiment 2) indicates that when the confounding effect of competition for soil resources is negated, there is a definite incurred benefit to seedlings of being sheltered at a micro-site scale. Of course, a cardboard box and an adult shrub provide different types of shelter for seedlings with cardboard boxes providing greater shelter from wind, sand-blasting and sand-burial than adult shrubs. Non-Mesemb seedlings also benefited from being sheltered, as they grew taller than those that were not sheltered. As with the Mesemb seedlings, the shelter provided by the cardboard boxes most likely protected them from the frequent strong winds and the concomitant 'sand blasting' that occurs, especially in heavily disturbed areas with low vegetative cover. Unlike Mesemb seedlings, non-Mesemb seedlings are unlikely to be prone to burial by sand deposition, since they are inherently much larger than Mesemb seedlings, and their photosynthesizing leaves are located relatively high above the soil surface.

Although the use of artificial interventions to promote seedling establishment on severely degraded landscapes appears to be more effective than simply leaving an area to recover 'naturally' or on its own, there are a number of other issues to consider. While it might be true that the introduction of adult plants to degraded sites provides a perpetual seed source, as such plants flower and set seed every year, the potential downside is that adult plants have to be removed from somewhere else. In cases where active mining is still taking place, plants can be removed from areas that are about to be mined. However, in the case of historically degraded areas, adult shrubs have to be removed from natural vegetation, which is not ideal, and if not done in a controlled way, could interfere significantly with the population dynamics which exist within the natural vegetation.

The use of artificial shelters while attempting restoration has mostly been applied to seedlings of tree species (Conner *et al.*, 2000; Oliet *et al.*, 2005; Valkonen, 2008). In the semi-arid regions of Ethiopia, tree seedlings planted in erosion gullies survive better and grow taller when they are sheltered by dry reeds planted around them (Reubens *et al.*, 2009). In the Mediterranean, a study has shown that the use of tree-shelter plastic tubes is not beneficial for Juniper seedlings, mainly due to its effect of limiting access to resources in the semi-arid climate (Jimenez *et al.*, 2005). These tubes have a small

diameter (7.5 cm – 10.5 cm; www.tubex.com) that accommodates the seedling or sapling stem. The use of larger plastic tubes (50 cm diameter) in experiments in this thesis increased shrub seedling establishment (Chapter 3), and in fact were responsible for accumulating fine sand due to their shape. This fine sand may have contributed to the nutrient availability of the seedlings within the shelters. In the Succulent Karoo, other studies where seedlings were sheltered found that brush-packing, where branches of dead bushes or shrubs are packed over the seedlings, promotes shrub seedling establishment (Visser *et al.*, 2004).

KICK-STARTING RESOURCE RICH PATCHES

In undisturbed vegetation in semi-arid regions, individual or clumps of shrubs elevate resource richness in patches (Aguar & Sala, 1999) and also provide physical shelter to establishing seedlings (Brooker *et al.*, 2008). The experiments in Chapter 4 indicate that on degraded sites, additional soil resources benefit seedling establishment, but in most cases, only when the micro-site is sheltered sufficiently. Therefore, when attempting to re-establish patch dynamics in degraded landscapes, it is important to first provide sufficient overall site stability and then micro-site shelter, before attempting to increase seedling survival by adding soil resources. Since plants themselves are responsible for creating focal points for resource accumulation in semi-deserts (Dean *et al.*, 1999), it stands to reason that once they have been successfully established that they will naturally assist the return of patch dynamics by positive feedback loops (Pueyo *et al.*, 2009). Therefore, by providing additional soil resources in the form of water and nutrients for these establishing seedlings, the rate of seedling establishment can be increased and revegetation and patch dynamic processes achieved more rapidly.

The chief aim of a restoration practitioner should be to utilize existing ecological knowledge efficiently and effectively. It is therefore important to consider the relative impacts of soil resources on seedling establishment, in order to construct appropriate objectives for their use. The relationship between water and nutrient availability to plants is an interesting one. The effect of water can most easily be seen in terms of plant survival, while the effect of nutrients usually influences plant growth. However, nutrients cannot be extracted from the soil by plants in the absence of water (Grubb, 1977), thus water is a pre-requisite for, but does not guarantee, plant growth. Of course plants that receive an adequate water supply but no nutrients will also eventually die (see

Experiment 3, Chapter 4). For example, in Experiment 5 (where all the plots were sheltered), the increased water availability in the gravel treatment led to greater survival of non-Mesemb seedlings, but no difference in the growth of the seedlings. However, in the same experiment, additional nutrients increased both the survival and growth of non-Mesemb seedlings. It is possible that the additional nutrients allowed the seedling root systems to grow faster than those that did not receive additional nutrients, thereby allowing them to access water moisture deeper in the soil profile and thus also survive longer than seedlings without extra nutrients.

Limited water availability is an inherent challenge when attempting restoration in semi-arid regions due to the low rainfall in these regions (Ward, 2009). However, plants in these regions cope with the low rainfall by pooling the water resources in the soil below the patches, and preserving it through shading and plant litter mulches (Ward, 2009). The combined effect of greater infiltration of rainwater in patches and reduced evaporation (Whitford, 1999) leads to water effectively being available to plants for longer after a rain event. Greater restoration success can be achieved by emulating these processes, rather than by attempting to transform the semi-desert into a tropical rainforest temporarily (in terms of water supply at least). The main objective for increasing the availability of water for plants during restoration should not be to supply enough water for the plant to grow and flourish in the periods between rainfall events, but rather to allow them to survive through to the following rainfall event (Agassi & Levy, 1991; Poesen & Lavee, 1994). These experiments have shown that changing the soil properties slightly can have the desired effect on seedlings, and result in greater survival and therefore establishment.

Although the polymer gel yielded no significant results in Experiment 4, in this experiment not one of the micro-sites was sheltered. In Experiment 5, where all the micro-sites were sheltered, both gravel and kelp led to significantly different establishment success rates of seedlings. The addition of kelp led to larger Mesemb and non-Mesemb seedlings, while the addition of gravel led to greater survival of non-Mesemb seedlings. It may be worth doing further research with the polymer gel in sheltered micro-sites, since the polymer gel has many more times the water holding capacity than kelp. Additional trials are needed to determine the appropriate rate at which the gel needs to be applied. The fact that gravel increased survival of non-Mesemb seedlings significantly is an important finding, since gravel is in abundance at mining operations as it is a by-product of the

mining process. It is, therefore, readily available to be used for restoration. Furthermore, it solves the problem faced by many mining operators of having to dispose of the gravel in an environmentally friendly manner.

As with altering the water dynamics of the soil for restoration purposes, soil nutrient levels in semi-arid regions should be altered with caution. Namaqualand for example has relatively nutrient poor soils (Watkeys, 1999). An oversupply of nutrients can at best be a waste of finances, and at worst negatively impact the species that are targeted for establishment by promoting weed growth. Species that were used in the experiments in this thesis were not pioneer or annual species, since the goal was to target the species that do not re-establish soon after disturbance on their own. Excessive nutrients can lead to an over-abundance of pioneer and early succession species, to the detriment of later succession species that were targeted. It can also lead to extra-limital or exotic species from flourishing, which should obviously be avoided. Results from field studies provide general guidelines as to what levels of nutrients are beneficial for establishing seedlings. In Namaqualand the nutrient (N, P, K) levels in patches are approximately double those which exist in inter-patches (P.J Carrick & R. Krüger, *unpublished data*). Therefore, when applying nutrients in the context of restoration, this guideline should be followed. In horticultural or agricultural contexts, nutrients are applied at far greater concentrations, and this often motivates the use of greater nutrient levels in restoration. However, the evidence from these experiments shows that the addition of ecologically relevant levels of nutrients is beneficial to the seedlings that are targeted for establishment (Chapter 4). Thus, it is both efficient in terms of cost and effective in terms of restoration success.

THE ECOLOGICAL RELEVANCE OF PHYSIOLOGICAL TRAITS

Throughout this thesis species have been grouped into two functional guilds, i.e. Mesemb species and non-Mesemb species (see Chapter 2). The vastly different response of these two groups to the experimental treatments has validated their use. For all experiments where seeds were sown, Mesemb species yielded (approximately 10 times) fewer seedlings than non-Mesemb species. It also appears that Mesemb seeds have greater dormancy, and tend to not all germinate in the first year of sowing, but rather over a number of seasons. Non-Mesemb seeds in contrast tend to germinate more easily, with the majority germinating in the first year of sowing.

Germination trials that were carried out in the laboratory on seeds of these species, however, are not wholly agreeable with these generalizations. These germination trials formed part of the preliminary investigations towards the experiments described in this thesis, where the primary purpose was to determine the germination rates of the species used, and to explore possible dormancy and dormancy breaking techniques for these species. However, when comparing germination rates of Mesemb and non-Mesemb seeds in the control treatments in one of the experiments (in a germination chamber with a 10 / 25 °C, 12 hr night / 12 hr day temperature and light regime), there was not a great difference between the range of germination rates between species within each functional guild. After 71 days, the germination of Mesemb species ranged from 0-75%, and that of non-Mesemb species ranged from 0-83% (R. Krüger & P.J. Carrick, *unpublished data*). There was also no significant difference (Student's t-test, $p=0.898$, $n=16$) between the mean germination rates of Mesemb species (34.9%) and non-Mesemb species (33.0%).

However, field and laboratory conditions yielded contrasting results. In laboratory growth chambers, seeds are germinated in petri-dishes and are wet the entire time, while similar water potentials are only experienced by seeds in the field in short pulses after rainfall events. The disparity between laboratory and field results highlights the pitfalls of using laboratory experiments to draw conclusions for field application. Had only the laboratory results been used to inform the number of seeds to be sown per m^2 , Mesemb and non-Mesemb seeds would have been sown in equal numbers, as was done in the experiments in this thesis. However, the field experiments indicate that Mesemb seeds should be sown in far greater numbers (c. 10 x greater) to achieve the same level of recruitment success. This result has been shared with restoration practitioners in the region who now sow Mesemb seeds at significantly higher densities than non-Mesemb seeds.

This pattern is reflected under natural conditions, where Mesemb plants produce many times the number of seeds than are produced by non-Mesemb plants. Mesemb plants produce hundreds of capsules, each with multiple seeds (about 10 seeds per capsule for species like *Amphibolia rupis-arcuatae* and up to several hundred seeds per capsule for species like *Jordaniella spongiosa*, pers. obs.). Non-Mesemb species produce seeds that are usually orders of magnitude lower in number than Mesemb species although they are usually larger in size. This represents a typical seed number-seedling survival (SNSS)

tradeoff between the two functional guilds. Since seeds size is negatively correlated with the number of seeds that a plant can produce (Coomes & Grubb, 2003), the more seeds it produces the smaller these seeds will be, and vice versa. However, seed size is also positively correlated with seedling survival, since larger seeds develop into larger seedlings which are potentially more resilient under low resource or adverse non-resource conditions (Coomes & Grubb, 2003). Thus, plants that produce a high number of small seeds are considered superior colonizers, while plants with fewer but larger seeds generally have a greater competitive ability (Coomes & Grubb, 2003).

Since Mesemb seedlings are unaffected by additional nutrient and water availability in micro-sites (Chapter 4), it would appear that Mesemb species have not evolved dispersal strategies which target a specific type of micro-site. Rather, the timing of dispersal is probably the most critical aspect of the Mesemb dispersal strategy. Since the capsules only open and release seeds when they are wet (Esler, 1999), this ensures that seeds are released when there is likely to be enough moisture for them to germinate. Also, most of the Mesemb species flower quite late in the spring, and the fruit bodies that become capsules take months to mature. In this manner, seed are prevented from being released during the odd rainfall event which might occur during the hot, dry summer months, when seedling establishment success is highly improbable.

In contrast, the dispersal mechanisms of non-Mesemb species appear to promote the dispersal of seeds to micro-sites that are optimal for their establishment, while the timing of dispersal appears to be of less importance. Physical shelter (Chapter 3) and additional soil resources (Chapter 4) enhance non-Mesemb seedling establishment, and both these factors are present in micro-sites under plants or in plant patches to which the majority of non-Mesemb seeds are dispersed. Wind is a frequent phenomenon in Namaqualand (Botha *et al.*, 2008), and thus seeds that are wind-dispersed can be dispersed all year round. This also ensures that seeds are dispersed to the micro-sites where they will germinate by the start of the winter season, in order to benefit from a full winter season's growth before the onset of the hot, dry summer. Non-Mesemb seedlings are also better equipped than Mesemb seedlings to cope with the negative effects of establishing in patches. Their larger seeds have more stored resources which promote faster and more extensive root growth. This, in turn, enables them to delay competition with the adult shrubs under which they establish by using the seed resources to grow through the web

of shallow roots of both Mesemb and non-Mesemb species. Furthermore, their greater growth rates, linked to the larger seed size and greater leaf area for photosynthesis, also allow them to grow through the adult canopy more quickly and thereby avoid being limited by light (Carrick, 2004).

Thus, the timing of germination appears a critical factor for the successful establishment of Mesemb species, while the dispersal to favorable micro-sites appears important for non-Mesemb species. Furthermore, although the results of the experiments in Chapter 3 indicate that non-Mesemb seedlings with physical protection on a micro-site scale establish with greater success, overall site stability is also crucial for Mesemb seedling establishment. Thus, on a severely degraded landscape (for example, as the result of strip-mining) where there is no or very little vegetation, any attempt to establish Mesemb species would be futile, even with landscape stabilizing interventions like shade cloth windbreaks. Non-Mesemb species, on the other hand, could be established with the erection of artificial physical shelters. Depending on the quality of soil, and whether topsoil had been re-applied to the site, the non-Mesemb species should help to stabilize the site within a few growing seasons. Once they have done so sufficiently, Mesemb seeds can be sown in the gaps between existing plants at the beginning of the rainy season, where they are more likely to establish successfully. Further evidence from Chapter 4 suggests that providing additional nutrients could help the slow growing Mesemb seedlings to grow faster and thus reach reproductive age more quickly.

WORKING WITH RATHER THAN AGAINST ECOLOGICAL PROCESSES

Restoration ecology is underpinned by the idea that working with ecological processes is better than working against them (Bradshaw, 1997) by trying to set up new processes. This idea has been explored at a micro-site level in this thesis, by attempting to re-establish ecological processes that are prevalent in semi-arid regions, such as patch dynamics and the facilitation of seedlings by adult plants. The results from this thesis indicate that these processes can be used successfully for restoration purposes, although there are often caveats that arise due to differences between functional guilds and overall stability of restoration sites.

Ecological dynamics are complex and it is often difficult to identify cause and effect. Because of this, different conclusions can arise from studies in different geographical

areas or when undertaken in the same area but in different years. In Namaqualand for example, some researchers have concluded that facilitation does not occur (de Villiers *et al.*, 2001a), while others, using a different approach, contend that it does occur (Eccles *et al.*, 2001; Schurr *et al.*, 2004). Carrick (2003) found that facilitation effects change along a browsing intensity gradient, while Schmidt (2002) has shown that it can differ in two consecutive years with very different rainfall amounts. Although Namaqualand has more predictable annual rainfall than sites in the adjacent Nama Karoo biome and most other semi-arid regions worldwide (Hoffman & Cowling, 1987), interannual differences can still lead to significant impacts on seed production and predation (Milton, 1995a), seed viability (R. Krüger & P.J. Carrick, *unpublished data*) and seedling survival (Schmidt, 2002). This indicates that micro-scale ecological processes are easily overridden by macro-scale processes, such as weather patterns.

Global weather patterns, however, also influence local weather systems. Global patterns that cycle over a number of years should be taken into account when attempting restoration. It has been proposed that several alternative equilibrium states can be reached by the vegetation of a particular area, depending on the type and extent of the restoration intervention (Didham *et al.*, 2005; Suding *et al.*, 2004). Where severe degradation has taken place, tinkering with micro-scale processes such as shelter, nutrient levels and water availability, may not be enough to successfully alter the successional trajectory of a given site, and it may be useful to harness larger scale processes to 'flip' such areas towards a trajectory that will result in a 'more desirable' alternative equilibrium state. It has been suggested that macro-scale processes associated with phenomena like *El Niño* can be used to trigger long-lasting effects in semi-arid regions (Holmgren & Scheffer, 2001). If small-scale processes, such as those manipulated in the experiments described in this study, can be used to significantly improve restoration success, then it's reasonable to expect macro-scale processes, associated with phenomena like *El Niño* to have similarly significant effects.

Using such macro-scale processes in local restoration efforts may seem implausible for several reasons because it is often difficult to predict the local expression of global processes such as *El Niño*. However, the advent and continual improvement of global climate models has made this a more accurate science, and in future it may become accurate enough to be utilized by restoration practitioners on a very local scale. For now,

it may still be worth investing more restoration effort in years where *El Niño* is likely to increase annual rainfall totals. Alternatively, and possibly more importantly, during the phase of *La Niña*, when below average rainfall is more likely, valuable resources may be squandered by restoration efforts.

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APPENDIX



Figure 5.1 A satellite image of the area surrounding Hondeklipbaai (located in the top left corner of the image). Large-scale degradation can be seen; old excavated prospecting trenches, excavated mine blocks and dumps of overburden soil (source: Google Earth 2010).



Figure 5.2 An aerial view of a mine block north of Kleinsee. The block has been excavated down to the bedrock, with the excavated soil placed adjacent to the block in steep-sided dumps (source: Google Earth 2010).

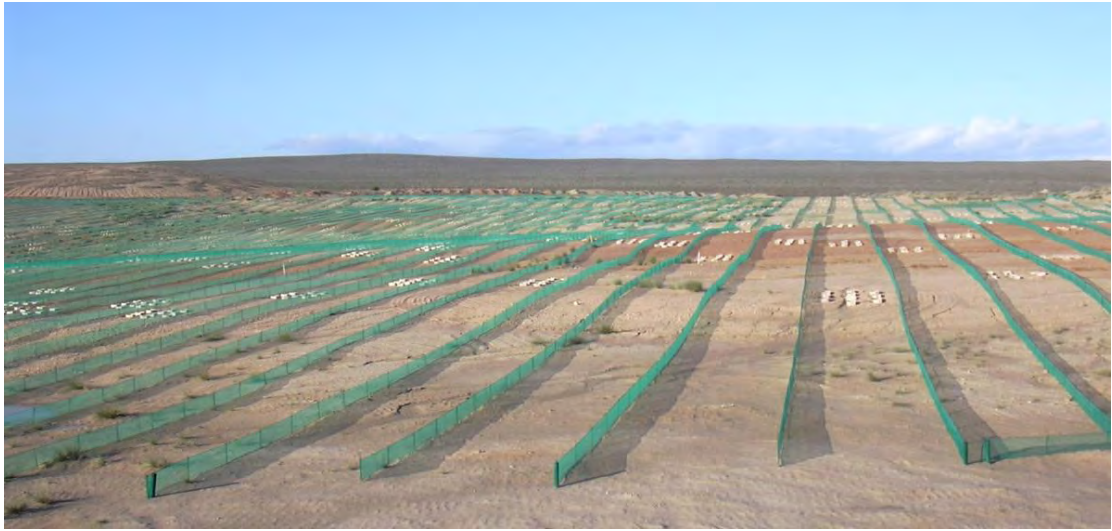


Figure 5.3 A previously mined area where the soil has been placed back in the mine block, and shade-cloth nets have been erected perpendicular to the prevailing winds in order to prevent soil erosion. Groups of plots with box shelters can be seen in between the rows of shade-cloth nets (source: Namaqualand Restoration Initiative).



Figure 5.4 A closer view of a group of plots, all sheltered by boxes and with different soil treatments.



Figure 5.5 Plots with different kinds of shelter (from left to right): plastic tube shelter, box shelter and transplanted adult shrub shelter (source: Namaqualand Restoration Initiative).