The Influence of Soil Properties on the Growth and Distribution of *Portulacaria afra* in Subtropical Thicket, South Africa

By

Carina Helene Becker

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Supervisor: Dr. C. Coetsee
Co-Supervisor: Prof. R.M. Cowling

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Abstract

Subtropical Thicket is the dominant vegetation biome in the Eastern Cape, and extends through to parts of the Western Cape. It is dominated by *Portulacaria afra* (spekboom), a woody succulent plant recognised for its importance as an ecosystem engineer and its carbon sequestration potential. Due to excessive grazing from domestic stock, spekboom has been completely removed from some areas. The Subtropical Thicket Restoration Programme (STRP) initiated a large scale restoration programme of planting spekboom cuttings in these degraded areas. Their efforts have been met with varying levels of success and improvement of the programme relies on continuous monitoring and scientific evaluation. I investigated the influence of selected soil properties on spekboom growth, mortality and landscape distribution, at both restoration sites and natural intact areas, and through experiments. Site or location was the most important factor influencing spekboom success at restoration plots, whereby sites in the eastern end of spekboom distribution perform better. Moving westwards slope orientation emerged as an important factor, whereby north facing slopes are preferred by spekboom. Although high levels of soil salinity (NaCl) restricted spekboom growth and affected its health, it could tolerate the levels it was exposed too. Soil pH, above 7, and phosphorous concentration, above 70 $mg.kg^{-1}$, were the only limiting factors to spekboom survival found in the restoration sites. This preference for acidic soils was mirrored in intact Thicket. However in general, soil is not a major factor influencing spekboom growth and distribution, and spekboom is tolerant of a wide range of soil conditions. Spekbooms constraint is most likely a function of climate, which varies greatly across the biome. This study answered some vital questions regarding the possible influence of soil in spekboom growth and distribution. It disapproved the theory that a catena effect may be responsible for the lack of spekboom growing in bottomland areas. The study also indicates and supports the versatility of spekboom as a plant for restoring degraded lands across a range of different geologies and soil types. To maximise spekboom survival rates, restoration efforts should be focussed towards the eastern end of its distribution and to avoid planting in soils with pH levels higher than 7.

Keywords: Spekboomveld, *Portulacaria afra*, spekboom, Thicket, soil properties, restoration, salinity, landscape

Chapter 1 - General Introduction

Introduction

Changes in land-use by humans over the past 150 years has led to a global decline and loss of both species diversity and ecosystem functioning (Gurevitch et al., 2006). The services that ecosystems provide to humans are not always obvious, but include protection of soils, retention of soil moisture, nutrient cycling and storing, and carbon (C) sequestration (Bainbridge, 2007). Poor management of natural ecosystems may cause conversion to a transformed state, with a deterioration in service provision and functioning (Lechmere-Oertel, 2003). The Thicket biome in South Africa has been subject to landscape transformation (Midgley, 1991, Stuart-Hill, 1992) and has suffered some of the heaviest levels of degradation of all the South African biomes (Vlok et al., 2003).

The Thicket biome is the dominant biome of the Eastern Cape Province of South Africa and is unique in the sense that its exceptionally high biomass of its associated Subtropical Thicket vegetation enables it to store large amounts of above- and below-ground C (in excess of 200 tons per hectare). This is on par with mesic forest ecosystems and quite extraordinary for a xeric ecosystem (Mills et al., 2005a, Mills and Fey, 2004a).

Historically, Thicket has supported a large array of indigenous herbivores (Kerley et al., 1995), but incorrect land management practices relating to browsing by domestic herbivores has resulted in large scale degradation (Hoffman and Everard, 1987). Degradation transforms Thicket to an open savanna-like state with lower productivity and carrying capacity (Hoffman and Cowling, 1990, Jackson and Hobbs, 2009). The loss of vegetation cover has severe implications for the soil. The diminished input of leaf litter reduces soil fertility, biomass of below- and above-ground C, water infiltration, soil moisture and a loss of topsoil. This increases soil crusting, sodium (Na) and pH levels (Lechmere-Oertel et al., 2005a, Lechmere-Oertel et al., 2008, Mills and Cowling, 2006, Mills and Fey, 2004b).

Research and planting trials by local farmers has shown that through creating fertile islands by planting the keystone Thicket species *Portulacaria afra* (also locally referred to as spekboom, and referred to as such hereafter), soil conditions can be improved. If this treatment is followed by years of rest it is possible to restore Thicket to a functioning state (Hall et al., 2003, Swart and Hobson, 1994, Todkill, 2001, Van der Vyver, 2011). This is a result of spekboom improving the quality of the soil and assisting in soil erosion control (Todkill, 2001). The plant also sequestrates C, which assists in offsetting global changes arising from elevated atmospheric carbon dioxide (CO_2) and could provide an income via C credits on international markets (Marais et al., 2009, Mills et al., 2010b, Mills and Cowling, 2006, Mills et al., 2007). The potential to earn C credits resulted in the South African government starting a planting programme, using spekboom cuttings, across a variety of landscapes in degraded Thicket. Survivorship success of these plantings has been quite varied (13-72 %)(Marais et al., 2009), and consequently research is being aimed at factors effecting survivorship (Mills et al., 2010b, Powell, 2009).

One theory is that an interaction between soil characteristics and the position in the landscape could influence the growth of spekboom (Mills et al., 2011). Although the plant can grow on a variety of geologies (Vlok et al., 2003), observations and studies from natural intact areas indicates that it generally prefers warm, north facing slopes, dominating crests of hills and decreasing with distance down slope (Cowling, 1984, Mills et al., 2011, Oakes, 1973). These findings have stimulated a host of questions by researchers regarding spekboom establishment across the biome. For instance, why does it grow on some south facing slopes (for example near Grahamstown) and not others (for example near Oudtshoorn)? What soil or environmental factors are responsible for spekboom's patchy distribution and the survival of cuttings? There could be a number of explanations for the distribution of spekboom, ranging from underlying rock geologies, soil types, nutrient content, soil depth, temperature (frost damage), drainage patterns, competition or interactions between these factors. As so much uncertainty regarding the distribution remains, further research is required to optimise survivorship and improve cost effectiveness of restoration programmes (Marais et al., 2009, Powell, 2009).

The Thicket Biome

Although the Thicket biome's history and classification has been a long and complicated one, the term 'Thicket biome' is fairly new and was proposed by Low and Rebelo (1996). Acocks (1975) considered it to be of Karoo origin, Rutherford and Westfall (1986) thought it to be connected to Savanna, but Midgley et al. (1997) linked it to forest, because it is not fire-prone and functionally quite similar. It has therefore been labeled with many names including Valley Bushveld (Acocks, 1975, Aucamp and Tainton, 1984), Subtropical Transitional Thicket (Cowling, 1984, Lubke et al., 1986), Subtropical Thicket (Midgley et al., 1997, Palmer, 1990, Vlok et al., 2003) and was even called the "missing biome" by Everard (1991). Tinley (1975) has been acknowledged as the first to introduce the concept of Subtropical Thicket as being a biome in its own right (Vlok et al., 2003) and biome status was recognized as such by Low and Rebelo (1996), who also included Acocks' Valley Bushveld in this concept (Vlok et al., 2003). Acocks (1975) termed it Valley Bushveld (in a number of forms), Noorsveld and Spekboomveld. Inland of Valley Bushveld is Spekboomveld (dominated by spekboom) and Noorsveld (dominated by *Euphorbia coerulescens*) (Kerley et al., 1995). Spekboomveld is generally confined to moderately deep, well-drained fertile soils, in hot, semi-arid valleys, between 500 – 1000 m above sea level (Kerley et al., 1995, Stuart-Hill, 1992, Vlok et al., 2003). In 2002 the Subtropical Thicket Ecosystem Planning Programme (STEP) made major strides in the understanding of Subtropical Thicket (Lloyd et al., 2002, Vlok et al., 2003), and in total 112 various Subtropical Thicket types were described and mapped. In revising the vegetation classification for South Africa, Mucina et al. (2006) created the term Albany Thicket biome and merged STEP's 112 vegetation types into 14 types. The terminology in this thesis will follow a combination of Vlok et al. (2003) Spekboom Thicket (Valley Thicket with high abundance of spekboom) and Spekboomveld (Arid Thicket with high abundance of spekboom); and Gamka Spekboom Thicket (where Arid Thicket mosaics with Succulent Karoo).

1. Vegetation

The vegetation of the Albany Thicket biome is generally centred on the coastal forelands of the Eastern Cape Province (covering 25 % of the province) and the most eastern part of the Western Cape. It is described as "a dense, impenetrable, near woody, semi-succulent and thorny vegetation type of an average height of 2-3 m" (Hoare et al., 2006), which is confined to areas receiving less than 850 mm rainfall annually (Lubke et al., 1986). The growth form diversity is high; *Aloe* and *Euphorbia* species emerge from the succulent shrub canopy which is dominated by *Portulacaria afra*, *Crassula ovata,* as well as members of the Celastraceae, Ebenaceae and Anacardiaceae families (Vlok et al., 2003). The canopy component consists of long-lived trees such as *Euclea undulata, Gymnosporia* spp*., Pappea capensis, Putterlickia pyracantha, Searsia* spp. and *Schotia afra* (Midgley and Cowling, 1993, Sigwela et al., 2009, Vlok et al., 2003). The trees are often accompanied by climbers and woody lianas (Cowling, 1984). The understorey is comprised of shade-tolerant herbs, mostly succulents (which contribute in excess 20 – 30 % cover) with sparse C_3 and C_4 grass cover. Plant endemism is 20 %, most of which are succulent species (Vlok et al., 2003).

Thicket is able to tolerate the xeric conditions due to its ability to modify the landscape (Aucamp and Tainton, 1984), whereby the closed canopy structure of shrubs and low trees ameliorates the extreme conditions of the environment (Vlok et al., 2003), by providing a moister, cooler and nutrient-rich microclimate beneath the canopy (Lechmere-Oertel, 2003). In this way it is able to maintain a high level of productivity throughout the year, when compared to other vegetation types with similar climatic conditions.

Thicket occurs as a solid form, covering large areas, and as a mosaic form with other adjacent vegetation types such as Fynbos, Karoo, Forest and Savanna. Different major Thicket types are associated with a rainfall gradient from xeric (Arid Thicket) via Valley Thicket, to mesic (Mesic Thicket) (Vlok et al., 2003). Regeneration of canopy members, except for the tree-like succulents (Cowling et al., 2009) seems to occurs more through resprouting than from seedling establishment (Midgley and Cowling, 1993). Although seeds are produced and bird dispersed (Cowling et al., 1997, Sigwela et al., 2009), seedlings are rarely encountered, especially in the Arid and Valley forms (Midgley and Cowling, 1993, Sigwela et al., 2009). Where they do occur, it’s at low densities and limited to the microclimate under bushclumps (Midgley and Cowling, 1993, Weatherall-Thomas, 2009). Very little or no regeneration via seedlings has been observed in transformed or degraded Thicket. The lack of seedling establishment could be attributed to the dry climate (Stuart-Hill and Danckwerts, 1988, Weatherall-Thomas, 2009). Due to the climate, it is common for trees and shrubs to have deep rooting systems, storage organs and succulence (Hoare et al., 2006). Many members of the Mesembryanthemaceae and Crassulaceae families; as well as *Cotyledon* spp. and spekboom, have the ability to employ Crassulacean Acid Metabolism (CAM) to photosynthesise in times of water stress, and it is these features that make semi-arid subtropical Thickets incredibly drought tolerant (Kerley et al., 1995).

Thicket is dominated by spekboom, a straggling, multiple branched small tree or shrub, with succulent stems and leaves, producing rose coloured flowers which are seldom fertilised, and therefore seed production is low (Mills et al., 2010b, Oakes, 1973).The plant is endemic to South Africa and has been recognised for its importance in ecological, agricultural and economic spheres (Beentje et al., 1994). Within Thicket this plant has been recognised as a keystone species and ecosystem engineer (Evans et al., 1997, Lechmere-Oertel, 2003, Van der Vyver, 2011), and produces most of the C-rich mulch beneath its dense canopy, by storing two-thirds of its C in the soil and plant litter (Baran, 2011). The plant is highly palatable and has been popular since the early 19th century for its supply of nutritious browse during long times of drought (Baran, 2011, Oakes, 1973, Van Wyk and Van Wyk, 1997, Von Maltitz, 1991), and has even been called a "miracle plant" (Vlok and Euston-Brown, 2002).

2. Climate

The majority of the Thicket biome's distribution lies in the Eastern Cape, which experiences a warm temperate climate (Cowling, 1984). Thicket is found in semi-arid areas and receiving a wide range of rainfall, 200 - 950 mm. Across the biome, at least 20 % of rain falls in winter (April – August) (Vlok et al., 2003), but the dominant rainfall pattern is bimodal, with spring and autumn peaks. Erratic and unreliable rainfall between prolonged droughts is a common feature of Thicket areas (Cowling, 1984, Vlok et al., 2003). The temperatures experienced in Thicket range from a mean minima of 0.9°C to a mean maxima of 32.6°C (Vlok et al., 2003) and frost rarely occurs, around 3 – 10 days of the year in the east and increasing further westwards (Hoare et al., 2006). Thicket occurs from near sea level to 1060 m (typically below 500 m), but is rarely found above 1000 m (Aucamp and Tainton, 1984, Cowling, 1984, Oakes, 1973).

3. Geology and soils

The Cape Fold Belt is the dominant geological feature within the Thicket biome (Whitfield and Norman, 2006). The mountains are composed mostly of the folded strata of the Cape Supergroup, which contains sandstone and quartzite of the Table Mountain and Witteberg Groups (quartzite and shale); which are characteristically found in sharply folded mountains systems, combined with the steep slopes and high percentage of quartz sand, give rise to coarse, sandy, unstructured soils that are shallow and nutrient poor (Hoare et al., 2006, Vlok and Schutte-Vlok, 2010, Whitfield and Norman, 2006). The lowlands are generally loamy to clayey, nutrient rich soils, mostly derived from shale (Vlok and Schutte-Vlok, 2010). Folded into the northern margin of the belt is the early Karoo Supergroup, which contains conglomerates, sandstones, shales and limestones of the Dwyka and Ecca groups. These give rise to deep, well-structured soils (Vlok and Schutte-Vlok, 2010, Whitfield and Norman, 2006).

Degradation and Transformation in Subtropical Thicket

South African biomes have experienced heavy levels of degradation, especially the arid interior environments (Vlok et al., 2003). More than one million hectares of the Thicket biome in the Eastern Cape has been converted from a dense, forest-like vegetation to an open desert-like state (Mills et al., 2010b). Aucamp and Tainton (1984) described this degradation as a “national tragedy”. The primary reason is the loss of vegetation cover, related to a loss of phytomass, and in cases of severe degradation the ecosystem loses functionality (Lloyd et al., 2002). Severe overgrazing impacts the endemics (Cowling and Holmes, 1991) and within the STEP domain 60.3 % of the original surface area of inland Thicket has been affected (Lloyd et al., 2002). Of Spekboom Thicket, approximately 46% has been heavily degraded and 36% has been moderately degraded (Lloyd et al., 2002, Mills and Cowling, 2006, Mills et al., 2011). Degradation and transformation in this biome stems from a number of processes, which include land clearing for cultivation, alien plant invasion, harvesting of fuel wood and medicinal plants, mining and urbanisation. However, it is excessive browsing by domestic stock (especially goats) since the early 1900’s that is the main factor (Aucamp and Tainton, 1984, Kerley et al., 1995, Mills et al., 2010b, Mills and Cowling, 2006). Kerley et al. (1999) and Le Maitre et al. (2007) hypothesized that landuse and in particular pastoralism, in Succulent Karoo and Thicket, to be ecologically and economically unsustainable

Thicket originally supported many indigenous herbivores, (Kerley et al., 1995) to which it is well adapted through the use of spines, resprouting after damage and vegetative growth (Cowling, 1984, Midgley, 1991, Stuart-Hill, 1992). However, Thicket is not very well defended against livestock, and livestock is largely responsible for the decline and desertification of Thicket (Stuart-Hill, 1992). Goats, in particular, browse quite differently to indigenous browsers. Stuart-Hill (1992) explains how undisturbed spekboom plants are characterized by having a 'skirt' or 'apron' of rooted side branches and over time they spread horizontally creating new individuals. Browsing of spekboom by goats takes place from the bottom upwards defoliating the lower portions of the canopy and consequently prevent the development of the ‘skirt’ or rooted branches. This removal of the protective ‘skirt’ exposes the understorey and changes the micro-climate beneath the canopy. The rich layer of accumulated organic mulch is then lost and the shrubs and trees are deprived of the organically enriched soil medium, which when combined with being exposed to continuous browsing, causes the plant to weaken and die (Mills et al., 2005a, Sigwela et al., 2009, Stuart-Hill, 1991, Stuart-Hill, 1992).The substantial changes in structure, loss of biodiversity, biomass and soil C (Lechmere-Oertel et al., 2008) locks the system in a degradation trajectory that can only be reversed by active restoration (Briske et al., 2006, Van der Vyver et al., 2012)

Spekboom’s slow growth rate contributes to explaining the poor resilience of subtropical Thicket, as it needs sufficiently long periods of rest after even moderate defoliation events (Aucamp, 1979, Swart and Hobson, 1994, Vlok et al., 2003). When sustained heavy browsing persists, it transforms the dense, closed canopy shrubland into an open “pseudo-savanna” community (Lechmere-Oertel, 2003, Lechmere-Oertel et al., 2005a), consisting of scattered trees of *P. capensis* and *S. afra,* which stand exposed among a layer of ephemeral herbs and short-lived grasses (known locally as “opslag”) (Kerley et al., 1995, Moolman and Cowling, 1994, Stuart-Hill, 1992). The transformation allows the invasion of exotic species, such as *Atriplex lindleyi* spp. *inflata,* and native karroid species, such as *Pentzia incana,* to dominate the area, (Hoffman and Cowling, 1990, Lechmere-Oertel et al., 2005a, Mills and Cowling, 2006, Mills and Fey, 2004a) and as a result spekboom, which normally comprised the bulk of the plant cover, is completely removed. In general, the disturbance caused by indigenous herbivores promotes heterogeneity of resources and species, whereas homogeneity is a result of overstocking and browsing pressure (Fabricius et al., 2002).

The loss of vegetation cover in degraded spekboom Thicket has severe implications for the soils in these environments. The loss in plant litter (by > 30 %), together with a reduction in the biomass of C (by > 75 %), leads to increased soil crusting (Mills and Fey, 2004b) and decreased water infiltration (by > 60 %) (Lechmere-Oertel et al., 2005a, Lechmere-Oertel et al., 2008, Mills and Fey, 2004b). Degradation results in decreased magnesium (Mg), soil moisture and calcium (Ca) levels (Palmer et al., 1988); as well as increased Na levels in the soil (Mills and Cowling, 2006). Degradation also increases the pH (i.e. 7.3 in general for degraded Thicket), compared to that of intact Thicket (6.0), which may be an indication of infertility, as phosphorous (P) availability decreases above a pH of 7.0 (Lechmere-Oertel et al., 2005b).

Degradation also has social consequences, whereby a reduction in plant productivity results in a reduction of natural capital which affects local communities through a reduction of wood availability, fruit and medicines (Hoffman and Cowling, 1990, Lechmere-Oertel et al., 2005a, Sigwela et al., 2009, Stuart-Hill, 1992). This transformation of the system is of great concern for the restoration and conservation of Thicket (Lechmere-Oertel et al., 2005a).

Restoration in Thicket

The rapid rate at which natural ecosystems are being destroyed has highlighted the importance and need of ecological restoration on a global scale (Cortina et al., 2006). The Society for Ecological Restoration defines ecological restoration as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Society for Ecological Restoration, 2004), and this encompasses the ecological aspects, such as improving ecosystem functionality, accelerating succession and restoring community structure; as well as restoring the socio-economic aspects of the social-ecological system (Aronson et al., 2006, Clewell and Aronson, 2006, Cortina et al., 2006). In South Africa, restoration is widely practised at all scales, but it has been highly localised and little has been published regarding the consensus of restoration protocols (Mills et al., 2007, Milton et al., 2003, Ntshotsho et al., 2011).

In Thicket the effects of degradation on soil properties, and the regeneration properties are poorly understood; and this lack of knowledge hinders the development of suitable restoration plans (Cortina et al., 2006, Lloyd et al., 2002, Mills and Fey, 2004a, Sigwela et al., 2009). Restoration ecologists stress the importance of the knowledge of the system and the processes that caused the degradation before attempting to aid in the recovery of the system (Bainbridge, 2007, Jackson and Hobbs, 2009, Thompson et al., 2009). Of major concern is little evidence of recovery of Thicket (Kerley et al., 1995), due to the slow growing nature of the plants, lack of shrub recruitment and a lack of spontaneous regeneration. These findings are supported by Weatherall-Thomas (2009) who concluded that the main limitations to seedling establishment is the lack of dispersal of seeds to safe sites for germination.

Restoration in semi-arid areas will not be achieved by simply removing the cause of the transformation (Kinyua et al., 2012, Mills et al., 2007); this is the initial step, and should be followed by re-introducing the key elements that provide structural features of the original habitat (Holmes and Richardson, 1999). Restoration requires active interventions to establish shrubs in order to improve conditions, especially within the soil (Holmes and Richardson, 1999, Lechmere-Oertel, 2003, Mills et al., 2007). However, attempts to reseed bare areas without improving the soil water conditions first will not succeed, and mechanical means to improve soil conditions is far too costly, especially on a large scale (Beukes and Cowling, 2003a, Herling et al., 2009, Mills et al., 2007). Figure 1.1 indicates how the cost of restoration increases exponentially as the state of the ecosystem deteriorates, and that restoring soil processes is the most expensive (Milton et al., 2003). Kerley et al. (1999) add to this by stating that due to the scale of degradation that has taken place within subtropical Thicket, "considerable management input" will be required for effective restoration to take place. Therefore the aim of Thicket restoration should be to preserve the remnant clumps of closed canopy Thicket and to attempt to increase these conditions as quickly as possible (Sigwela et al., 2009).

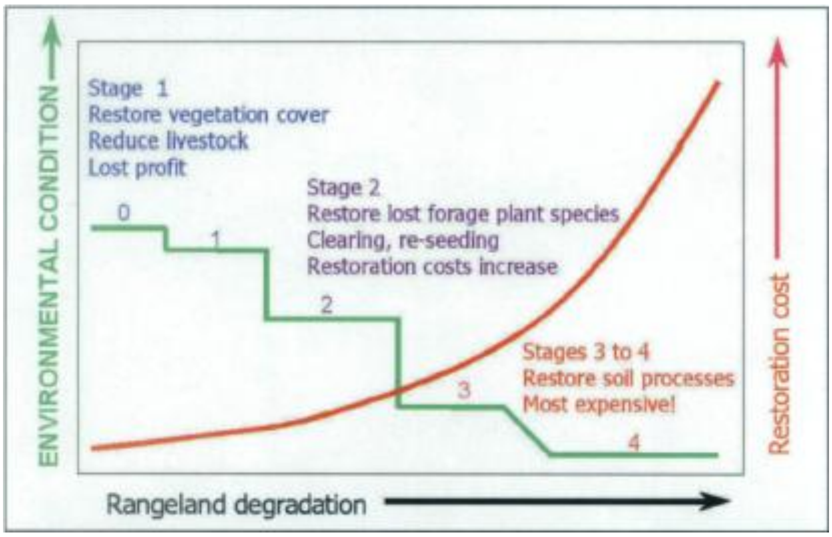

Figure 1.1: The costs of restoration increase exponentially as land degradation proceeds from reduced vegetation cover through vegetation change through desertification and soil loss (Milton et al., 2003)

The Subtropical Thicket Restoration Programme (STRP) was launched in 2004 through the Working-for-Woodlands program of the South African government, and functions under the auspices of the Eastern Cape Restoration Program (ECRP). The main aim of this program is to demonstrate that a restoration program at the farm scale is feasible, with the long-term goal of establishing the protocols and procedures to initiate restoration on a landscape scale (Mills et al., 2007). This is being done by planting cuttings of spekboom at varying densities (1 – 3 m intervals) and patterns, as well as constructing exclosures to determine browsing effects on plant establishment. It was decided to use this plant because of its ability to handle drought and being able to propagate easily from cuttings (Lechmere-Oertel et al., 2008, Oakes, 1973, Vlok et al., 2003). Spekboom also forms roots when it touches the ground and spreads outwards (Kerley et al., 1995, Mills et al., 2007, Stuart-Hill, 1992, Vlok et al., 2003). Mills et al. (2007) hypothesized that spekboom would improve above- and below-ground conditions by increasing leaf litter (Lechmere-Oertel et al., 2008); improving the soil organic C content and fertility by accumulating organic matter, which improves the nutrient and water holding capacity of the soil (Lechmere-Oertel et al., 2005b, Mills and Cowling, 2010a, Mills and Fey, 2004a). However, it must be kept in mind that transformed sites may not be suitable for spekboom growth if the top soil has been washed away (Mills and Cowling, 2006), and therefore some of the planting areas may not be successful.

The Working for Woodlands ECRP is underpinned by scientific experiments and research; and consists of the active engagement of a wide range of stakeholders of government ministries, private farmers, nature conservation and the Gamtoos Irrigation Board (GIB), the implementing agency for the Working for Woodlands project in the Eastern Cape. The GIB, through a contracting system, hires teams of previously disadvantaged individuals to implement the planting of spekboom cuttings, and is funded by the government's Expanded Public Works Program, administered initially by the Department of Water Affairs and Forestry (DWAF) and, since 2012, by the Department of Environmental Affairs (DEA). Since 2004 some ca. 1630 ha have been planted in protected areas of the Eastern Cape (Van der Vyver et al., 2012). Ntshotsho et al. (2011) complimented the ECRP as being one of the few programs in South Africa whereby “positive strides” have been made, because scientists, practitioners and managers are collaborating in real-world experiments and information sharing. Another attractive feature of Thicket restoration and C sequestration is that the initial costs are low, compared to that of forest restoration for example, because cuttings are being sourced from intact Thicket, so there is no need for nursery germination (Mills et al., 2007).

Over the last two decades there have been limited studies on subtropical Thicket recovery (Hall et al., 2003, Swart and Hobson, 1994, Todkill, 2001, Van der Vyver, 2011). All the studies, however, concluded that by creating fertile islands and/or the use of the ecosystem engineer spekboom to improve soil conditions, followed by years (30 – 50) of rest, the return of canopy plant biodiversity is achieved, as was recently re-affirmed by Van der Vyver (2011). These studies indicate that re-vegetating degraded slopes resulted in good plant survivorship, P levels increased and C rates were increasing promisingly (Mills and Cowling, 2006). The electrical conductivity of the soil, which is a scale used for estimating soil salinity (Allison et al., 1954), also recovered (Todkill, 2001). Apart from improving the quality of the soil, spekboom assists in soil erosion control, increases infiltration therefore improving base flows, and increases the land's wildlife carrying capacity (Van Luijka et al., in press). Van der Vyver et al. (2012) also indicate that woody canopy species can recruit spontaneously in spekboom restored thicket after ca. 40 years. This type of information is valuable to stakeholders because in order for STRP to achieve certification for C trading, it must prove that it is not creating a monoculture of spekboom (Bekessy and Wintle, 2008), which has been a concern because planting spekboom on its own does not qualify as restoration (Mills et al., 2007, Van der Vyver, 2011). To restore an ecosystem implies that all ecological processes, functions, biological complexity and diversity will be restored, which is difficult to achieve (Benayas et al., 2009, Ruiz-Jaen and Aide, 2005). However, even if restoration leads to a spekboom-dominated landscape, it would be a more preferable community than the transformed state, because it will be a source of food to livestock and wildlife (Mills et al., 2007).

Portulacaria afra and soil

Studies of soils in Southern Africa indicate that there are relationships between plant species distribution patterns, soil chemical properties (Hartmann et al., 1979, Mills et al., 2012, Palmer et al., 1988) and lithologically-controlled soil texture (Fraser et al., 1987, Lechmere-Oertel and Cowling, 2001). Earlier research showed that Thicket is largely restricted to growing on nutrient- and clay-rich soils derived from shales and mudstones (Cowling, 1984). Changes in vegetation are reflected across short distances where there is a sudden change from sandstone to shale. Shale-derived soils have higher silt and clay contents, which retain more water making it harder for plant roots to extract water, and in semi-arid areas factors influencing the availability of water influence the composition of vegetation (Medinski et al., 2010). Shales also contain high levels of Na (shale 1485 $mg.kg^{-1}$ vs sandstone 10 $mg.kg^{-1}$)

(Lechmere-Oertel and Cowling, 2001). Although spekboom tends to be more associated with these nutrient-rich soils, it was later realised that it is not restricted by any particular soil type, as it had been seen growing on all geologies, including the infertile quartzitic sandstones of the Cape Supergroup (Oakes, 1973, Vlok et al., 2003).

Baran (2011) compiled lists of all references to, or about, spekboom, dating back to the 1830's, and it was clear that this plant has dominated hill slopes, being concentrated higher up on mountains on stony ridges, often covering whole hills or mountains, and in many areas, spekboom also shows preference for specific slopes. However, there is little evidence that it grows in footslope/bottomland areas. Mills et al. (2011) noted that in the Fish River Reserve, Eastern Cape, spekboom was located on the crest of hills and seemed to decrease with distance down slope. In some areas there is a clear line where it ceases to occur, especially on footslopes or bottomland areas (Oakes, 1973) (R.M. Cowling, 2011 pers. Comm) (Figure 1.2). The variability of spekboom distribution in the landscape prompted Mills et al. (2011) to ask vital questions which are important for the planting of spekboom cuttings; such as what soil or environmental factors interact with spekboom survival? This plant's distribution may be affected by many soil and landscape factors and I will discuss them separately.

Figure 1.2: Location of Spekboom Thicket along a slope near Addo National Park. The black line indicates where spekboom (evident by the light green shrubs) ceases to grow as it reaches the footslope. Photo: C Becker

1. The effect of catenas

The concept of vegetation changes along gradients (or catena effect) is an old one and has been well described globally. Vegetation changes along slopes have been attributed to nutrient flows, temperatures, and soil profile, depth, salinity and moisture status (Ben-Shahar, 1990, Boix-Fayosa et al., 1998, Metternicht and Zinck, 1997, Ni and Zhang, 2007, Schimel et al., 1985, Yanagisawa and Fujita, 1999). Crests of mountains generally consist of shallow, leached, coarse, sandy soils, and through the sorting and moving of particles down slopes, lower slope positions often accumulate soil and nutrients (Chapin et al., 2011, Fraser et al., 1987, Metternicht and Zinck, 1997, Mills and Cowling, 2010a, Ni and Zhang, 2007, Schimel et al., 1985). The result is that there is an increase in soil depth and element concentration at the footslopes, especially with regards to organic matter, C, P, nitrogen (N) (Ben-Shahar, 1990, Schimel et al., 1985, Yanagisawa and Fujita, 1999) and Na (Fraser et al., 1987). The higher levels of Na increases the pH to a level where calcium carbonate precipitates and results in a Na-saturated dispersed clay fraction, which develops a hard, impermeable crust (Fraser et al., 1987, Mills and Fey, 2004b). Crusting is also result of a combination of soil texture mineralogy, electrical conductivity and organic matter (Medinski et al., 2010, Zhao et al., 2011). Mills and Cowling (2006) noted that within intact Thicket the pH ranges from 5.9 – 7, with extremes of 4.8 in the Baviaanskloof (Mills and Cowling, 2010a), to 8.0 near the boundary with the Succulent Karoo (Lechmere-Oertel and Cowling, 2001). Thus spekboom may be avoiding the higher pH at the bottom of slopes.

2. Soil nutrients

Palmer et al. (1988) studied aspects of soil-plant relationships near the Fish River Reserve, Eastern Cape, and found that areas where spekboom bush clumps grew are rich in minerals, especially Ca (from the high amounts of organic matter being deposited) and magnesium (Mg), and had high conductivity rates. They concluded that there are complex relationships between the vegetation and soil in the Fish River valley. The study of Mills et al. (2011), also in the Fish River, was aimed at determining possible relationships between spekboom and a range of soil properties. From this they discovered a uniform pattern that spekboom was constrained at both high and low levels of subsoil electrical conductivity, sand content, Ca, zinc (Zn) and aluminum (Al). These findings were supported by a later study (Mills et al., 2012) who notes that in Southern Africa woody vegetation growth is best at intermediate nutrient contents.

3. Soil salinity

Salinity is also a factor to consider when dealing with woody plant life forms (Medinski et al., 2010). There is a notion that spekboom could be limited by some salt or salinity factor, which has stemmed from a number of observations and planting experience by researchers (R.M. Cowling, 2011 pers. comm) and nursery managers (S.J. Milton, 2011 pers. comm). Ting and Hanscom (1977) observed through a number of tests that when spekboom receives salt (using a 2% NaCl solution) it responds in the same way as when it is water stressed, by slowing down transpiration rates during the day to almost a complete halt. This response to salinity has been observed in other members of the Didiereaceae family (Kafi and Rahimi, 2011, Rahdari et al., 2012). However, as Vlok et al., (2003) remark, it has an unusual ability to retain foliage even when severely water stressed moisture conditions persist.

4. Aspect and slope

Aspect and slope could be important factors because they result in further variations in the soil (Amezaga et al., 2004, Birch et al., 1999, Evans et al., 1997, Palmer et al., 1988), as well as the climate, whereby southern facing slopes at the mid latitudes of the Southern Hemisphere, experience cool, moist conditions and northern facing slopes are characteristically warmer and drier (Amezaga et al., 2004, Armesto and Martínez, 1978, Evans et al., 1997, Holland and Steyn, 1975, Sternberg and Shoshany, 2001). Previous work in the Fish River Valley has shown that Medium Succulent Thicket (vegetation between 2 – 2.5 m tall which is dominated by spekboom*, Euclea undulate* and *Grewia robusta)* is mainly associated with steep north and west facing slopes and Short Succulent Thicket (comprising very dense, 1 – 2 m tall, impenetrable thickets dominated by *Euphorbia bothae, Rhigozum obovatum and* spekboom) grows on north facing slopes (Evans et al., 1997). Spekboom also thrives on rocky, dry soils (Oakes, 1973). South facing slopes tend to more dominated by Cape evergreen sclerophyll plant communities of Renosterveld and allied shrublands (Armesto and Martínez, 1978, Holland and Steyn, 1975). The effect of temperature on spekboom distribution is not clear. Although spekboom can survive in areas subject to frost and occasional freezing temperatures, it grows much better in frost-free areas (Oakes, 1973).

Rationale and Aim of the Study

Knowledge of the relationship between spekboom and soils is valuable, especially with regards to the current work being done by STRP/ ECRP, which has shown that spekboom has the potential to restore the functioning of the ecosystem and to sequester C at a surprisingly fast rate (4.2 tons/ha/annum) for a semi-arid area (Marais et al., 2009). In 1976 at an arid Thicket site, a farmer planted cuttings and by 2005 these plantings, despite the aridity, covered 90% of the site, demonstrating excellent survivorship (Mills and Cowling, 2006). However, since the program's plantings began in 2004, this degree of success has not been mirrored at the experimental survivorship trials. Trials investigating a variety of factors (cut spekboom stem diameters, planting angle, clumping, planting density and planting angle) has yielded conflicting results, with survivorship ranging from 13-72 %. This is compounded by the fact that survivorship rates are not static, and that mortality continues to increase even three years post-planting (Powell, 2009). Most of the degraded soils in the planting areas have a high clay content and are therefore subject to soil capping (Mills and Fey, 2004a, Mills and Fey, 2004b) and run-off. Powell (2009) hypothesized that survivorship would be influenced by soil type and degradation state, in combination with planting depth; and that results from well-drained soils could produce significantly different results from clayey sites. Mills and Cowling (2010a) add to this by saying that the success of C sequestration (and the programme as a whole) will be strongly influenced by nutrient contents in the soil.

The previous section has shown that many landscape and environmental factors may be important in driving spekboom distribution, and that most of what is known about the interactions between these factors and spekboom comes from work done in the Fish River Reserve area. However, there has been little attempt to investigate the role of these landscape and environmental factors on spekboom distribution and survival for the broader Thicket biome (including the Succulent Karoo/Thicket interface) (Beukes and Cowling, 2003a). Thus this study aims to investigate this topic.

From a C investor's point of view, survivorship of a slow growing species is very important as it has profound implications (in terms of costs per hectare) on the feasibility of a restoration program. From a conservation point of view, central to the conservation of diversity is an understanding of the factors that control it (Cowling, 1983), especially the keystone plant species such as spekboom (Hoffman and Everard, 1987, Rogers et al., 1995, Vlok et al., 2003). A full analysis of all landscape and environmental factors is not within the scope of a master's thesis, therefore the aim of this thesis is to further the understanding of the role that soil could play in spekboom survivorship and landscape-scale distribution in spekboom dominated Thickets of the Eastern and Western Cape.

In Chapter 2 I investigated the influence of selected soil properties (pH, sodium, particle size, aspect, gradient, electrical conductivity, soil depth and infiltration) on the distribution of spekboom in Thicket landscapes across the biome, ranging from Grahamstown in the east, through to where it forms mosaics with the Succulent Karoo near Oudtshoorn, in the west. Here I specifically, asked the following questions: 1) Is the presence of spekboom related to soil factors? And 2) How do the different soil factors differ amongst north and south slopes as well as valley bottoms?

In chapter 3 the hypothesis that sodium or salinity are limiting factors are examined by a range of experiments on spekboom cuttings in a nursery. The following questions were addressed: 1) How is above-ground growth and plant affected by soils and water with different levels of Na and Cl? 2) How are root:shoot ratios affected by soils and water with different levels of Na and Cl?

As restoration of thicket with the use of spekboom cuttings has had such varying degrees of success, Chapter 4 investigates if there could be a relationship between spekboom cutting survival and active growth rates and selected soil properties (macro-nutrients, pH, particle size, aspect, gradient, soil depth and infiltration), which was carried out at a range of Working for Woodlands restoration sites near Calitzdorp, Addo and Baviaanskloof. I investigate whether: 1) Is the survival of spekboom related to one or more soil properties? 2) Is the growth of spekboom affected by one or more soil properties?

Chapter 5 is a general discussion that ties all the chapters together and where I asses any limitations of the study. I then proceed to provide possible management implications and directions for future research that arose/ resulted from this study.

The three central chapters will be submitted for publication in journals, and are thus stand-alone entities. Although I have tried to avoid repetition in the text, it does occur to some degree.

Chapter 2 – The influence of selected soil properties on the distribution of *Portulacaria afra* in the subtropical Thicket landscape

Abstract

In South Africa, Spekboomveld (a subtype of the Thicket biome), which is dominated by *Portulacaria afra* (spekboom), is generally restricted to warm, north facing slopes. Spekboom's distribution is patchy in some areas, where it tends to avoid growing on some south facing slopes and bottomland areas. One theory for this patchy distribution is that an interaction between soil characteristics and the position in the landscape could influence spekboom growth. My hypothesis is that 1) due to a catena effect, spekboom is avoiding bottomland areas that consist of fine textured, deep soils with high pH and nutrient levels, especially sodium, and that these areas are more saline than the surrounding slopes, and 2) slopes of different aspects and bottomland areas differ in their soil and environmental composition which could account for spekbooms preference for north facing slopes. This chapter analysed the differences in selected soil properties (sodium, particle size, slope, pH and electrical conductivity) on north and south facing slopes as well as bottomland (valley) areas. Ten sites between Grahamstown and Oudtshoorn were selected and soil samples at these three landscape positions were analysed. I did not find a strong catena effect at the Thicket sites because all the factors, other than pH, did not show clear differences between the slopes and bottomland areas. This suggests that spekboom prefers for more acidic soils (4.4 – 5.1). The extensive range of soil texture (particle size) found across the sites where spekboom grows reflects other studies findings on spekboom's tolerance for a wide range of soil conditions. There was also a clear trend in changing soil texture from east to west. Other environmental characteristics such as slope angle, interlinked with aspect, are probably a major factor, because it influences the amount of solar radiation a slope receives. This in turn influences the temperature and duration of sunlight exposure a slope is exposed too, whereby north facing slopes can receive as much as double the amount of sunlight than a south facing slope in cooler seasons. This, together with rainfall patterns would influence the micro-climate of the different landscape positions, and is likely the primary driver of spekboom's patchy distribution across the landscape.

Introduction

The Thicket biome is generally centred on the coastal forelands of the Eastern Cape Province and the most eastern part of the Western Cape. Thicket has been described as “a dense, impenetrable, near woody, semi-succulent and thorny vegetation type of an average height of 2-3 m” (Hoare et al., 2006). Thicket occurs in areas where fire and frost are absent or infrequent (Vlok et al., 2005). One of Thicket’s subtypes is spekboomveld, which is dominated by the leaf-succulent shrub *Portulacaria afra* (hereafter spekboom), and is largely restricted to warmer, north facing slopes (Milton et al., 1997). Spekboom is an important component of Thicket for a variety of reasons: it acts as a keystone species and ecosystem engineer (Evans et al., 1997, Lechmere-Oertel, 2003, Van der Vyver, 2011); it produces a carbon (C) -rich mulch beneath its dense canopy; and it supplies palatable, nutritious browse, especially during times of drought (Baran, 2011, Oakes, 1973, Van Wyk and Van Wyk, 1997, Von Maltitz, 1991).

Earlier research showed that Spekboomveld is largely restricted to hot, semi-arid valleys on moderately deep, nutrient- and clay-rich soils derived from shales and mudstones (Cowling, 1984). It has since been realised that it is not restricted by any particular soil type, as it has been observed growing on all geologies, including the infertile quartzitic sandstones of the Cape Supergroup (Vlok et al., 2003). Research from natural intact areas indicates that this plant generally prefers warm, north facing slopes, dominating crests of hills, on stony ridges, and decreasing with distance down slope (Baran, 2011, Cowling, 1984, Mills et al., 2011, Oakes, 1973). However, changes in its distribution are reflected across short distances and in some areas there is a clear line where it ceases to occur, especially on footslopes or bottomland areas (Oakes, 1973). These findings have stimulated a host of questions by researchers regarding spekboom establishment across the biome. For instance, why does it grow on some south facing slopes (for example near Grahamstown) and not on others (for example near Oudtshoorn)? These differences in vegetation composition of different slopes and valleys were noted by Van der Vyver (2011), who recommended that possible interactions between these areas should be investigated. There could be a number of explanations for the patchy distribution of spekboom, but one theory is that an interaction between soil characteristics and the position in the landscape could influence its growth (Mills et al., 2011). A catena effect is when soils particles are sorted and transported down a slope from the crest of the mountain to the bottomlands, resulting in lower slope positions accumulating soil and nutrients. The catena effect could account for spekboom’s slope preference, because bottomland areas would consist of deep soils with high concentrations of elements, especially sodium, and increased pH levels, as compared to the surrounding slopes (Ben-Shahar, 1990, Boix-Fayosa et al., 1998, Metternicht and Zinck, 1997, Ni and Zhang, 2007, Schimel et al., 1985, Yanagisawa and Fujita, 1999).

Thicket has suffered severe levels of degradation, whereby 46 % of spekboomveld has been heavily degraded by domestic herbivores (Lloyd et al., 2002, Mills and Cowling, 2006). In 2004 the Subtropical Thicket Restoration Programme (STRP) was launched to initiate restoration of Thicket on a landscape scale, using spekboom cuttings. However, the success of the plantings so far has varied greatly, and therefore any knowledge relating to spekboom's growth requirements or ecological processes is of vital importance to the current work being done by STRP (Marais et al., 2009, Powell, 2009). Most of the past Thicket research has been on the carbon sequestration aspect of spekboom and the effects of degradation (Curran et al., 2012, Hoffman and Cowling, 1990, Kerley et al., 1999, Lechmere-Oertel, 2003, Lechmere-Oertel et al., 2005a, Lloyd et al., 2002, Marais et al., 2009, Mills and Cowling, 2006, Mills and Cowling, 2010a, Mills and Fey, 2004a, Powell, 2009, Van der Vyver, 2011, Van Luijka et al., in press). There is a gap in the ecological understanding of where spekboom naturally grows in the landscape, and what factors could be influencing this.

This chapter seeks to investigate the influence of selected soil and environmental properties (pH, sodium, particle size, aspect, slope angle, electrical conductivity, soil depth and infiltration) on the distribution of spekboom in Thicket landscapes across the biome. Here I specifically asked the following questions: 1) Is the presence of spekboom related to soil factors? And 2) how do the different soil factors compare amongst north and south facing slopes as well as bottomlands?

Study Sites

The concept of a 'Thicket biome' is fairly new and was first proposed by Low and Rebelo (1996). Since then, the classification of Subtropical Thicket has undergone different reviews, such as the Subtropical Thicket Ecosystem Planning Programme's (STEP) valuable mapping of Thicket types in 2002 (Lloyd et al., 2002, Vlok et al., 2003); and Mucina et al. (2006) who founded the term Albany Thicket biome by merging STEP's 112 vegetation types into 14 types. The terminology in this chapter will follow a combination of Hoare et al. (2006), Vlok et al. (2003), and Vlok et al. (2005) classification systems of Arid and Valley Thicket forms.

Ten sights were chosen within the Subtropical Thicket biome of South Africa, extending from Grahamstown, being the most eastern site, to Oudtshoorn, being the most western site (Figure 2.1; Table 2.1). The sites were divided according to the major drainage systems (basins) in the Subtropical Thicket area, namely the Gouritz, Gamtoos, Sundays and Fish basins.

Fish river basin

Geology

Site 1, located just north of Grahamstown (Figure 2.1), along the Ecca pass, is situated on the Beaufort Group of the Adelaide Formation on the upper slopes, and the Ecca Group of the Fort Brown Formation on the lower slopes, both Karoo Supergroup lithologies. The Ecca Group consists mainly of black shales and some sandstones, which weathers to form a red, highly erodible soil. The Beaufort Group is composed of a monotonous sequence of grey shales and mudstones, with interbedded sandstones. The argillaceous rocks are usually bright in colour (red, purple or green) while the sandstones are often yellowish, which often distinguishes it from the underlying Ecca (Truswell, 1977, Van Eden, 1972, Whitfield and Norman, 2006).

Vegetation

This site is located in the Great Fish Noorsveld vegetation unit, which is dominated by the local endemic *Euphorbia bothae,* as well as other *Euphorbia* species, intermixed with sclerophyllous bush clumps (*Euclea, Grewia, Gymnosporia, Putterlickia*, *Schotia*), as well as groups of succulent shrubs (*Portulacaria afra,* C*rassula, Cotyledon*) (Hoare et al., 2006, Vlok et al., 2003). Spekboom was found to dominate both north and south facing slopes, as has been recorded by other researchers of the Fish river drainage area (Evans et al., 1997). The bottomland or footslope area was dominated by Acacia *karoo, Azima tetracantha* and *Pappea capensis* trees.

Climate

The site experiences all year rainfall with spring and autumn optima's and relatively dry winters, and has a MAP of 310 - 400 mm (measured between 1968 – 2004) (data from SA Weather Bureau). It has a warm temperate climate and frost occurs approximately 3 days/ year (Hoare et al., 2006). In summer (January) the minimum average temperature is 16°C and the maximum average temperature is 30°C. In July (winter) the minimum average temperature is 7°C and the maximum average temperature is 22°C. In winter temperatures can drop to -3°C (data from SA Weather Bureau).

Table 2.1: Co-ordinates (of the north facing slope), landowners and their respective farm or reserve names for the ten landscape sites

Site Number	Drainage basin	Latitude	Longitude	Farm/reserve names	Land owners
1	Fish	33.17972	26.57119	New Resolution Hatchery	A. Daveport
2	Sundays	33.23264	25.39569	Kaboega	I. Ritchie
3	Sundays	33.24655	25.36758	Kaboega	I. Ritchie
4	Sundays	33.54658	25.17161	Krompoort	A. Dorfling
5	Gamtoos	33.65012	24.35368	Baviaanskloof Nature Reserve	Eastern Cape Parks & Tourism Agency
6	Gamtoos	33.60255	24.06441	Rust 'n Vrede	C. Lamprecht
7	Gouritz	33.5133	22.28807	Buffelsdrift Game Lodge	A. van Schalkwyk
8	Gouritz	33.51808	22.26535	Buffelsdrift Game Lodge	A. van Schalkwyk
9	Gouritz	33.67757	22.23622	Chandelier Game Lodge	G. Ferreira
10	Gouritz	33.68282	22.23772	Chandelier Game Lodge	G. Ferreira

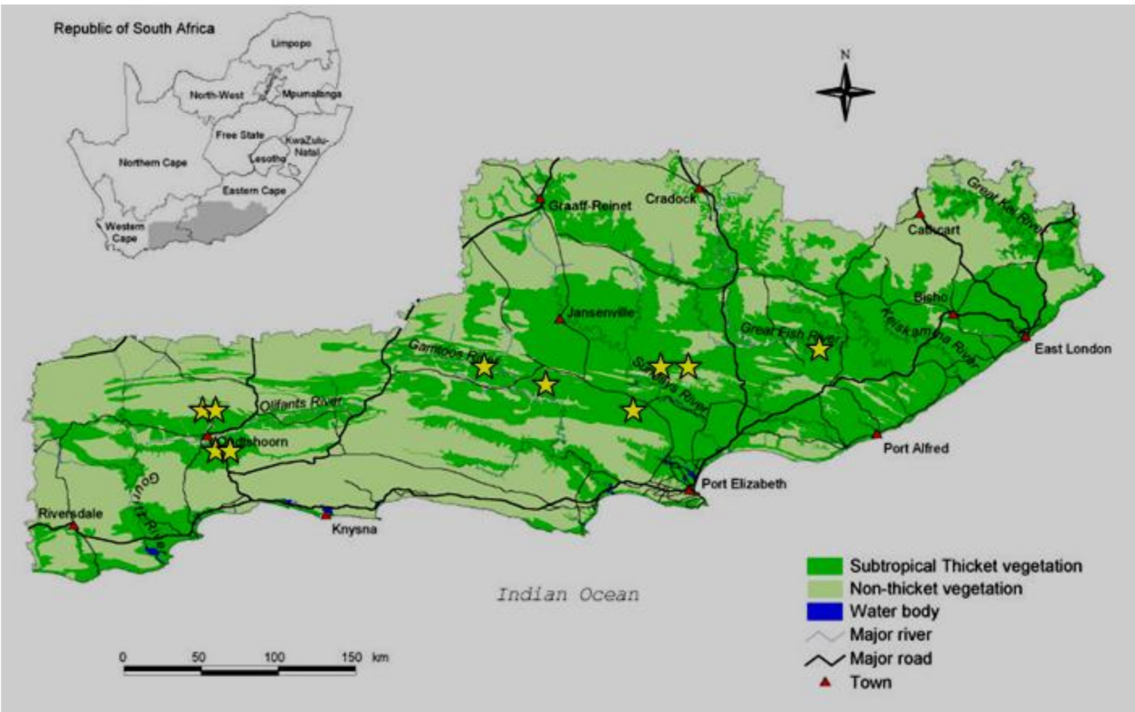

Figure 2.1: Location of the 10 landscape study sites, depicted as yellow stars, in South African Subtropical Thicket. Dark green areas represent Subtropical Thicket vegetation, lighter green areas represent other (non Thicket) vegetation (Knight and Cowling, 2003).

Sundays river basin

Geology

Sites 2 and 3 located on the eastern borders of the Addo National Park (Figure 2.1), are situated on a series of undulating hills. These are on a Dwyka and Ecca transition (both of Karoo lithologies), which gives rise to deep, well-structured soils (Vlok and Schutte-Vlok, 2010, Whitfield and Norman, 2006). The unsorted Dwyka tillite with minor shales, consists of dark grey, fine grained rocks containing clasts of various shapes, sizes and origins. The soils they produce are often saline and prone to crusting (Esler et al., 2006). The transition with the Ecca group contains sandstone and shale (Truswell, 1977, Whitfield and Norman, 2006).

Site 4 is situated on farm Krompoort, which is situated in a valley to the north-west of Uitenhage, on the northern foot slopes of the Groot Winterhoek mountains. The geology of the site consists of Bokkeveld Group red shales (Cape Supergroup), sandstones and siltstones of the Ceres and Traka Subgroups (Truswell, 1977).

Vegetation

Sites 2 and 3 are part of the Sundays Thicket vegetation unit, whereby the undulating plains, low mountains and foothills are covered with tall, dense trees and shrubs; and succulents are common. There is a wide variety of lianas, and spekboom dominance increases with increasing aridity. At these two sites, spekboom was found to dominate north facing slopes, and was present on south facing slopes but not as dominant. The bottomland area was well vegetated with trees (*Acacia karoo* and *Euclea undulata*), shrubs (*Plumbago auriculata, Lycium ferocissimum*) and grasses (*Panicum maximum*).

Site 4 falls within the Sundays Spekboomveld, an arid form of Succulent Thicket (Hoare et al., 2006, Vlok et al., 2003), and will also be referred to as Sundays Thicket. This type of Thicket is loosely organised into a mosaic of vegetation patches comprising evergreen, trees (< 5 m), emerging from a matrix of woody and succulent shrubs, dominated by spekboom; and patches of bare ground (Lechmere-Oertel et al., 2005a). Spekboom was found to dominate both slopes at this site. The bottomland area was fairly open with scattered *Acacia karoo* and *Searsia longispina* trees, but was dominated by *Pentzia incana* and *Lycium ferocissimum.*

Climate

Sites 2 and 3 experience a similar MAP of 250 – 400 mm (measured between 1971 – 2011), which falls throughout the year with small peaks in late summer and spring. The number of frost days is approximately 8. The minimum and maximum average temperatures in January are 17°C and 31°C, respectively; and temperatures greater than 40°C are frequently recorded in summer. In July minimum and maximum average temperatures are 5°C and 22°C, respectively (data from SA Weather Bureau).

Site 4 receives all year rainfall with spring and autumn maxima with a MAP of 250 - 317 mm (measured between 1970 – 2009) (Van der Vyver, 2011). The minimum and maximum average temperatures in January are 15°C and 28°C, respectively. In July minimum and maximum average temperatures are 5°C and 20°C, respectively (data from SA Weather Bureau), and can approach freezing (Lechmere-Oertel et al., 2005b).

Gamtoos river basin

Geology

Sites 5 and 6 (Figure 2.1) are located on the footslopes of the Kouga Mountain Range within the Baviaanskloof Mega-Reserve and consist of steep slopes with shallow, red, clayey and often rocky soils, which are derived from a variety of parent materials, usually mudstones, shales, slates, phyllite and sandstones from the Bokkeveld Goup (Cape System) (Truswell, 1977).

Vegetation

The vegetation at site 5 is predominately Gamtoos Valley Thicket, which is dominated by *Euphorbia grandidens, Aloe speciosa, Cussonia gamtoosensis, Sideroxylon inerme* and *Ptaeroxylon obliquum* (Hoare et al., 2006), interspersed with Baviaanskloof Spekboom Thicket. Spekboom dominated both slopes at this site. The vegetation at site 6 was a mixture of Baviaanskloof Spekboom Thicket (especially on north facing slopes), where spekboom dominated the vegetation, and Baviaanskloof Sandolienveld (occurring more on south facing slopes) where spekboom occurred scattered across the slope. Baviaanskloof Spekboom Thicket is dominated by spekboom*, Pappea capensis, Schotia latifolia, Aloe speciosa, Panicum maximum, Putterlickia pyracantha,* and *Cenchrus ciliaris.* Due to the steepness of the slopes that graded into each other, there was no suitable bottomland area at site 5. The bottomland area at site 6 was narrow and erosion was taking place nearby. The area was dominated by *Pentzia incana* and *Cenchrus ciliaris* with scattered *Asparagus* species.

Climate

Rainfall at sites 5 and 6 is commonly associated with post-frontal events, bringing soft soaking rain in the spring and autumn months and thunderstorms in mid to late summer. Rainfall peaks in the equinoctial months, is less reliable in summer and little falls in the winter months. The MAP is 230 - 300 mm (measured between 1985 – 2012). Frost days vary from 5 – 65 days. The minimum and maximum average temperatures in January are 16°C and 31°C, respectively. In July minimum and maximum average temperatures are 5°C and 20°C, respectively (data from SA Weather Bureau).

Gouritz river basin

Geology

Sites 7 and 8 are just north of Oudsthoorn (Figure 2.1), on Buffelsdrift Game Reserve, located on well consolidated and characteristically red pebbled Enon Conglomerates of the Uitenhage (Cretaceous) group (Torien, 1979). Sites 9 and 10 are south of Oudtshoorn, on Chandelier Game Lodge, which lies on Bokkeveld red shales (Cape Supergroup) (Torien, 1979).

Vegetation

The vegetation at sites 7 and 8 is Kruisrivier Spekboom-Pruimveld (Valley Thicket with Spekboom Mosaics), where spekboom is abundant amongst woody trees and shrubs (e.g. *Carissa haematocarpa, Euclea undulata, Nymannia capensis, Pappea capensis, Rhigozum obovatum*) in a matrix of Succulent Karoo communities, in which *Pteronia incana* is often abundant. Grasses are present, such as *Cenchrus ciliaris* and *Sporobolus africanus,* and leaf succulents such as *Aloe ferox, Cotyledon orbiculare* and *Sarcostemma viminale* are also abundant. The Thicket vegetation is restricted to growing on the north facing slopes, and occurs as fragmented patches amongst Succulent Karoo, Renosterveld, Sandolien or Fynbos vegetation on the adjacent south facing slopes (Vlok et al., 2005). The bottomland areas were fairly open and dominated by *Pentzia incana* with scattered *Acacia karoo* and *Euclea undulata* trees. *Sarcostemma viminale*, *Lycium ferocissimum* and *Galenia africana* were also present.

The vegetation at sites 9 and 10 is Kandelaars Arid Spekboomveld (Arid Thicket with Spekboom Mosaics), where spekboom and woody trees and shrubs (*Carissa haematocarpa, Euclea undulata, Gymnosporia szyszylowiczii, Nymannia capensis, Putterlickia pyracantha, Rhigozum obovatum* and *Searsia undulata*) are also abundant on the north facing slopes, while Succulent Karoo communities dominate the south facing slopes (Vlok et al., 2005). The bottomland area consisted of scattered *Acacia karoo* and *Searsia longispina* trees, between *Aloe ferox, Carissa haematocarpa, Galenia africana* and *Sarcostemma viminale* species*.* At all the sites in this basin, there was a clear pattern of spekboom not growing on south facing slopes.

Climate

Sites 7 to 10 are located in a more semi-desert region with a MAP 230 - 290 mm (measured between 2001 – 2012) and falls within the winter rainfall region, although it also experiences summer thunderstorms. The minimum and maximum average temperatures in January are 15°C and 32°C, respectively; and temperatures greater than 44°C occur. In July minimum and maximum average temperatures are 2°C and 20°C, respectively (data from SA Weather Bureau).

Materials and Methods

At each study site, transects (n = 15) were used to collect soil samples and other physical data for each north and south facing slope and for a bottomland area (hereafter called valley). Data collection took place in March, April and May 2012. The sites were selected with the assistance of some of the landowners as well as by using Google Earth to locate sites which consisted of a north facing slope, an opposite south facing slope and the valley between them. Transects on the slopes (five soil samples per transect, totalling 15 samples per site) were positioned so that they were mid-slope and followed the contour so as to maintain the mid-slope position. Each transect was positioned so that the whole transect would maintain the same direction (either north or south) and that it would not curve around the mountain. Transects in the valley were located on the footslopes of the mountain, where the ground levelled out and below the line where spekboom ceased to grow. Care was taken to avoid sampling too close to rivers or erosion ditches.

At the start of each transect GPS co-ordinates were recorded. Replicates were spaced at a minimum of 20 m apart (in some cases this may have been slightly more than 20 m in order to find a suitable spot to auger and take the relevant readings), which created a transect of 100 m. At each point the following (other than the soil sample and infiltration rate, discussed below) was recorded:

1) slope aspect with the use of a compass,
2) soil depth measured by hammering a dropper in the ground until it could go no further and recording the depth in centimetres,
3) Slope angle (except in the cases of the valley areas which were flat) was measured using the triangle principle with the use of a measuring tape, a dropper and spirit level (FAO., 1998),
4) Plant species within the immediate vicinity of the soil sample,
5) As well as any other interesting observations.

Soil sampling and preparation

Soil samples were collected with the use of an auger, and in cases where the soil was too hard or rocky, with the use of spades and picks, to a depth of 20 cm (where possible, as on some steep slopes soils were extremely shallow). The soil samples were taken in open ground between plants, so as not to sample soil directly under the canopy as this could affect soil nutrient analysis (Belsky, 1994), especially in the case of spekboom, beneath which carbon and litter is high. The samples were transported in labelled plastic bags back to the Nelson Mandela Metropolitan University laboratory at Saasveld, where they were stored until May, 2012. Each soil sample was well mixed and sieved through a 2 mm sieve to remove organic material and roots, and then left to air dry to maintain constant weight and minimal biological activity (Boone et al., 1999).

At the beginning of each transect, a separate soil sample was collected in order to calculate bulk density (BD):

Bulk density ($g.cm^{-3}$) = W / V

Due to the rocky structure of the soil, the excavation method of Elliott et al. (1999) was adapted; whereby a set volume was excavated (V), oven dried, and weighed in grams (W). The bulk density was used to convert the concentration data for sodium (Na) to content value ($g.m^{-2}$).

Laboratory analysis

All of the samples were analysed for Na, particle size, resistance and pH. The analyses were undertaken at the Elsenburg Laboratory, Institute for Plant Production, Stellenbosch, South Africa. Extractable Na was extracted with 1 % citric acid and analysed by using a Thermo ICP iCAP 6000 Series Spectrometer (Thermofisher Scientific, Surrey, UK). The pH was determined in KCl (McLean, 1982, Rhoades, 1982). Clay content was determined by the hydrometer method, sand by sieving and silt by the difference (Day, 1956, Elliott et al., 1999). Electrical resistance was determined in a saturated soil-water paste and is inversely proportional to the salt concentration, which can therefore be considered to be an index of the salt hazard of the soil. The results were given in ohms (The non-affiliated soil analysis working committee, 1990) which was then converted to electrical conductivity (EC) and expressed as mS.m.

Infiltration rates

Adjacent to where each soil sample was taken, infiltration readings were taken. Steady infiltration under tension was determined at a pressure head of 2.0 cm of water using a mini-disk infiltrometer (MDI) (Decagon Devices, Pullman, WA) (Decagon Devices, 2003, Li et al., 2005, Madsen and Chandler, 2007).The infiltrometer was applied to a smooth, flat area on the soil surface, assuring that it made solid contact with the soil surface. The starting water volume was recorded (at time zero) and the volume was recorded at regular time intervals of 30 seconds as the water infiltrated, for a total of five minutes. From this the overall average rate of infiltration, ml infiltration per minute was calculated.

Statistical analysis

Statistica 10 (Statsoft Inc. 2010) was used for the statistical analysis. A full factorial ANOVA was used to determine how the soil variables differed in the three different landscape positions and across the four drainage basin areas (and their interaction). If no significant interaction between position and drainage basin was found, a main-effects ANOVA was performed. In addition, Scheffe's procedure for pair wise comparison was done post-hoc.

Results

The full factorial ANOVA's indicated significant interactions between the drainage basin and landscape position for gradient, pH, sand, silt and clay. Depth and infiltration only had significant differences in either drainage basins or landscape positions, but not on the interaction between basin and landscape position. Electrical conductivity and Na were the only variables that did not show any significant differences across the landscape or across the different drainage basins, and are thus not reported on in detail. The electrical conductivity had a narrow average range of 18 $mS.m^{-1}$ on south facing slopes, to 23 $mS.m^{-1}$ on north facing slopes. Na displayed a similar pattern, whereby the averages ranged from 3 $g.m^{-2}$ on north facing slopes to 9 $g.m^{-2}$ in the valleys.

Table 2.2. displays the results for the soil bulk density measurements of each landscape position in the four basins.

Table 2.2: Average bulk density (BD) measurements of the transects across three landscape positions. North = north facing slopes, South = south facing slopes, Valley = footslope area.

Site	Drainage basin	Landscape position	BD ($g.cm^{-3}$)
1	Fish	North	1.01
1	Fish	Valley	1.43
1	Fish	South	1.12
2	Sundays	North	1.02
2	Sundays	South	1.03
3	Sundays	North	1.02
3	Sundays	Valley	1.11
3	Sundays	South	1.24
4	Sundays	North	1.07
4	Sundays	Valley	1.24
4	Sundays	South	1.62
5	Gamtoos	North	1.41
5	Gamtoos	South	1.13
6	Gamtoos	North	1.02
6	Gamtoos	Valley	1.00
6	Gamtoos	South	1.12
7	Gouritz	North	1.29
7	Gouritz	Valley	1.61
7	Gouritz	South	1.31
8	Gouritz	North	1.27
8	Gouritz	Valley	1.41
8	Gouritz	South	0.99
9	Gouritz	North	1.21
9	Gouritz	Valley	1.20
9	Gouritz	South	1.15
10	Gouritz	North	1.11
10	Gouritz	Valley	1.23
10	Gouritz	South	1.03

Soil depth

Both landscape position ($F_{2, 134}$ = 3.06, p = 0.050) and drainage basin ($F_{3, 134}$ = 2.66, p = 0.051) were drivers of soil depth (Figure 2.2). Valley areas had the deepest soils (22.08 ± 12.75 cm) and were significantly deeper than soils from south facing slopes (16.96 ± 8.57 cm; p = 0.04), but not soils from north facing slopes (19.80 ± 8.74 cm). North facing slopes were on average deeper than south facing slopes. The Sundays basin had the shallowest soils (16.15 ± 10.43 cm), which differed significantly from the Fish basin (22.27 ± 9.19 cm; p = 0.04) and the Gamtoos basin (22.36 ± 7.47 cm; p = 0.01); but the Gamtoos and the Fish basins had soils of similar depths.

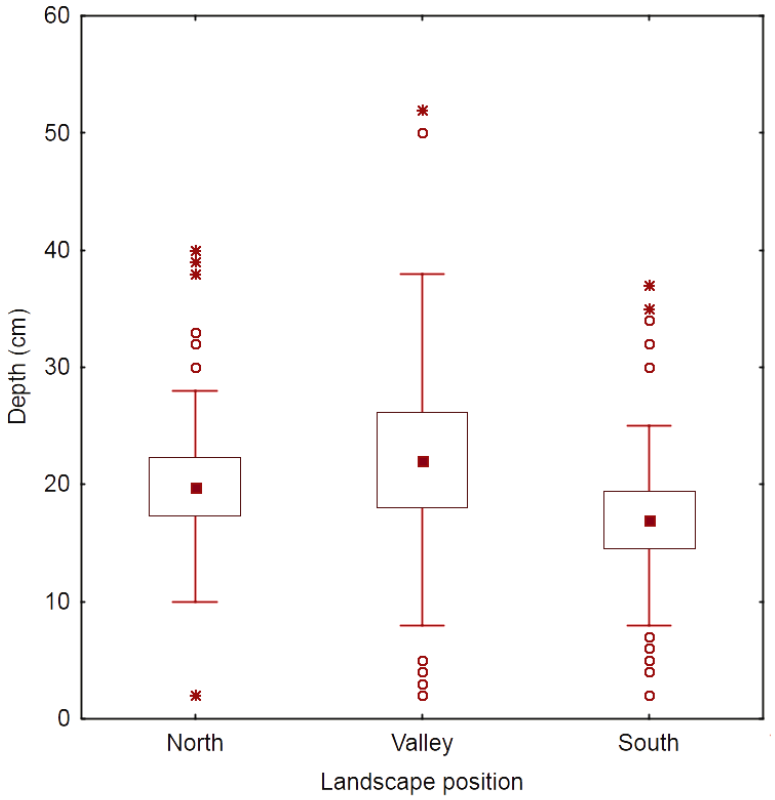

Figure 2.2: Box plots showing average soil depth for all four drainage areas at the three different landscape positions. North = north facing slopes, South = south facing slopes. Filled boxes indicates averages, box indicates average ± 0.95 confidence intervals, whiskers indicates the non-outlier range, circles indicate outliers and stars indicate extremes.

Slope angle

The interaction between the landscape position and drainage basin was significant ($F_{6, 128}$ = 6.30, $p < 0.001$). The valley positions were generally flat and therefore automatically recorded as 0°, hence no differences between the drainage areas. The south facing slopes were generally found to be steeper than the north facing slopes (Figure 2.3). The Gouritz basin was the only area where the north and south facing slopes had a similar slope. Excluding the valleys, the north facing slopes in the Fish area had the gentlest slopes (10.32 ± 0.85°). The south facing slopes in the Sundays area were the steepest (39.19 ± 21.09°), and were significantly steeper than all the other north facing slopes; well as the south facing slopes in the Gouritz area (17.14 ± 8.31°).

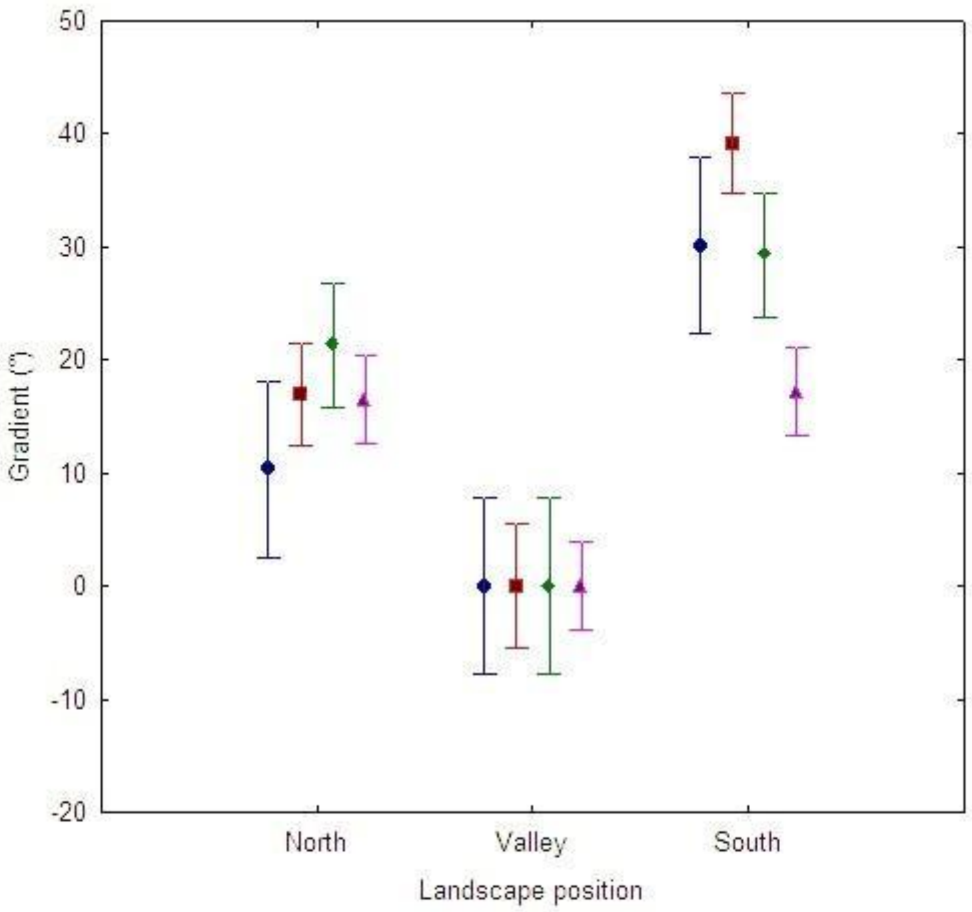

Figure 2.3: Plot of interaction of drainage basin and landscape position for slope. North = north facing slopes, South = south facing slopes. Filled shapes indicate averages, vertical bars indicate 0.95 confidence intervals. Fish drainage basin, Sundays drainage basin, Gamtoos drainage basin, Gouritz drainage basin.

Infiltration

There was no significant interaction between the landscape position and the drainage basin, but there were significant differences in infiltration between the different drainage basins ($F_{3, 134}$ =7.55, $p < 0.001$). Infiltration did not vary with landscape position, and valleys and slopes had similar values ($p > 0.15$). Average infiltration changed from east to west (Figure 2.4), the Fish basin being the most east and the Gouritz the most western site. The average infiltration in the Fish (1.23 $\pm$ 0.64 $ml.min^{-1}$), and Gamtoos (2.02 $\pm$ 1.20 $ml.min^{-1}$) basins differed significantly from the Gouritz basin (3.52 $\pm$ 2.47 $ml.min^{-1}$; $p < 0.01$). Thus infiltration in the Gouritz basin is more than double that of the Fish basin.

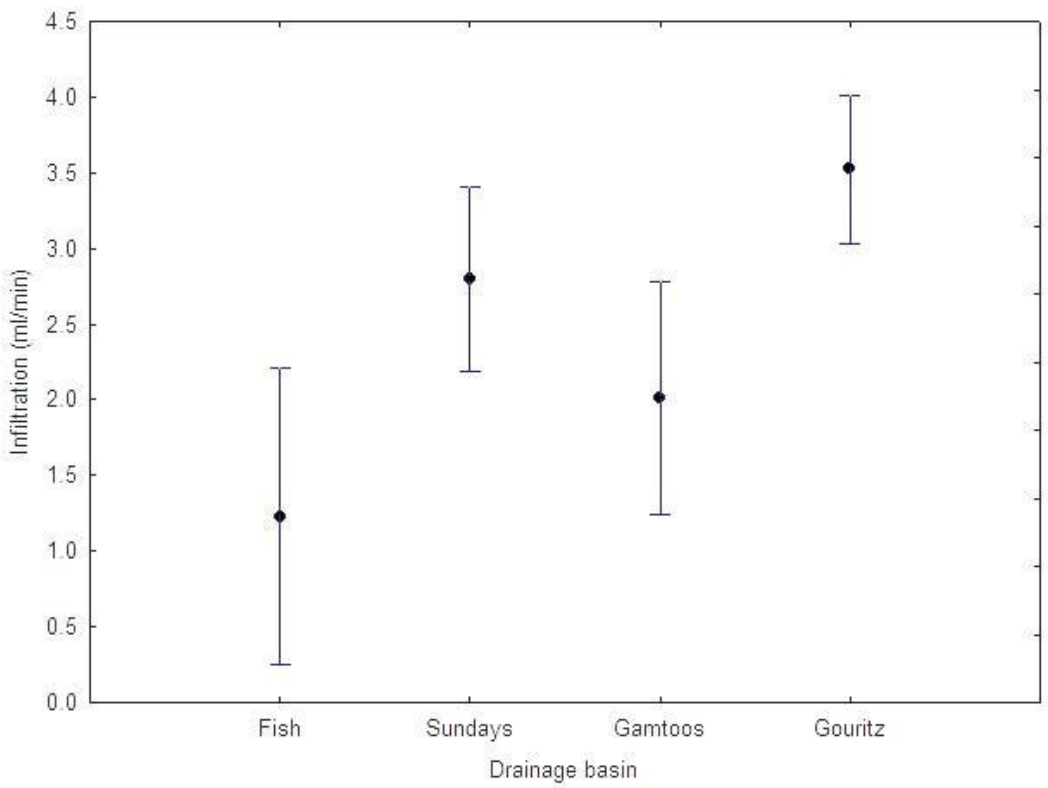

Figure 2.4: Plot showing average infiltration rate for the four drainage areas. Filled circles indicate averages, vertical bars indicate 0.95 confidence intervals.

Soil pH

The interaction between the landscape position and drainage basin area was significant ($F_{6, 123} = 2.65$, $p < 0.019$). The trend was that the valleys were more alkaline than both slopes, except in the Gouritz area, where south facing slopes (average pH 5.78 $\pm$ 0.91) were similar to the valleys (average pH 5.96 $\pm$ 1.49). There was a significant difference between the Gouritz south and north facing slopes (average pH 4.4 $\pm$ 0.81; $p < 0.01$); as well as between the valleys and north facing slopes ($p < 0.01$). These north facing slopes in the Gouritz were also the most acidic of all the recordings (Figure 2.5). The other north facing slopes all had similar readings between 5.11 - 5.19. The Gamtoos and Fish basins in general had very similar pH levels across the different landscape positions.

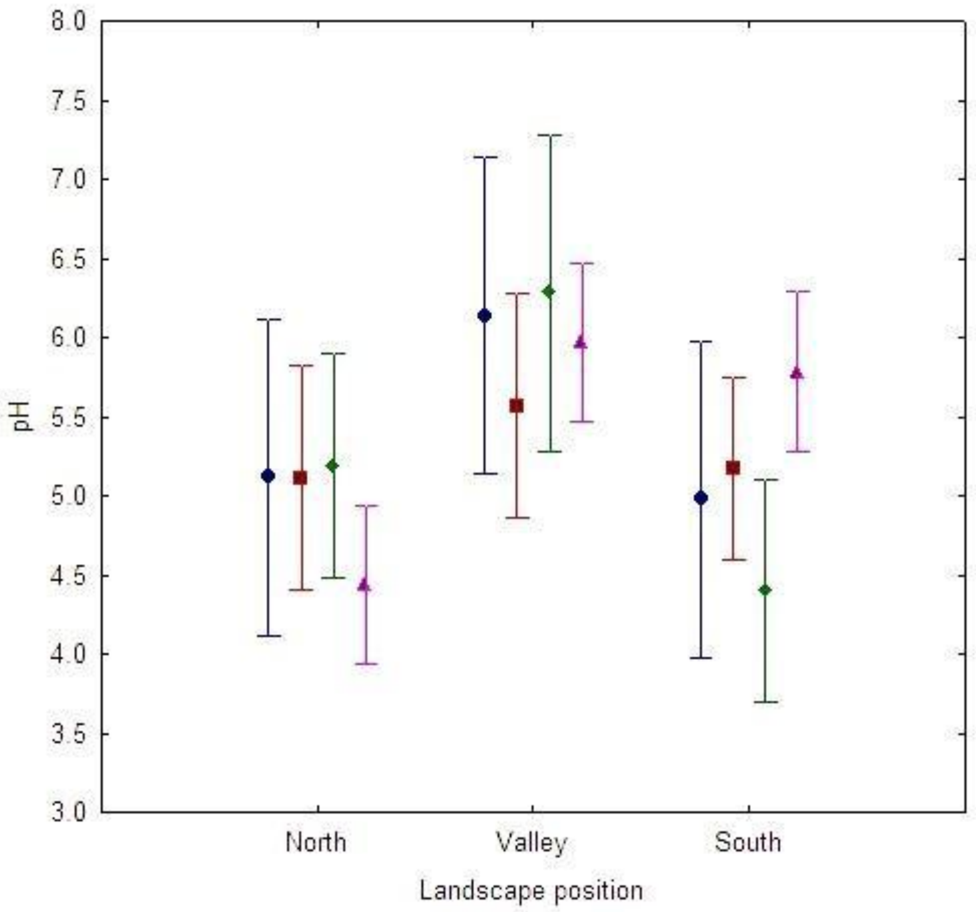

Figure 2.5: Plot of interaction of drainage basin and landscape position for soil pH. North = north facing slopes, South = south facing slopes. Filled shapes indicate averages, vertical bars indicate 0.95 confidence intervals. Fish drainage basin, Sundays drainage basin, Gamtoos drainage basin, Gouritz drainage basin.

Particle size

Sand content

The interaction between the landscape position and drainage basin area was significant ($F_{6, 128} = 10.97$, $p < 0.001$). Sand content on north facing slopes varied greatly across the drainage areas (Figure 2.6). In the Gamtoos, the north facing slopes had the lowest average sand content (50.90 $\pm$ 30.41 %) and were significantly lower ($p < 0.001$) than all other locations, except for the north facing slopes in the Fish. The Gouritz south facing slopes had the highest average sand content (76.25 $\pm$ 5.54 %). All the valleys contained similar sand content, ranging from 78.90 – 82.00 %. The south facing slopes also had high levels of sand, ranging from an average of 75.13 % in the Sundays to 82.60% in the Gamtoos. The Sundays and Gouritz south facing slopes were similar in their average sand contents (75.13 $\pm$ 8.40 % and 76.25 $\pm$ 5.54 %, respectively); as well as the Fish and the Gamtoos south facing slopes (82.00 $\pm$ 7.87 % and 82.60 $\pm$ 3.90 %, respectively).

Silt content

There was a significant interaction between the landscape position and drainage basin ($F_{6, 128} = 7.55$, $p < 0.001$) for silt content. The results for silt content showed very similar trends to the results for the sand content, yet also some differences were found. Silt content on north facing slopes varied greatly across the drainage basins (Figure 2.7), and clearly followed an east-west trend of decreasing silt content ($p < 0.05$), from the Fish area (19.80 $\pm$ 6.72 %) to the Gouritz area (6.35 $\pm$ 2.75 %). The Fish and Gamtoos basins had similar readings for both their valleys and south facing slopes, as was the case with the Sundays and the Gouritz areas. The valley and south facing slopes did not have the extreme variability as the north facing slopes had, with narrow ranges of 6.35–8.40 % for valleys, and 7.60–10.10 % for south facing slopes.

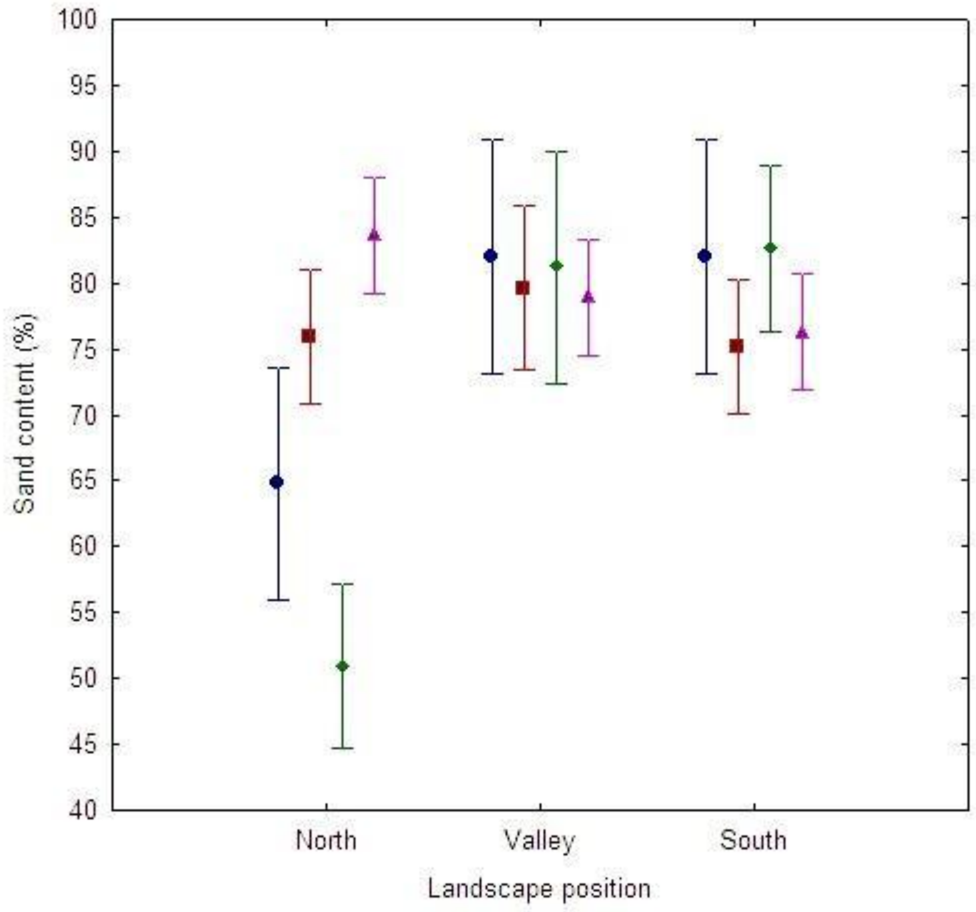

Figure 2.6: Plot of interaction of drainage basin and landscape position for sand content. North = north facing slopes, South = south facing slopes. Filled shapes indicate averages, vertical bars indicate 0.95 confidence intervals. Fish drainage basin, Sundays drainage basin, Gamtoos drainage basin, Gouritz drainage basin.

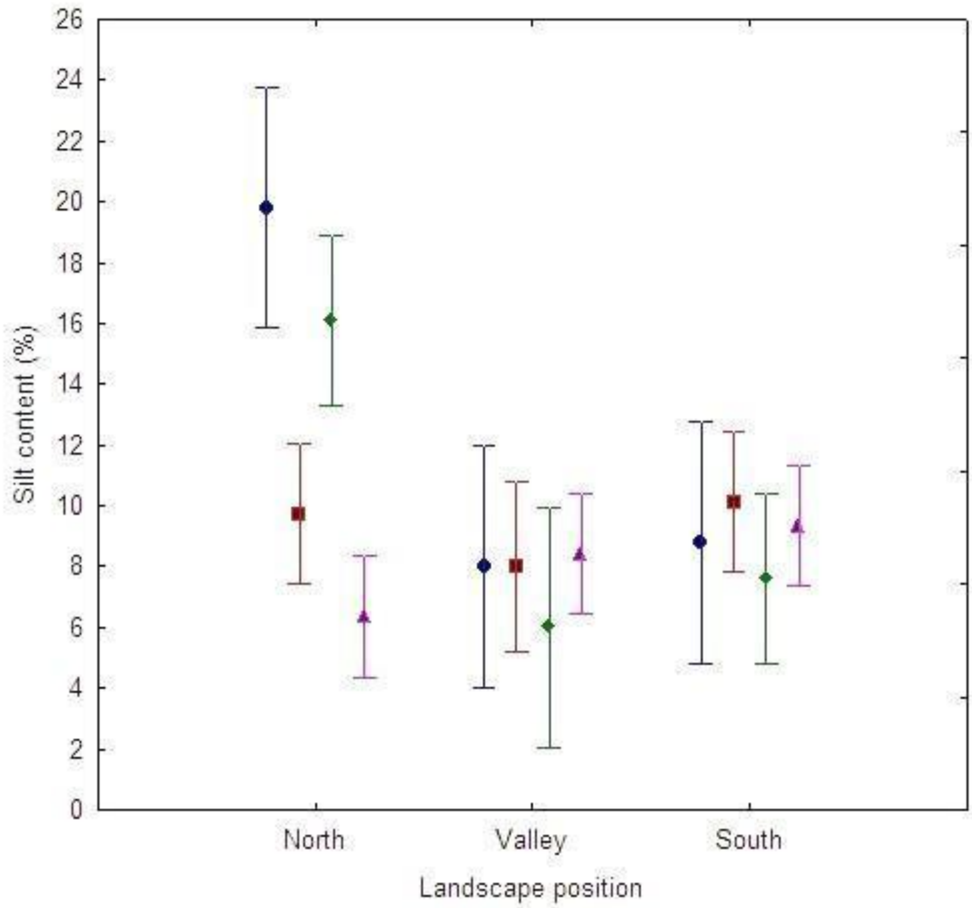

Figure 2.7: Plot of interaction of drainage basin and landscape position for silt content. North = north facing slopes, South = south facing slopes. Filled shapes indicate averages, vertical bars indicate 0.95 confidence intervals. Fish drainage basin, Sundays drainage basin, Gamtoos drainage basin, Gouritz drainage basin.

Clay content

There was a significant interaction between the landscape position and drainage basin ($F_{6, 128}$ =5.30, p < 0.001) for clay content. The average clay content varied significantly between the Gouritz (10.00 + 2.20 %) and Gamtoos (18.10 + 10.71 %) north facing slopes (p = 0.04), but these were the only significant differences in clay on the north facing slopes. The south facing slopes also varied in their clay contents, although the Fish and Gamtoos had very similar values (9.20 + 5.02% and 9.80 + 1.32 % respectively) and the Sundays and the Gouritz had similar results (14.73 + 5.12 % and 14.40 + 5.07 % respectively). For the Fish and the Gamtoos areas, the trend was that silt content increased from the south facing, to the valley, to the north facing positions. In the Gouritz this was the exact opposite, and in the Sundays it increased from the valley, to the south facing, to the north facing slopes (Figure 2.8).

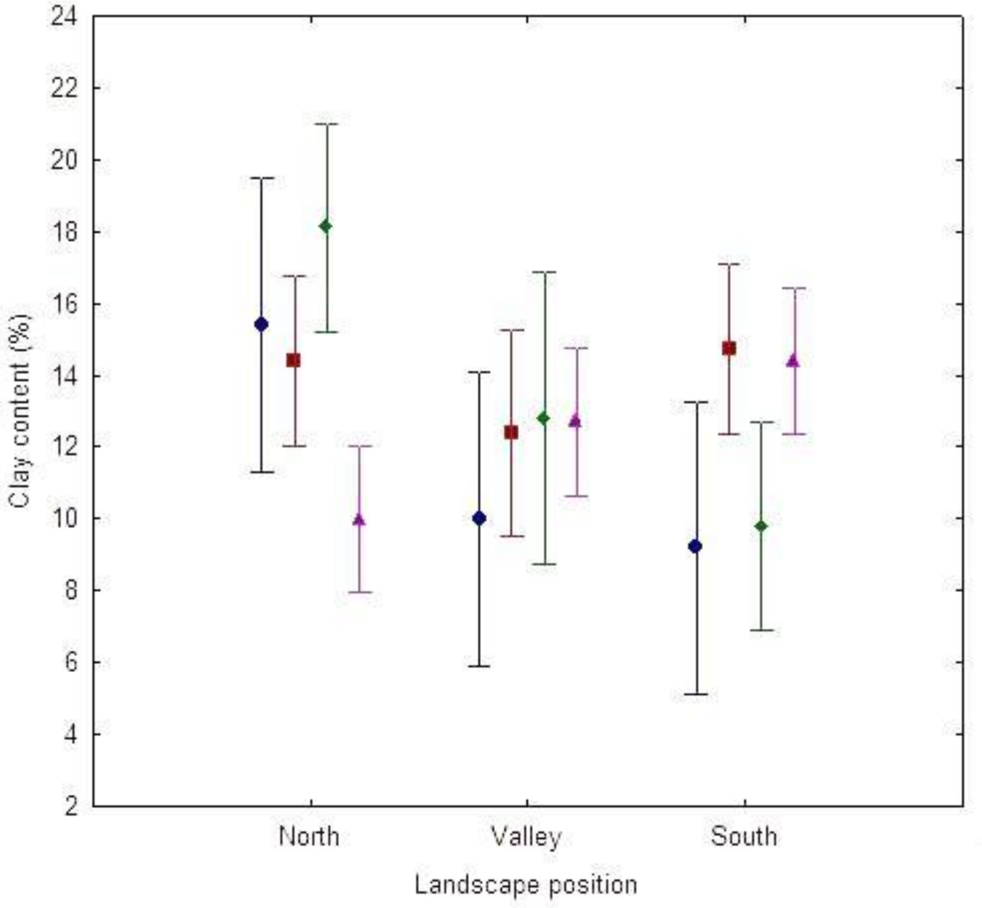

Figure 2.8: Plot of interaction of drainage basin and landscape position for clay content. North = north facing slopes, South = south facing slopes. Filled shapes indicate averages, vertical bars indicate 0.95 confidence intervals. Fish drainage basin, Sundays drainage basin, Gamtoos drainage basin, Gouritz drainage basin.

Discussion

The focus of this chapter was to investigate if spekboom presence at the landscape scale could be related to selected soil and environmental factors. Of the soil variables investigated in this study, I found that only pH and the slope to be significant determinants of the distribution of spekboom at a landscape scale. There was a clear trend in changing texture and infiltration rates in the drainage basins from east to west, but not at the landscape scale. Electrical conductivity (EC) and Na were the only variables that did not indicate any significant differences between the different landscape positions or drainage basins.

Soil pH

The overall trend was that the valleys (where spekboom does not grow) were more alkaline than the slopes. Valley areas were the only factor analysed that seemed to follow the catena effect theory, unlike Na and electrical conductivity, whereby bottomland areas have higher pH levels. The valleys ranged in their average pH 5.8 – 6.3. It is clear that the sites where spekboom grows (all the north facing slopes and the south facing slopes of the Fish, Sundays and the Gamtoos) have lower pH values. Even when regarding the south facing slopes, there is a trend that where spekboom dominates (Fish and Gamtoos basins), soils are more acidic than that of the Sundays, where it is not as dominant. It is also clear that the areas where spekboom does not grow have higher pH values. Research on woody plant forms indicates preference ranges of 5.5 – 7 (Medinski et al., 2010, Mills and Cowling, 2006). Research from other intact thicket areas also supports this (pH range 4.8 – 6.04) (Lechmere-Oertel et al., 2005b, Mills and Cowling, 2010a, Rutherford et al., 2012). Thus spekboom may be avoiding the soils with higher pH values.

Particle size

The importance of soil texture or particle size, especially of clay, has already been mentioned. All three size classes of sand, silt and clay, showed interesting and generally quite similar results, whereby all the valleys and south facing slopes had similar results, and the north facing slopes had great variation between the different drainage basins. The north facing slopes had clear west to east trends, whereby sand decreased, and silt and clay increased, although the trend with clay was not as pronounced as in the case of silt. These results could be due to the underlying geology (Bell, 1982), where soils from the Enon conglomerate (Uitenhage group) tend to have a lower coarse sand content and greater fine sand content than Bokkeveld shale derived soils (Mills and Fey, 2004a).This supports the suggestion that spekboom is tolerant of a wide range of soil conditions and grows on a variety of geologies (Mills et al., 2011, Vlok et al., 2003). All the valleys had very similar results, regardless of basin. It was only clay content that differed slightly between the different valleys. The wide range of particle size contents on the north facing slopes poses an interesting question: as all the north facing slopes were dominated by spekboom, that would indicate a wide range of tolerance to different soil textures. But why then is spekboom not growing in the valleys, whose various particle size content range falls within this 'tolerance range'? The silt and sand contents showed a trend that the valley areas had similar recordings to those found on the north facing slopes in the Gouritz basin. Although spekboom does grow well on these slopes, it is the area where it mosaics with Succulent Karoo vegetation, and is not as dominant in the vegetation as it is in Spekboomveld in the Sundays and Fish basins. It is also the most western end of Thicket's distribution, therefore one could deduce that the north facing slopes in the Gouritz indicate an almost 'threshold point' regarding soil texture.

Texture can have a major influence on plants as it determines where water is stored, infiltration rates and the tendency of the soil to crust (Mills and Fey, 2004a, Perrolf and Sandstroem, 1995, Powell, 2009). There was a wide range of sand content (~ 40 – 80 %) that spekboom was found on, which is not unusual, as previous research has shown sand in intact Thicket to range from 35 % (Mills and Cowling, 2010a) to 84 % (Rutherford et al., 2012). Coarser soils allow rapid infiltration of water , as well as holding it at higher water potentials, thus making it more readily available to plant roots to extract, as compared to fine textured soils (HilleRisLambers et al., 2001, Palmer, 1990). Coarser soils also favour plants with deeper root systems, such as woody vegetation (Lechmere-Oertel and Cowling, 2001). In the Fish River Reserve Mills et al. (2011) found that spekboom cover is constrained at extreme (both high and low) levels of sand content, and that spekboom is most competitive in intermediate levels.

The high range for silt content (7 – 20 %) was surprising, given the fact that even low silt contents in sandy soils can produce a seal, thereby limiting the entry of water into soil (Perrolf and Sandstroem, 1995). Also, results from other intact Thicket indicates silt contents of 8 - 13 % in the Sundays (Mills and Cowling, 2006, Mills and Fey, 2004a, Rutherford et al., 2012) and 11 % in the Baviaanskloof (Gamtoos basin) (Mills and Cowling, 2010a). Clay did not show the wide range in results as sand and silt did, and it also did not follow the same trends regarding the valley areas. The true Spekboomveld north facing slopes ranged in their clay contents from 14 – 18 %, whereas the Gouritz basin slopes were considerably lower at 7 %. This supports other research in intact Thicket, where clay ranges from 5 % near Jansenville (Rutherford et al., 2012), to 8 % near farm Krompoort (Mills and Cowling, 2010a) to 16 % in the mosaics with Succulent Karoo (Beukes and Ellis, 2003b). Although the plant can grow on a variety of geologies (Vlok et al., 2003), it tends to be more associated with nutrient and clay rich soils derived from shale and mudstones (Cowling, 1984); which are known to contain higher silt and clay contents than sandstone derived soil. (Lechmere-Oertel and Cowling, 2001). However, there were also some irregularities with clay on the south facing slopes, where the slopes that did have spekboom present were lower in their clay contents than the slopes that did not have spekboom. It was also unusual that the south facing slopes in the Gouritz and Sundays had contents of 14 %, which would be within the range of spekbooms 'tolerance', yet spekbooms presence is limited to non-existent in these areas. The same argument stands for the valleys, where it would be expected that soils would contain higher amounts of fine material, especially clay from being washed down slope (Ben-Shahar, 1990, Van der Merwe et al., 2002, Yanagisawa and Fujita, 1999).

Slope

Steep slopes (of approximately 19° or more) have been recorded as where spekboom-dominated Thicket grows (Mills et al., 2011, Oakes, 1973, Rutherford et al., 2012, Vlok et al., 2003), which was generally reflected in my results. However, if this was the case then all the south facing slopes should be covered with spekboom, which is not the situation either. One theory is that the amount of solar radiation a slope receives could influence a plant's responses, because it affects surface energy budgets, temperatures and soil moisture balances; and could be regarded as one of the fundamental variables of the plant environment (Ciolkosz, 2009, Granger and Schulze, 1977, Zachar, 1982). In the middle latitudes (around 33°) solar radiation differences in aspects are greatest, and south facing slopes show declining energy load with increasing slope angle (Holland and Steyn, 1975), which is especially prevalent in winter (Schulze, 1975). Such contrasting and permanent differences in radiant energy may cause a variety of microenvironments that consequently affect vegetation development (Granger and Schulze, 1977). The considerably lower radiation loads on southern aspects in autumn through to spring, creates a more mesic soil moisture regime (Granger and Schulze, 1977). This results in the establishment of mesic thicket species to the detriment of spekboom, which is most competitive in arid environments (Mills et al., 2011). The differences in radiation loads could thus account for the different vegetation composition on north and south slopes. However, if this was purely the situation, one would expect the south facing slopes in the Gouritz basin of only 17° to be more dominated by spekboom than the much steeper slopes (30 - 50°) of the other three basins, because according to this theory, these south facing slopes of the Sundays, Fish and Gamtoos would barely receive any sunlight during the winter months. Yet this is the opposite, and the Gouritz is the only basin where south facing slopes were completely devoid of spekboom.

The situation in the Gouritz area could be due to a more complex relationship with temperature and rainfall patterns, as this basin receives less rainfall than the other basins further east. It is also more prone to frost than the other areas. Holland and Steyn (1975) noted that as rainfall declines, Cape sclerophyll plant communities become more restricted to the upper reaches of south facing slopes. The effect of temperature on spekboom distribution is not clear. Although spekboom can survive in areas subject to frost and occasional freezing temperatures, it grows much better in frost-free areas (Oakes, 1973). It is as Holland and Steyn (1975) remark, in South Africa where Karoo, Cape sclerophyll plant and forest communities mingle, each community occupies the topographic situation most suited to the physiological requirements of its species.

Electrical conductivity and sodium

Electrical conductivity (EC) and Na were the only variables that did not indicate any significant differences between the different landscape positions or drainage basins. EC is a measure of the salt content of the soil (Flynn, 2005), and accumulation of salts are due to geologic, climatic and topographic factors (Metternicht and Zinck, 1997). I found it surprising that EC did not differ among the landscape positions, or drainage basin areas of different geologies. However, according the US Salinity Laboratory classifications for soils, all the soils sampled in this study are deemed non-saline (below 400 $mS.m^{-1}$) (Metternicht and Zinck, 1997), irrespective of landscape position.

Na had similar results as EC, where there was very little variation in its concentration between the slopes and valleys. As in the case above with EC, it was partly expected that Na would be higher in the valley areas (Fraser et al., 1987). The current literature regarding soil characteristics in Thicket focuses on C, pH, N, P and Ca; and there is no work where Na is included in the analyses; therefore there is no information on Na in intact Thicket areas to compare my results to. My results disprove my hypothesis that Na and salinity would be higher in the lower lying areas due to a catena effect, which has also been documented in the Northern Sonoran Desert (Parker, 1991).

Soil Depth

The results for soil depth indicated that valleys were deeper than the slopes, which generally conforms to the norm, where crests of mountains consist of shallow soils and due to the movement of particles down slope, lower slope positions accumulate soil (Chapin et al., 2011, Fraser et al., 1987, Metternicht and Zinck, 1997, Ni and Zhang, 2007). However, I think this is a debatable point. Firstly, the level of significance was very borderline, and the significant difference in soil depth between valleys and south facing slopes was very small. The same applies to the difference, which was not statistically significant, between the north facing slopes and the valleys. The slopes also had a large range of soil depths, up to 40 cm in some areas. In general Spekboomveld is reported as being confined to moderately deep soils (Kerley et al., 1995, Stuart-Hill, 1992, Vlok et al., 2003). Thus I would say this is not a clear indication that soil depth is a driver of spekboom presence.

Infiltration

Infiltration, as in the case of soil depth, did not show any differences between the slopes and valleys, which is also unusual. Infiltration is also difficult to measure because it is easily influenced, for example, by unseen rocks just under the device or soil crusting. The results showed a wide range of average infiltration rates from east to west (1.23 – 3.52 $ml.min^{-1}$), which is probably due to a combination of the variety of soil types and differences in vegetation cover (Perrolf and Sandstroem, 1995) across the four basins. The soils in the Fish, Sundays and Gamtoos basins are dominantly derived from shales and mudstones, which give rise to clay-rich/ clay loam soils, which can be more prone to sealing and limiting water entry into the soil. The mountains in the Gouritz basin generally consist more of coarse, sandy soils derived from Enon conglomerates (Uitenhage group), which allow rapid infiltration of water (HilleRisLambers et al., 2001, Palmer, 1990).

Conclusion

Across the Thicket biome spekboom dominates landscapes in the form of Spekboomveld or Spekboom Thicket (Vlok et al., 2003), and it does so across an exceptionally wide range of climatic and soil conditions, from approximately 200 to 500 mm mean annual rainfall, on nutrient-rich, alkaline shale-derived soils as well as nutrient-poor, acidic sandstone-derived soils (Mills et al., 2011). It was therefore suggested by Mills et al. (2011) that spekboom is tolerant of a wide range of soil conditions and is unlikely to be constrained by a host of soil properties. To answer whether spekboom distribution is related to soil factors, I found that other than pH, slope (interlinked with aspect) and possibly texture, there are no clear trends emerging, and there is a large degree of overlap in soil properties where spekboom does and does not occur. To answer whether spekboom distribution is related to position in the landscape, I found that pH and slope were factors that determined spekbooms preference for hill slopes and not valleys.

Mills et al. (2011) ruled out a catena effect in the Fish River Reserve because spekboom is located more on the crests of hills than in mid-slopes where nutrient contents would be intermediate. I also agree with their argument regarding catena effects, because with most of the variables I analysed this theory was contradicted, where the lower slope positions did not respond as was expected (increased saline and Na levels, decreased infiltration, increased clay content). It could be argued that the catena effect where lower positions accumulate soil and nutrients applies to mountain slopes that consist of shallow, leached, coarse, sandy soils (Ben-Shahar, 1990, Chapin et al., 2011, Fraser et al., 1987, Metternicht and Zinck, 1997, Ni and Zhang, 2007, Schimel et al., 1985, Yanagisawa and Fujita, 1999), and in this study area this is not applicable to the dominantly clay-rich, shale derived soils. However, it should be noted that in some areas it was difficult to find suitable valley locations because the slopes were so steep and grading into each other. Therefore to find a suitable location for the transect sometimes meant being a bit further up the footslope and quite close to spekboom, which could affect the results.

As Mills et al. (2011) concluded, what constraints spekboom in the Fish River Reserve is probably a function of correlated factors related to position in the landscape (e.g. temperature or frost) and/or competition from other plants, and this could well be the case for the broader biome. The nature of the constraint or patchy distribution of spekboom requires further investigation, especially regarding the influence of frost, temperature/ solar radiation, together with rainfall patterns, which vary considerably across the biome (from a predominantly more summer rainfall area in the east to the more winter rainfall area in the west).

Chapter 3 - Response of *Portulacaria afra* cuttings to varied soils and salinity conditions

Abstract

A significant factor to the success of any restoration project is an understanding of the ecology of the key species that are used for such work. *Portulacaria afra* (spekboom), a dominant species in drier Subtropical Thicket of South Africa, is a poorly understood plant species that is being extensively used for restoration of degraded, semi-arid Thicket. Observations have indicated that spekboom does not grow well in saline soils (Hobson et al., 1975) characteristic of lower lying, bottomland areas, where salts in the soil tend to accumulate after being washed down slope, or from evaporation in the soil. This chapter explores the notion that soil salinity (NaCl), sodium (Na) or soil type could be affecting spekboom survivorship, growth, and overall plant condition in restoration sites. This was done by measuring some parameters of growth (i.e. stem diameter, leaf number, leaf colour and root:shoot ratio) of 240 spekboom cuttings being subjected to various salinity levels over a 10 month period. Two different soil types, a Na-clay rich, and a Na-poor sandy soil were watered with rainwater (low in NaCl) and borehole water (high in NaCl) to create four treatment combinations of increasing salinity. Soil type did not emerge as a significant factor, but the water type did have a significant impact. Plants in the rainwater treatments always responded positively compared to the plants in the borehole water treatments, in terms of an increase in leaves (39 % vs 29 %, respectively) and an overall increase in stem diameter (~ 80 % vs ~ 40 %). The treatments receiving the rainwater also had on average 60 % of their plants changing to a greener leaf colour, while the plants in the borehole water treatments became more yellow, which is indicative of plant stress. The plants in the rainwater treatments also had increases in their root weights, while the plants in the borehole water treatments decreased in root weight after 10 months (from their original weight). Although the borehole water treatments showed limited signs of growth, their high survival rate was un-expected, indicating a degree of tolerance to high salinity conditions. My experiment indicates spekboom tolerates different soil types but its growth is negatively affected under saline conditions. These findings have important implications for restoration managers.

Introduction

Where Spekboomveld (*Portulucaria afra*- dominated vegetation) occurs in the Albany Thicket biome of South Africa, *P. afra* (hereafter spekboom) is largely restricted to hill slopes, preferring the crests and midslopes of hills, and decreases with distance down slope (Mills et al., 2011, Oakes, 1973). Spekboom is a leaf succulent species that exhibits both Crassulacean Acid Metabolism (CAM) and C_3 photosynthetic pathways (Guralnick et al., 1984, Ting and Hanscom, 1977). CAM succulents generally occupy shallow soils and rocky terrain (Ware, 1990), which is characteristic of many hill slopes of Spekboomveld (Vlok et al., 2003). Spekboom is generally absent from bottomland habitats, although exceptions do exist. Owing to the weathering of parent rock, which releases soluble salts (mainly calcium, magnesium and chlorides of sodium), and through the sorting and moving of soil particles down slope, bottomland localities accumulate high concentrations of elements. Known as 'catena effect' (Ni and Zhang, 2007, Schimel et al., 1985, Yanagisawa and Fujita, 1999), and in semi-arid areas this often creates large areas of saline, impenetrable soil surfaces in bottomland areas (Allison et al., 1954, Ben-Shahar, 1990, Fraser et al., 1987, Metternicht and Zinck, 1997, Mills and Cowling, 2010a, Munns and Tester, 2008, Parker, 1991). Catena's are often found in the Karoo (Esler et al., 2002, Le Maitre et al., 2007, Milton and Dean, 1995). Goundwater sampled from valleys and flat areas in the Karoo has higher concentrations of chloride (Cl) and Na, than that of the surrounding hill slopes (Adams et al., 2001). Hobson et al. (1975) have observed that spekboom avoids saline and lime-rich soils. This stimulated the hypothesis that spekboom distribution could be constrained by salt (NaCl) or sodium (Na) levels in the soil.

While other species of the Didiereaceae – the family to which spekboom belongs - such as *Portulaca oleracea,* are relatively well researched in terms of its ability to handle saline environments (Dagar, 2000, Kafi and Rahimi, 2011, Nyffeler, 2007, Rahdari et al., 2012, Yazici et al., 2007), it too is susceptible to high salinity levels and has been classified as "moderately salt tolerant" (Dagar, 2000, Kafi and Rahimi, 2011, Shannon and Grieve, 1999, Yazici et al., 2007). Information regarding spekboom's tolerance is extremely limited or 'unknown', according to Dagar (2000). Ting and Hanscom (1977) observed that spekboom responds the same to salt stress (using a 2 % NaCl solution) as it does to water stress, displaying an almost complete termination of transpiration and limited growth. When stressed, spekboom switches from a C_3 mode of gas exchange to CAM type CO_2 uptake in order to conserve water and energy (Guralnick et al., 1984, Guralnick and Ting, 1986, Guralnick and Ting, 1987, Kerley et al., 1995, Oakes, 1973).

Soil salinization is one of the world's oldest and most serious environmental problems, affecting almost 1 billion hectares of land (Munns and Termaat, 1986, Ottow et al., 2005). This is especially the case in arid and semi-arid regions (Allison et al., 1954, Ashraf and Harris, 2004, Belkheiri and Mulas, 2011, Munns and Tester, 2008), where it's common for large areas of saline soils to form, especially in areas where grazing has accelerated erosion and runoff (Walters, 1951). Evaporation rates increase with the removal of vegetation, causing salts in the soil to concentrate in the upper layer of the soil, which inhibits plant growth and survival (Allison et al., 1954, Van de Koppel et al., 1997). Especially in arid areas, the concentration of salts in the soil is a major factor influencing the distribution of vegetation (Kargar Chigani et al., 2012, Medinski et al., 2010). Salt stress affects plant processes such as photosynthesis, nutritional balances, metabolism and concentrations of ions, which can result in oxidative stress and plant death (Ashraf and Harris, 2004, Belkheiri and Mulas, 2011, Jennings, 1968, Medinski et al., 2010, Munns and Tester, 2008, Ottow et al., 2005, Tuna et al., 2007, Van de Koppel et al., 1997).

Salinity is a condition characterized by a high concentration of soluble salts, such as Cl, Ca, carbonates of Na, sulphates (SO_4) or magnesium (Mg), on the soil surface, in the subsoil, and in groundwater (McKenzie, 2003, Metternicht and Zinck, 1997). NaCl and calcium sulphate ($CaSO_4$) are examples of these soil salts (McKenzie, 2003). Soils are classified as saline when the electrical conductivity (EC) is 400 mS/m or more and when the pH is generally less than 8.5 (Allison et al., 1954, Munns and Tester, 2008), and are often recognised by the presence of white crusts on the soil surface (Allison et al., 1954). Soils can also be sodic, whereby the soil contains high levels of Na (McKenzie, 2003).

Since 2004 the Subtropical Thicket Restoration Programme (STRP) in South Africa has been using spekboom cuttings to initiate restoration of spekboom-dominated thicket on a landscape scale, and therefore any knowledge relating to the relationship between spekboom and soils is valuable (Marais et al., 2009, Mills et al., 2010b). The rationale for this study is to provide guidelines to restoration managers of the STRP who need to know where restoration work is likely to produce the best survival rates and subsequent returns on investment.

The aim of this chapter is to investigate the responses of spekboom cuttings when grown in soil with high and low levels of Na and how the response interacts with high and low levels of NaCl in water. The specific objectives of this study are to investigate: 1) How is above-ground spekboom growth affected by soils and water with different levels of Na and Cl?

2) How are root:shoot ratios of spekboom affected by soils and water with different levels of Na and Cl?

I hypothesise that plants growing under low saline conditions would survive and grow the best, by increasing in stem diameter, leaf number, and root to shoot ratio. They would also portray a healthier state through greener leaf colour. On the other hand the plants subjected to high salinity conditions would most likely senesce or die, and if they do survive, they would not increase in stem diameter or root to shoot ratio. Their overall condition would be poor with yellow leaves and low leaf numbers.

Materials and Methods

Location and climate

The experimental trial took place at the Renu-Karoo nursery in Prince Albert (33° 11’ 51.46” S; 22°01’ 46.62” E), which is located in the rain shadow of the Swartberg Mountains, and the mean annual precipitation (MAP) range is low, between 165 - 200 mm (data from S.A. Weather Bureau). The rainfall pattern is equinoctial, with the highest peaks between March and April, and between October and November. The overall mean annual temperature is 16°C, and the temperatures range from below 0°C to above 30°C. Frost incidence is approximately 26 days. The experimental plots were located in the open areas at the nursery and had no covering, in order to create the most natural conditions possible, regarding exposure to sunlight, temperatures and natural rainfall. The total amount of rainfall recorded at the nursery over the experimental period was 134.5 mm, which fell mostly over the summer months of December (25 mm), January (8 mm), February (3.5 mm), March (26 mm) and April (33 mm).

Experimental planting design

To determine the effect of water and soil salinity on spekboom, 240 rooted spekboom plants were planted in planting bags of different soils supplied by the Renu-Karoo Nursery. Two soils were used: a clay-rich, sodium-high (hereafter referred to as clay soil), and a sand-rich, sodium-poor soil (hereafter referred to as river sand). It should be noted that although both soil types are local to the area, none of their associated habitats supports spekboom. Spekboomveld grows on the quatzitic slopes immediately south of the town.

The plants were watered with two concentrations, extremely high and low (hereafter referred to as borehole and rainwater respectively) of saline water. The plants were watered for a period of 10 months, from spring (end August) 2011 to beginning of winter (end June) 2012. It was decided not to let the experiment run for a full year as frost in winter has the potential to damage plants (S.J. Milton, pers. comm.).

All rooted plants were supplied by the nursery. Plants were removed from the potted soil and all excess soil carefully removed from their roots, so as not to damage the roots. All the plant stems were measured, just above where the roots begin to grow, and cut to a length of 20 cm. The point on the base of the stem, from where the start of the stem was measured, was marked. Care was taken that each plant consisted of a single stem, and side branches were removed. The diameter of the stem was measured at the base of the stem at the marked point with the use of vernier callipers. All plants had a minimum of 10 leaves, and the colour of the leaves was recorded at the beginning and the end of the period.

Samples of each soil and water type were sent to Elsenburg Laboratory, Institute for Plant Production, Stellenbosch, South Africa, for analysis (Table3.1). The soils were analysed for extractable sodium (Na) with 1 % citric acid by using a Thermo ICP iCAP 6000 Series Spectrometer (Thermofisher Scientific, Surrey, UK), and texture, where clay content was determined by the hydrometer method, sand by sieving and silt by the difference (Day, 1956, Elliott et al., 1999) (Table 3.1). The two types of water used consisted of borehole water and rainwater. These two water types were analysed for Na (3120 B Inductively Coupled Plasma Method) and chloride (Cl) (4500-Cl B Argentometric Method) (Clesceri et al., 1989). The results of the analysis of the water types showed that the rainwater had a Na content of 1 mg/L and a Cl content of 3.55 mg/L; and the borehole water had a Na content of 348 mg/L and a Cl content of 1242.50 mg/L.

The rooted plants were divided so that 120 were planted into each of the two soil types. Black planting bags (size 2 L) were used, and small stones were placed in the bottom of the bag to aid drainage, and then filled with the relevant soils, leaving a space from the rim of the bag (~ 4 cm) for water. Open areas at the nursery were selected and black plastic sheeting was laid down on the ground which prevented plant roots that might escape the planting bags from growing into the ground. Eight areas were laid out in this manner (see Figure 3.1) and the plots were laid out as follow: each plot contained 30 plants, 15 planted in clay soil and 15 in river sand, which were randomly put into five rows of six plants each. The groups were labelled A – H, where four groups were watered with borehole water, and four groups were watered with rain water. Watering was done by hand and with a watering can. This created four treatment combinations to be tested, with 60 plants in each treatment. For the first month the plots were watered twice weekly with their respective water types. After the first month, they were watered once weekly.

Plant measurements

In order to ascertain the effect of the treatments on plant growth and survival, both non-destructive and destructive measurements were taken. In agronomy, the typical variables to consider for salinity tolerance are survival, plant height and leaf injury (Ashraf and Harris, 2004).

For each plant, stem diameter was measured at the base of the stem where it was marked; and this was done at the commencement of the experiment, after five months, and at the end of the time period (called T1, T 2 and T3, respectively). As the difference in diameter between T1 and T2, and between T2 and T3 was so marginal, the difference between T1 and T3 was used instead to indicate increase in stem growth. These results were grouped into diameter classes of 0 mm, 1 – 4 mm, 5 – 8 mm, and equal to or greater than 9 mm. It should be noted that although the diameter of a plant did not increase, it did not necessarily die. The number of mature or fully developed leaves on each plant was counted at T2 and at T3, and the difference between T2 and T3 (either an increase or decrease) was expressed as a percentage of the total number of leaves at the end of the experiment (T3) for each plant.

It is generally accepted in the agronomy literature that changes in leaf colour are an indication of plant health or nutrition deficiencies (Allison et al., 1954, Murakami, 2005). In the case of spekboom changes in leaf colour from a grey green colour to yellow are due to age and stress (Baran, 2011). Therefore, leaf colour was deemed a suitable parameter to be measured, which was performed by comparing leaves to a RAL Colour Chart (Colour Coatings South East Limited, n.d.), using the colour of the majority of the leaves, but taking care not to use the colour of a new shoot, which could differ in colour from mature leaves. I recorded the colour at the commencement and termination of the experiment. Similar colours were grouped together to create five colour classes, whereby “Colour 0” comprised dead plants, “Colour 1” was yellow, “Colour 2” was yellow-brown, “Colour 3” was yellow to burnt orange, “Colour 4” was light grey-green, and “Colour 5” was dark green. Frequency tables were used to display the before and after results, which also indicate that at the start of the experiment the plant leaves ranged in colours.

Root to shoot ratio’s were measured for a sub-sample of 10 randomly selected plants just before planting began. At the end of the experimental period 10 randomly selected plants from each treatment combination were selected, and the root to shoot ratio was calculated, in order to see the effect of salinity on plant growth and condition in spekboom. The root to shoot ratio (R:S) is defined as the dry weight of the root biomass divided by the dry weight of the shoot biomass, after drying in an oven at 65°C for 48 hours (Rogers et al., 1995).

Statistical analysis

Statistica 10 (Statsoft Inc. 2010) was used for the statistical analysis. Frequency tables were used to display leaf colour changes. Full factorial ANOVA was used to determine the effects of soil and water (and their interaction) on leaf numbers. Differences in stem diameter were analysed across treatments using the Pearson‘s Chi-square test. The Kruskall-Wallis test, a non-parametric ANOVA, was used to identify significant differences of R:S ratio within treatments.

Table 3.1: Analysis of the two soils used in experimental planting trail.

Soil Name	Sodium (Na) (mg/kg)	Sand (%)	Silt (%)	Clay (%)
River sand	8	90	3	7
Clay	473	70	11	19

Figure 3.1: Layout of experiment (1 plot). Photo: C.Becker.

Results

There were significant treatment effects on spekboom growth and survival. The water treatment significantly affected above-ground growth parameters, but soil type did not play a significant role in any of the parameters measured.

Stem diameter

There was a significant effect of treatment on stem diameter growth (X^2 (9) = 57.3, p<0.0001) (Table 3.2). The most commonly seen increase in stem diameter over the test period was in the 1 – 4 mm class, of which both treatments receiving rainwater dominated this class. Overall, approximately 40 % of the plants (97 of the 240) did not increase in stem diameter, but as the 0 mm class encompasses both living and dead plants that did not increase in size, it is not possible to say what percentage died. However, the 0 mm class was dominated by the two groups receiving borehole water, which both had more than 60 % of their individuals in this class. Table 3.2 indicates the number of individuals in each class, as well as the percentage, in brackets, out of 60. The groups that received borehole water also had the least total stem diameter growth (37 % for the river sand group and 38 % for the clay soil group). The groups receiving rainwater had the highest percentages of growth (85 % for the river sand group and 78 % for the clay soil group). The river sand and rainwater treatment also dominated the 5 – 8 mm and the > 9 mm classes (16 % and 10 % respectively).

Table 3.2: Changes in stem diameter from commencement to termination of experiment (T1-T3) across treatments W1 = rainwater, W2 = borehole water, S1 = river sand, S2 = clay soil. Plants with stem diameter growth is the total number of plants that did increase in size (≥1 mm) out of 60 plants. Numbers in brackets indicates a percentage of the treatment (60 plants per treatment).

Treatment	**Diameter classes (mm)**				**Plants with stem diameter growth**
	0	1 - 4	5 – 8	> 9	
W1-S1	9 (15)	35 (58)	10 (16)	6 (10)	51 (85)
W1-S2	13 (22)	37 (62)	9 (15)	1 (2)	47 (78)
W2-S1	38 (63)	16 (27)	6 (10)	0 (0)	22 (37)
W2-S2	37 (62)	19 (32)	2 (3)	2 (3)	23 (38)
Totals	97	107	27	9	

Leaf number

The increase in the number of leaves was expressed as a percentage increase of leaves of each plant at termination of the experiment. The full factorial ANOVA indicated that the interaction between the soil type and the water type was not significant; therefore a main effect ANOVA was performed. The results indicated that only the water type had an effect on the number of leaves gained over the study period ($F = 9.06$, $df = 1$, $p = 0.003$). The treatments receiving rain water had a significantly ($p = 0.003$) higher average increase in leaf numbers (39.4 %), compared to the groups receiving borehole water (29.5 %). Figure 3.2 and Figure 3.3 (C,D,E,F) displays the results of the different treatment combinations at the end of the experiment, whereby the highest increase in leaf numbers was found with the plants in clay soil and receiving rainwater (44 ± 26 %). The group in the river sand receiving rain water had a lower increase (34 ± 21%) in leaves. The two groups receiving the borehole water yielded very similar results, irrespective of the soil types; river sand (30 ± 23 %) and clay soil (28 ± 31 %). The difference in appearance of the plants can be seen in Figure 3.3, from the start of the experiment (Figure 3.3 A) to termination of the experiment (Figure 3.3 C,D,E,F).

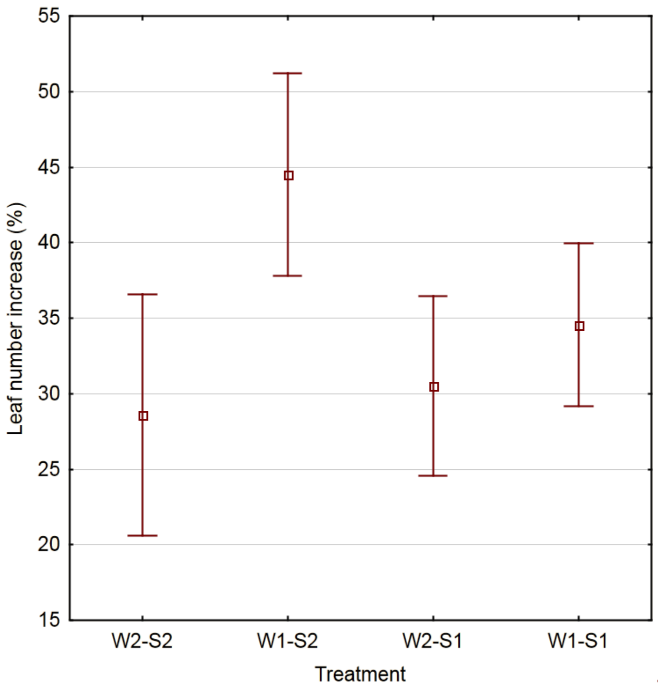

Figure 3.2: The percentage leaf numbers increase for the four treatment combinations: W1 = rainwater, W2 = borehole water, S1 = river sand, S2 = clay soil. Squares indicate means, whiskers indicate mean ± 0.95 confidence interval.

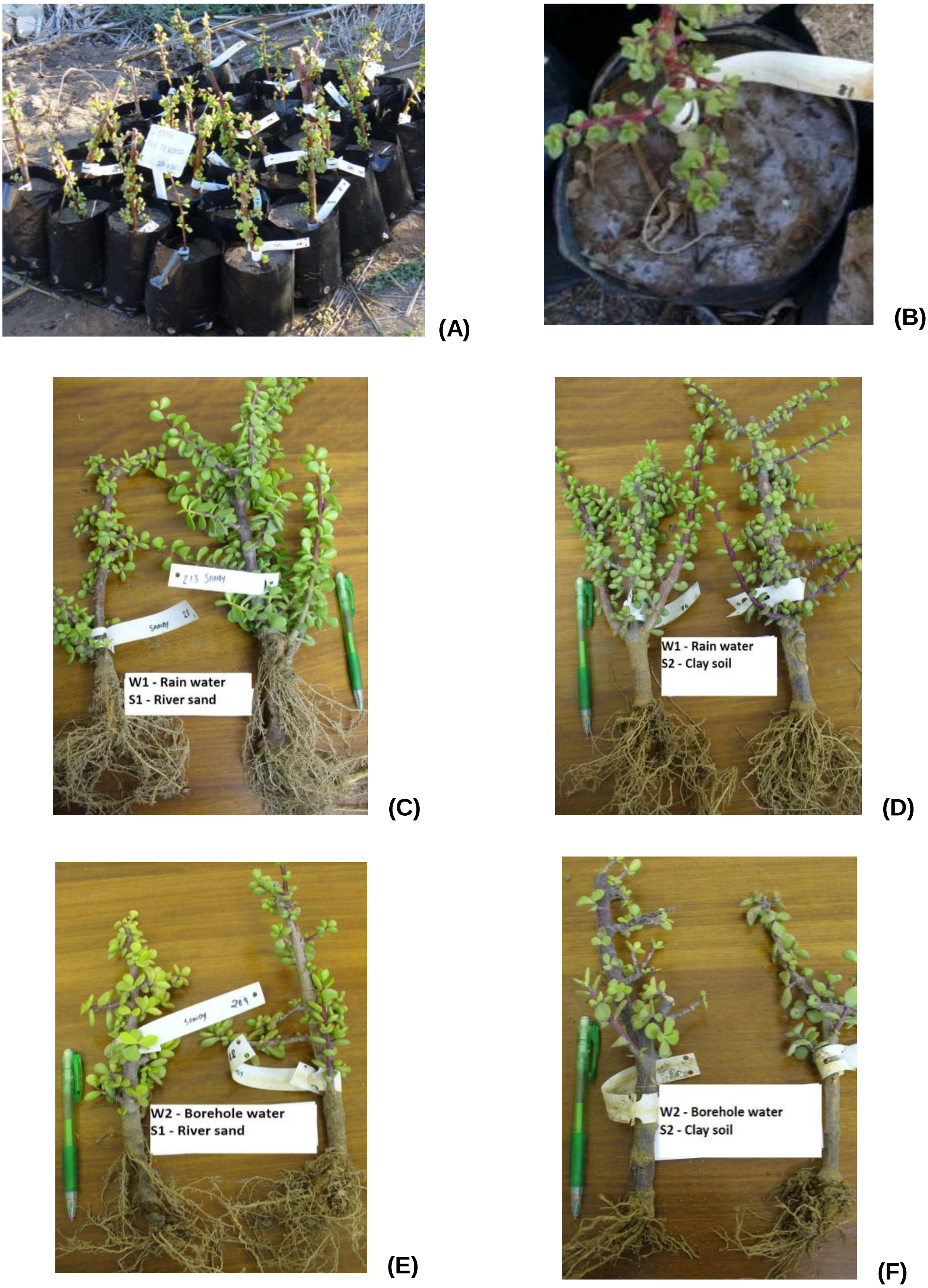

Figure 3.3: Photos of spekboom plants before and after treatments. A = example of plants at start of experiment. B = salt accumulation on soil of plant in the borehole and clay soil treatment after five months. Photos C, D, E, F = examples of plants from each of the four treatment combinations after the 10 month period. Photos: C. Becker

Leaf colour

Table 3.3 displays how the leaves changed colour over the test period. At commencement of the experiment most plants were in the C2 category (165 plants), followed by the C1 category (29 plants), therefore mostly in the range of the colour yellow. There was a definite change from T 1 to T3, as evident in the totals row, where C4 contained the most individuals (93 plants) at T 3. The two groups which received rain water had more than half of their individuals in the C4 category, in particular the clay soil where 75 % of the plants were in this category. The two rainwater groups also did not have any plants in the C5 category at T 3, even though they did have at T1. The two groups receiving borehole water had most of their individuals in the C1 category, especially the plants in river sand (60 %). All groups increased in plant numbers in the C1 category, in particular the groups that received borehole water.

Table 3.3: Changes in leaf colour from the commencement of the experiment (T1) to termination (T3). Figures in brackets indicate percentage plants per treatment group (n=60). Percentages in bold indicate the highest percentage per treatment. Colour behind the code provides the nearest example of the colour. W1 = rainwater, W2 = borehole water, S1 = river sand, S2 = clay soil.

	Treatment	**Leaf colour**					
		C1	C2	C3	C4	C5	C0 (dead)
T1	W1-S1	8 (13.3)	48 **(80.0)**	0 (0.0)	3 (5.0)	1 (1.7)	
	W1-S2	7 (11.7)	35 **(58.3)**	0 (0.0)	7 (11.7)	11 (18.3)	
	W2-S1	9 (15.0)	37 **(61.7)**	0 (0.0)	7 (11.7)	7 (11.7)	
	W2-S2	5 (8.3)	45 **(75.0)**	0 (0.0)	4 (6.7)	6 (10.0)	
	Totals	29	165	0	21	25	
T3	W1-S1	17 (28.3)	11 (18.3)	0 (0.0)	32 **(53.3)**	0 (0.0)	0 (0.0)
	W1-S2	10 (16.7)	3 (5.0)	0 (0.0)	45 **(75.0)**	0 (0.0)	2 (3.3)
	W2-S1	36 **(60.0)**	10 (16.7)	0 (0.0)	7 (11.7)	2 (3.3)	5 (8.3)
	W2-S2	21 **(35.0)**	17 (28.3)	2 (3.3)	9 (15.0)	2 (3.3)	9 (15.0)
	Totals	84	41	2	93	4	16

Measuring the number and the colour of leaves served two purposes: as an indicator of growth, and indirectly by displaying the number of dead plants at the termination of the experiment. However, plant death was a difficult variable to quantify, because the number of dead plants (assessed as plants without leaves) fluctuated over the 10 months, and this is not well reflected in the graphs and figures. After five months, a total of 18 plants were recorded as dead, and of these, six were growing again at the end of the 10 months. Of the six that recovered, four were in the clay soil and receiving borehole water group. This fluctuated again, and by the end of the 10 month period, 16 plants were dead in total, (Table 3.3) nine of which came from this particular treatment.

Root to shoot ratio

The R:S ratio was not significantly (p = 0.07) affected by either soil or water type, although there was a trend that both treatments receiving rain water had higher R:S ratios than the borehole water receiving treatments (Table 3.4). Table 3.4 displays the average dry weights of the roots and shoots of the sub-sample before planting began and of the different treatment combinations after 10 months. There is a clear indication that the overall ratio decreased, which was generally due to the increase in shoot mass. It also displays that the treatments receiving the rainwater had a slight increase in root mass, whereas the treatments receiving the borehole water had marked decreases in root mass, to less than half the weight of the original sub-sample group. The average shoot and root mass's indicate that the plants in the clay soil and receiving the rainwater had the most increase in mass (average shoot weight was 24.30 $\pm$ 22.50 g and average root weight was 7.00 $\pm$ 8.33 g), while the plants in the clay soil but receiving borehole water had the least increase in shoot weight (16.80 $\pm$ 13.21 g), and the highest decrease in root weight (2.90 $\pm$ 2.18 g). Figure 3.3 displays the well developed roots and shoot growth of the groups receiving rainwater (Figure 3.3 C and D) which is clearly contrasted to the groups receiving the borehole water (Figure 3.3 E and F).

Table 3.4: Average dry shoot and root weights and R:S ratio's ± Standard Deviation, of spekboom rooted cuttings from the different treatment combinations. W1 = rainwater, W2 = borehole water, S1 = river sand, S2 = clay soil. Initial weight is the average weight of 10 randomly selected plants before they were planted at the commencement of the experiment.

	Shoot (g)	Root (g)	R:S
Initial weight	12.62 ± 9.84	6.75 ± 5.90	0.54 ± 0.17
W1 S1	19.60 ± 10.60	7.10 ± 5.15	0.37 ± 0.19
W1 S2	24.30 ± 22.50	7.00 ± 8.33	0.32 ± 0.23
W2 S1	21.10 ± 9.94	3.20 ± 2.30	0.18 ± 0.14
W2 S2	16.80 ± 13.21	2.90 ± 2.18	0.20 ± 0.15

Discussion

The aim of this chapter was to test the hypothesis that Na or NaCl could be limiting to spekboom growth, in order to provide the STRP managers with information regarding site selection for future spekboom planting sites, as well as to provide possible explanations for the current state of some planting sites. This chapter's hypothesis stemmed from a number of observations by researchers and nursery managers. One such observation came from an experimental planting site near Calitzdorp, where it was clearly visible that spekboom cuttings were surviving in conglomerate soils on the slopes and not in alluvium soils in the bottomland areas (J.H. Vlok, pers.comm). An initial analysis of the two soils revealed that the alluvium soil had a Na content of 247 mg/kg and the conglomerate type soil that had a Na content of 99 mg/kg (C.H. Becker, unpublished data), and therefore a possible connection with Na was suspected. If this was the case, the assumption could be made that the plants growing in the clay soil in this experiment should not have survived, considering that the Na content was almost double (473 mg/kg) that of the Calitzdorp alluvium soil. From the results, it is clear that although there were a few plants that died, the response was not as obvious as was expected. A possible explanation for this is that spekboom tends to associated more with nutrient- and clay-rich soils derived from shales and mudstones (Cowling, 1984, Vlok et al., 2003), and these shale-derived soils have high silt and clay contents, as well as high levels of Na (Lechmere-Oertel and Cowling, 2001, Vlok et al., 2003). Therefore, the influence of Na on spekboom is unclear, and the type of soil Na is present in could also affect its influence on plants (Shannon and Grieve, 1999).

Detailed studies of Na accumulation in plant cells would provide better indications of its influence on spekboom. From these results, the soil type did not play a significant role but the water type did, and this is probably due to the influence of the borehole water, with its high Na and Cl contents (see salt accumulation on the soil in Figure 3.3.(B)). Cl is a relatively mobile element in the soil that does not generally constrain plant growth (Jobbágy and Jackson, 2001). However, it could be a factor to consider in these experiments, as the chloride levels in the borehole water were extremely high.

Stem Diameter

A striking difference in stem diameter measurements was seen between the two water types, where both rain water receiving treatments had more than double the increase in growth than the borehole treatments. There was little difference between the soil types within each water treatment. There was a limitation in using stem diameter, because the 16 dead plants were not reflected in the 0 mm class, which consists of both living and dead plants. In a study on spekboom truncheon survivorship, Powell (2009) also found that stem diameter had no significant influence on survivorship, which explains why many of the 'healthy' and actively growing plants did not increase in stem diameter over the 10 months. However, the use of stem diameter did provide valuable information, and it was clear that treatment played a significant role on the increase in diameter. The increase in stem diameter supported the hypothesis that spekboom plants growing in low saline conditions grow better than those in high saline conditions.

Leaf number

As with stem diameter, the significant difference was between the two water types used, where the treatments receiving the rainwater had a 10% higher increase in leaf numbers than the treatments receiving the borehole water, irrespective of the soils they were in (Figure 3.3. C,D,E,F). This response to salinity could be due to an accumulation of NaCl in the shoot (from transpiration) and subsequent decrease in essential nutrient uptake (Jennings, 1968, Munns and Termaat, 1986).

The phenomenon of fluctuating spekboom death rates has been observed at restoration planting trials where survivorship rates are not static and continue to fluctuate even three years post planting (Powell, 2009). Between the five month and 10 month period there were a few plants in the clay soil and treatments receiving borehole water that recovered, and it was interesting to see that the treatment that was subjected to the highest salt levels had some plants that were able to recover, indicating an almost “dormant” physical state in the plants. A possible explanation is that these plants did not handle the transplanting well (i,e root damage or bad handling) but were able to recover. At the end of the experiment this treatment had the most dead plants and the lowest increase in leaf numbers, which supports observations by Munns and Termaat (1986) that the impact of salinity on a plant changes over time. This supports my hypothesis that survival would be best in the river sand and rain water receiving treatment and poor in the clay and borehole water receiving treatment.

Leaf colour

The changes in leaf colour of the spekboom cuttings indicate that the treatments receiving the rainwater were healthier that the treatments receiving the borehole water (Figure 3.3. C,D,E,F), because by the end of the experiment there were two dominant colour classes, yellow (C1) and grey-green (C4). These results indicate that the treatment in the clay soil and receiving rainwater were the healthiest, and of all the treatment combinations, this treatment would be the closest at mimicking the natural conditions that spekboom would be found in. In general it was thought that the treatments with the clay soil and receiving the borehole water would indicate the most stress. However, according the leaf colour analysis, this treatment did not have such drastic changes in leaf colour, but the treatment with the river sand (and receiving borehole water) had most of its individuals turn yellow. These results could indicate that soil type could be a factor and that overall they grew better in the clay soil. There was an overall reduction in plants in the dark green class, indicating that all treatments caused some degree of stress in the plants.

One factor that could not be accounted for and which could influence the results, was the previous soil and watering history of each individual plant by the nursery staff before the experiment commenced; thus, some plants could have had an improvement in conditions with the onset of the experiments. However, the randomisation of re-planting should account for those discrepancies. Even though the use of changes in leaf colour of spekboom has not been used as an indicator of health, in my experiments it proved to be a reliable indicator of the plants’ response to salt stress. Changes in leaf colour due to salt stress have also been observed in *P. oleracea* (Rahdari et al., 2012), and as Munns (2002) indicates, salt effects on plants are visible as yellowing or death of older leaves. This is because high concentrations of Na or Cl accumulate in the leaves and result in leaf burn or injury (Shannon and Grieve, 1999).

Root to shoot ratio

Root:shoot ratios indicate where, and what quantity, of plant tissues have a supportive function verses the quantity that have growth functions (Allaby, 1998). In this experiment all the treatments had lower ratios than the original sub-sample, but it is worthwhile to notice that the roots and shoots responded differently under the different treatments (Figure 3.3 C,D,E,F). The most noticeable change was the major decrease in root weight of the plants receiving borehole water, especially in the case of the plants in the clay soil. Similar results were found with salinity experiments on *P. oleracea*, where increasing salinity had significantly negative effects on root measurements of growth, length and dry weight (Kafi and Rahimi, 2011). Salts on the outside of roots have immediate effects on cell growth and metabolism, because high salt concentrations in the soil make it harder for roots to extract water from the soil (Belkheiri and Mulas, 2011, Munns and Tester, 2008, Shannon and Grieve, 1999). Soil structure can also be affected by Na levels, where an excess causes the structure of the soil to collapse (dispersion), making it difficult for plant roots to penetrate the soil (Allison et al., 1954).

The shoot weights did not show as clear trends as the root weights did, which contradicts some literature, and indicates that in saline conditions, shoot growth of plants is generally more affected than the root growth (Munns and Termaat, 1986). Kafi and Rahimi (2011) found that in *P. oleracea,* shoots underwent more stress than the roots, although they do comment that this could be influenced by the amount of water in the soil, which influences the impact of NaCl. However, the spekboom plants in the most saline treatment did have the lowest shoot weight.

The of use of root:shoot ratios is valuable as a rough indicator of physiological process, but the interpretation thereof is not straight forward (Mokany et al., 2006). The reasoning is that plants with a higher proportion of roots can compete more effectively for soil nutrients (such as nitrogen or phosphorous), but, plants with a higher proportion of shoots can collect more light energy (Allaby, 1998, Lloret et al., 1999). It is generally accepted that the indication of a healthier plant would come from an increase in root:shoot ratio, provided the increase came from a greater root weight and not from a decrease in shoot weight (Harris, 1992, Wood and Roper, 2000). In this experiment there was an overall reduction in ratio, but the plants receiving the rainwater did increase in both root and shoot weight, whereas the plants receiving the saline water decreased in root weight. My experiments, through a host of different variables, also indicate spekboom's limited growth under saline conditions.

Therefore, although these salt stressed plants may not physically die, and just manage to survive, this information has implications for the STRP, whereby carbon sequestration values are partly based on root carbon values (Mills and Cowling, 2006).

Conclusion

Across the Thicket biome spekboom grows on a wide range of soil conditions, from nutrient-rich, alkaline shale-derived soils to nutrient-poor, acidic sandstone-derived soils (Mills et al., 2011). It was therefore suggested by Mills et al. (2011) that spekboom is tolerant of a wide range of soil conditions. My results reflected this, where soil type did not emerge as a significant factor of spekboom plant health and growth. The theory that high Na levels in the soil would affect spekboom growth does not seem plausible, which is very likely true because spekboom naturally grows more on nutrient- and clay-rich soils derived from shales and mudstones (Cowling, 1984, Vlok et al., 2003); which contain high levels of Na (Lechmere-Oertel and Cowling, 2001, Oakes, 1973, Vlok et al., 2003).

The type of water was the determining factor in these experiments, where it was clear that the borehole water with its high NaCl levels had negative effects on all aspects of plant growth measurements, which supports observations of spekboom's reduced cellular and metabolic activities under salt stress (Ting and Hanscom, 1977). The most striking effects were seen by the reduced root weight and the change in leaf colour, which is most likely due to the effect of salts on the root and accumulation within the plant (Belkheiri and Mulas, 2011, Munns and Tester, 2008, Shannon and Grieve, 1999). Spekboom's fluctuating death rates can also complicate survival data calculations. All these factors have a bearing on the success of the STRP and carbon sequestration data. Spekboom appears to tolerate different soil types, which has a positive implication for restoration site selection. Its degree of salinity tolerance was considerably higher than was expected, which, depending on the degree of soil salinity, can also have positive implications for the recovery of saline bottomland areas. To achieve the best growth and success rate however, I would not recommend planting them in saline areas.

Chapter 4 – The influence of selected soil properties on mortality and growth of *Portulacaria afra* at restoration sites

Abstract

In South Africa, Spekboomveld (a subtype of the Thicket biome), which is dominated by *Portulacaria afra* (spekboom), has been heavily degraded by excessive grazing from domestic stock. The large scale degradation and complete removal of spekboom, a keystone species, stimulated the formation of the Subtropical Thicket Restoration Programme (STRP) in 2004. This programme has overseen the planting of spekboom cuttings in degraded Thicket landscapes in the Western and Eastern Cape. Survival of spekboom at planting sites has been varied, ranging from 13-72 %, and variability is compounded by the fact that survivorship rates are not static. Knowledge regarding the feasibility of site locations, and the influence of soil and climatic factors on spekboom survival, is crucial for the economic feasibility of the programme. This chapter aims to investigate if there could be a relationship between spekboom cutting establishment and selected soil properties (macro-nutrients, pH, particle size, aspect, gradient, soil depth and infiltration) at three restoration sites; around Calitzdorp, Addo National Park, and in the Baviaanskloof Nature Reserve. My results indicated that site location was the most important factor for spekboom growth and mortality, whereby plants performed better in the east (Addo) with almost complete mortality in the west (Calitzdorp). The declining survival rate westwards is most likely attributed to climatic variability across the biome. Spekboom generally performs better on north facing slopes, but in Addo it grows well on both north and south facing slopes. Of the soil properties considered, soil pH, clay content and phosphorous concentration are important, and spekboom grows best at a soil pH under 7, phosphorous levels below 70 $mg.kg^{-1}$, and clay content above 12 %. My results indicated that when compared to site location and landscape position, soil does not have a strong influence on spekboom success. The information gathered indicates that the STRP should focus on planting sites located in the eastern end of spekboom distribution order to maximise spekboom success rate and returns on investment.

Introduction

South African biomes have experienced severe levels of degradation, especially those associated with the semi-arid interior (Vlok et al., 2003). More than one million hectares of the Thicket biome in the Eastern Cape has been converted from dense, closed-canopy vegetation to an open desert-like state (Mills et al., 2010b). Approximately 46% of Thicket dominated by *Portulacaria afra* (hereafter spekboom) – hereafter referred to as Spekboomveld - has been heavily degraded (Lloyd et al., 2002, Mills and Cowling, 2006, Mills et al., 2011). Degradation in this biome stems from a number of processes, but the main factor is the reduction in abundance of spekboom through excessive grazing by domestic stock (especially goats) since the early 1900's (Aucamp and Tainton, 1984, Esler et al., 2006, Kerley et al., 1995, Mills et al., 2010b, Mills and Cowling, 2006). Spekboom is a keystone species in most Arid Thicket and some Valley Thicket types in the semi-arid Subtropical Thicket of the Eastern Cape and parts of the Western Cape (Lechmere-Oertel, 2003, Lechmere-Oertel et al., 2005a). Within these areas spekboom is an important species for livestock and wildlife ranching as it is a major supplier of browse (Aucamp, 1979, Von Maltitz, 1991), especially during times of drought (Aucamp, 1979, Oakes, 1973, Stoltz, 1991, Stuart-Hill, 1989).

In semi-arid Subtropical Thicket, resilience to severe overgrazing is low (Stuart-Hill, 1989, Stuart-Hill, 1991, Vlok et al., 2003). This is compounded by the problem that seedlings are generally rare, especially in the Arid and Valley Thicket forms (Midgley and Cowling, 1993, Von Maltitz, 1991), and this leads to a lack of regeneration in disturbed landscapes where the protective canopy has been removed (Aucamp, 1979). Seedlings of spekboom are seldom observed (Von Maltitz, 1991) and on the rare occasions when seedlings do emerge, they seldom mature and become incorporated into the canopy. Germination trials in laboratory settings have also yielded very poor results (Oakes, 1973). Although spekboom recruits poorly from seedlings, it has exceptional abilities to produce roots from cuttings (Lechmere-Oertel et al., 2008, Swart and Hobson, 1994, Vlok et al., 2003). It also has the ability to form a 'skirt' of rooted branches at ground level around itself (Von Maltitz, 1991), which binds the soil together as well as providing a microsite beneath the plant conducive to further re-colonisation (Sigwela et al., 2009). However, even with these features, it does not seem to re-colonise highly degraded areas (Stuart-Hill, 1991). This has created a situation where a harsh micro-climate, reduction in soil quality (Mills and Fey, 2004a) and the low seedling recruitment capabilities, may prevent the natural return of spekboom. Consequently, active interventions such as manual planting are required to restore degraded spekboom Thicket.

The Subtropical Thicket Restoration Programme (STRP) was launched in 2004 through the Working-for-Woodlands program of the South African government, and functions under the auspices of the Eastern Cape Restoration Programme (ECRP). The programme hires teams of previously disadvantaged people to implement the planting of spekboom cuttings at varying densities (1 – 3 m intervals) and patterns, as well as constructing exclosures, which are used to determine browsing effects on plant establishment (Mills et al., 2007). This restoration work is unique in the sense that planting takes place in semi-arid environments on degraded soils which are susceptible to regular droughts, and not in moister habitats as is the case in most restoration programmes (Bainbridge, 2007). An excellent success case study from an Arid Thicket site revealed that 29 years after the landowner had planted spekboom cuttings, the site, despite receiving less than 300 mm annual rainfall, had a 90% spekboom cover (Mills and Cowling, 2006). However, since the STRP's plantings began in 2004, this degree of success has not been mirrored at the planting sites. Trials investigating a variety of factors (e.g. cut spekboom stem diameters, planting angle, clumping, planting density and planting angle) has yielded conflicting results, with survivorship ranging from 13-72 %.

Every species' distribution is determined by its own ability to survive under specific environmental conditions (Medinski et al., 2010, Vázquez and Givnish, 1998). Thus a knowledge of the ecological requirements and factors that control it, (Cowling, 1983) especially a keystone species such as spekboom, is central for restoration success (Hoffman and Everard, 1987, Rogers et al., 1995, Sigwela et al., 2009, Vlok et al., 2003). Differences in soil characteristics, such as soil type, depth and degradation state, could manifest in different spekboom cutting survival, growth and C sequestration rates (Cowling and Mills, 2010, Mills et al., 2010b, Mills et al., 2011). Powell (2009) suggested that spekboom planted on well-drained soils could produce significantly different results from the survival results he obtained on clay-rich soils. Some heavily degraded sites are not suitable for spekboom establishment and growth when the loamy top soil has been eroded (Mills and Cowling, 2006, Rutherford et al., 2012), leading to poor spekboom survival. The success of the STRP and calculations regarding the rate of C sequestration are all reliant on the survival rates of spekboom (Mills and Cowling, 2010a). Survival rates have implications for the costs per hectare; therefore knowledge regarding the relationship between spekboom and the soils it is planted in is extremely valuable.

Following concerns arising from the variable survival of spekboom cuttings, the aim of this chapter is to investigate if there could be a relationship between spekboom cutting establishment and selected soil properties (macro-nutrients, pH, particle size, aspect, gradient, soil depth and infiltration) at three restoration sites. I specifically investigate whether the mortality and growth of spekboom truncheons in restoration initiatives is related to one or more soil properties.

Study Sites

Three of STRP's restoration planting sites were chosen for the study. All the sites were planted with spekboom truncheons two to five years ago (2007 – 2011). Sites were specifically chosen that had not been replanted (owing to high mortality) since the initial time, so that results would not be confounded by including different-aged plantings. The STRP sourced the truncheons from nearby intact thicket areas, where after the harvested branches were cut to a length of 60 cm and planted to a depth of 20 – 30 cm. However in some soils this depth could not be reached due to the soil structure and rockiness, but a minimum of 15 cm was aimed for (Mills et al., 2010b). Sites were located within the STRP's restoration exclosures, which consist of a quarter hectare plot that has been fenced in to prevent grazing from livestock and wildlife.

Vegetation

The vegetation at all three sites is some form of Spekboom Thicket (for site-specific details, see below). All sites have been heavily degraded by livestock browsing and exist now as an open savanna with scattered remnant trees and dominated by annual grasses and karroid shrubs, mostly *Pentzia incana*. Spekboom has been eliminated from all three of the sites. Three plots on Kaboega and Kuzuko farms were located below remnant stretches of the original Thicket vegetation. Below I describe the intact vegetation from each site.

Site 1, hereafter referred to as the Calitzdorp site, is located in Kruisrivier Spekboom-Pruimveld (Valley Thicket with Spekboom Mosaics), where spekboom is abundant amongst woody trees and shrubs (e.g. *Carissa haematocarpa, Euclea undulata, Nymannia capensis, Pappea capensis, Rhigozum obovatum*) in a matrix of Succulent Karoo communities, in which *Pteronia incana* is often abundant. Grasses are present, such as *Cenchrus ciliaris* and *Sporobolus africanus,* and leaf succulents such as *Aloe ferox, Cotyledon orbiculare* and *Crassula* spp are also abundant. The Thicket vegetation is restricted to north-facing slopes, and occurs as fragmented patches amongst Succulent Karoo, Renosterveld, Sandolien or Fynbos vegetation on the adjacent south facing slopes (Vlok et al., 2005).

Although the second site (hereafter referred to as the Baviaanskloof site) has been highly transformed, the natural vegetation would be Baviaanskloof Spekboom Thicket on the north facing slopes. Baviaanskloof Spekboom Thicket is dominated by spekboom, *Pappea capensis, Schotia latifolia, Aloe speciosa, Panicum maximum, Putterlickia pyracantha,* and *Cenchrus ciliaris.*

The third site (hereafter referred to as the Addo site) is located within the Sundays Spekboomveld, an arid form of Succulent Thicket (Hoare et al., 2006, Vlok et al., 2003). This type of Thicket is loosely organised into a mosaic of vegetation patches comprising evergreen trees (< 5 m), emerging from a matrix of woody and succulent shrubs, dominated by spekboom; and patches of bare ground (Lechmere-Oertel et al., 2005a). Other than spekboom, dominant species in the intact form include *Pappea capenis, Euclea undulata, Schotia afra, Crassula ovata,* and *Boscia oleoides.*

Figure 4.1: Google Earth imagery of location of restoration sites, numbers in brackets indicates number of plots laid out per site.

Site 1: Calitzdorp

Geology

The Calitzdorp site is located 5km to the East of Calitzdorp (Figure 4.1) in the Klein Karoo on well consolidated and characteristically red pebbled Enon Conglomerates of the Uitenhage (Cretaceous) group (Torien, 1979). This site is located within the Gouritz River drainage area (Driver et al., 2011).

Climate

This site is located in a semi-desert region and falls within the winter rainfall region, although it also experiences summer thunderstorms. The mean annual precipitation (MAP) of 140 mm, is most pronounced in autumn. The minimum and maximum average temperatures in January are 15°C and 32°C, respectively; and temperatures greater than 44°C occur. In July the minimum and maximum average temperatures are 2°C and 20°C, respectively (data from SA Weather Bureau).

Site 2: Baviaanskloof Nature Reserve

Geology

The Baviaanskloof site incorporates various restoration exclosures on the footslopes of the Kouga Mountain Range (Figure 4.1 and Figure 4.2), on the privately owned farm of Zandvlakte, within the Baviaanskloof Mega- Reserve. The geology consists of steep slopes with shallow, red, clayey and often rocky soils that are derived from a variety of parent materials, usually mudstones, shales, slates, phyllite and sandstones from the red shale Bokkeveld Goup (Cape System) (Esler et al., 2006). This site is located within the Gamtoos River drainage area (Driver et al., 2011).

Climate

The sites experience rain throughout the year but summers are stressful for plants owing to high temperatures. Rainfall here is commonly associated with post-frontal events, bringing soft soaking rain in the spring and autumn months and thunderstorms in mid to late summer. Rainfall peaks in the equinoctial months, is less reliable in summer and little falls in the winter months. The MAP is 230 - 300 mm (measured between 1985 – 2012). Frost days vary from 5 – 65 days. The minimum and maximum average temperatures in January are

16°C and 31°C, respectively. In July minimum and maximum average temperatures are 5°C and 20°C, respectively (data from SA Weather Bureau).

Figure 4.2: Location of the plots at Site 2, in the Baviaanskloof (numbers in brackets indicates the number of plots sampled per fenced plot. Shaded area on the right is the Eastern section of Bavianskloof Nature Reserve**.**

Site 3: Addo National Park

Geology

The Addo site consists of various restoration exclosures in the vicinity of Darlington Dam in the Addo National Park, as well as on the park's eastern border, on the privately owned farms of Kuzuko, Doringhoek and Kaboega (Figure 4.1 and Figure 4.3). Most of the plots I sampled are located on a Dwyka and Ecca transition (both of Karoo lithologies), which give rise to deep, well-structured soils (Vlok and Schutte-Vlok, 2010, Whitfield and Norman, 2006). The unsorted Dwyka tillite with minor shales consists of dark grey, fine grained rocks containing clasts of various shapes, sizes and origins. The soils they produce are often saline and prone to crusting (Esler et al., 2006). The transition with the Ecca group contains sandstone and shale. The other plots are located where these formations intercede with the Witteberg group, which contains predominately quartzitic sandstone and shale (Truswell, 1977, Whitfield and Norman, 2006). The Witteberg Group is characteristically found in sharply folded mountains systems. The steep slopes combined with the high percentage of quartz sand, give rise to coarse, sandy, unstructured soils that are shallow and nutrient poor (Hoare et al., 2006, Vlok and Schutte-Vlok, 2010, Whitfield and Norman, 2006). This site is located within the Sundays River drainage area (Driver et al., 2011).

Climate

The farms of Kaboega and Doringhoek experience a MAP of 250 – 400 mm (measured between 1971 – 2011) which falls throughout the year with small peaks in late summer and spring. The minimum and maximum average temperatures in January are 17°C and 31°C, respectively; and temperatures greater than 40°C are frequently recorded in summer. In July minimum and maximum average temperatures are 5°C and 22°C, respectively (data from SA Weather Bureau).

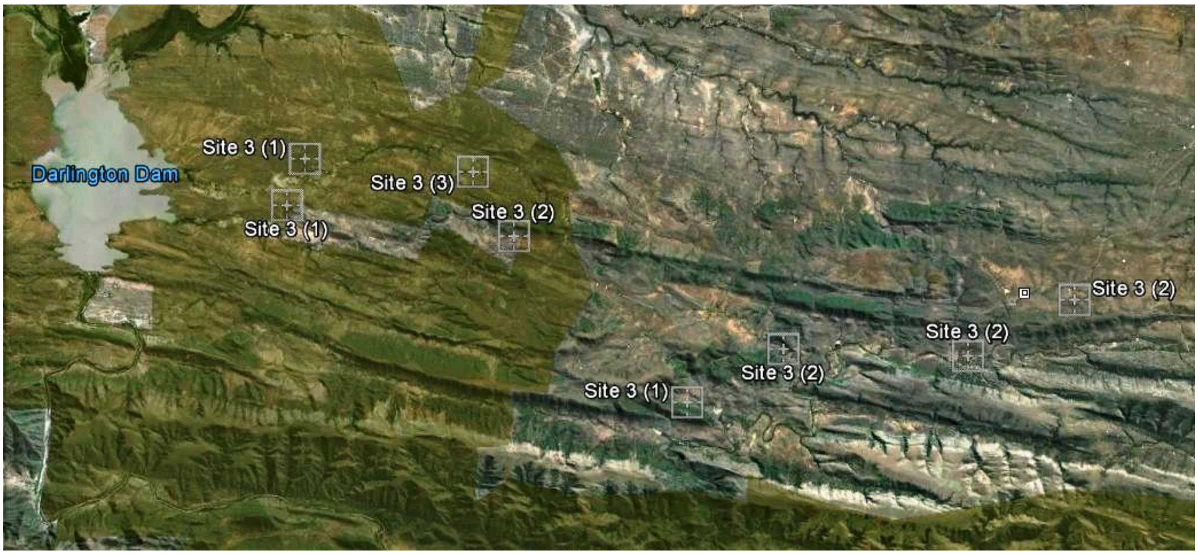

Figure 4.3: Location of thicket wide plots in and around Addo. The number in brackets represents the number of plots I sampled per restoration exclosure. Shaded area indicates Addo National Park.

Materials and Methods

Plant data collection

Data collection took place between September and October 2011, and consisted of marking out plots at the Calitzdorp site, and within the restoration exclosures in Addo and Baviaanskloof. The STRP applied different planting methods to different rows in these restoration exclosures. It was not possible to include all these variables and methods in this study, and therefore sampling plots were randomly located throughout the exclosures covering sections of all the rows planted. Plots of 20 m X 25 m were marked out with the use of poles and tape, and due to the spacing of the planted spekboom cuttings, this was calculated to contain 120 plants (10 rows of 12 cuttings). Plants were classified into “dead”, “surviving” (which refers to plants that still have leaves which were generally wrinkled, but there were no signs of active growth), and “actively growing” which refers to plants that showed signs of new growth, which was evident by the red colour of new shoots. As plants were spaced 1 m apart, if a plant was not found around the 1 m mark, it was considered to be dead. These classes were then calculated to obtain a percentage of plants dead, surviving and actively growing out of 120. At the Addo site, seven plots were taken in restoration exclosures on north facing slopes and seven on south facing slopes. In Baviaanskloof, planting on south facing slopes only began in 2011; therefore these areas could not be used in this study as they were too ‘young’, thus only seven plots on north facing slopes were collected. At Calitzdorp, the layout differed slightly because of the unusual landscape situation. Here two different soils occurred in matrix (especially on the south facing slope) and during a preliminary examination spekboom appeared to be growing better on the less clayey of the two soils (conglomerate vs. alluvium). Due to different area sizes represented by the two soils, nine plots were sampled on the conglomerate soil (five on the north facing slope and four on the south facing slope) and six on the alluvium soil (all on the south facing slope).

Soil sampling and preparation

Three soil samples were taken in a diagonal line from within each 20 x 25 m plot, from the “top” (which was considered to be the point closest to the crest of the hill), from the “middle” (the centre of the plot) and the “bottom” (which was considered to be the point closest to the footslope of the hill). Soil samples were collected with the use of an auger, and in cases where the soil was too hard or rocky, with the use of spades and picks; to a depth of 20 cm. The samples were transported in labelled plastic bags back to the Nelson Mandela Metropolitan University laboratory at Saasveld. Each soil sample was well mixed and sieved through a 2 mm sieve to remove organic material and roots and then left to air dry to constant weight which curbed minimal biological activity (Boone et al., 1999).

Laboratory analysis

Soil analyses took place at the Elsenburg Laboratory, Institute for Plant Production, Stellenbosch, South Africa and all samples were analysed for extractable phosphorous (P), calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K), as well as pH and texture. Extractable P, Ca, Mg, Na and K were extracted with 1 % citric acid and analysed by using a Thermo ICP iCAP 6000 Series Spectrometer (Thermofisher Scientific, Surrey, UK). The pH was determined in KCl (McLean, 1982, Rhoades, 1982). Clay content was determined by the hydrometer method (Day, 1956, Elliott et al., 1999), sand by sieving and silt by the difference (Day, 1956, Elliott et al., 1999).

Infiltration rates

Adjacent to where each soil sample was taken, infiltration readings were taken. Steady infiltration under tension was determined at a pressure head of 2.0 cm of water using a mini-disk infiltrometer (MDI) (Decagon Devices, Pullman, WA) (Decagon Devices, 2003, Li et al., 2005, Madsen and Chandler, 2007). The infiltrometer was applied to a smooth flat area on the soil surface, assuring that it made solid contact with the soil surface. The starting water volume was recorded (at time zero) and the volume was recorded at regular time intervals of 30 seconds as the water infiltrated, for a total of five minutes. From this the overall average rate of infiltration, ml infiltration per minute was calculated.

Statistical analysis

A conditional inference tree analysis was applied to the quantity of dead (referred to as mortality) and quantity of actively growing spekboom. A conditional inference framework uses the conditional distribution of statistics in an unbiased way (Hothorn et al., 2006), that involves a two-stage algorithm that 1) partitions observations by univariate splits in a recursive way and 2) fits a constant model in each cell of the resulting partition. The foundation for selection among covariates measured at different scales is the association between responses and covariates. The recursion ends when no significant relationship between any of the coviarates and the response can be detected after using multiple test procedures. This method has a well defined theoretical background and provides an unbiased, non-parametric model, and was thus deemed a suitable model to use. All statistical analysis were performed with base R (R Development Core Team, 2010) and related packages including lattice (Sarkar, 2008), Hmisc (Harrell, 2010) and party (ctree) (Hothorn et al., 2006).

Results

This section consists of the influence that various soil, location and environmental factors had on actively growing and dead spekboom plants. Figure 4.4 provides a visual representation of the average percentages of dead and surviving plants. Surviving in this graph includes plants that were actively growing.

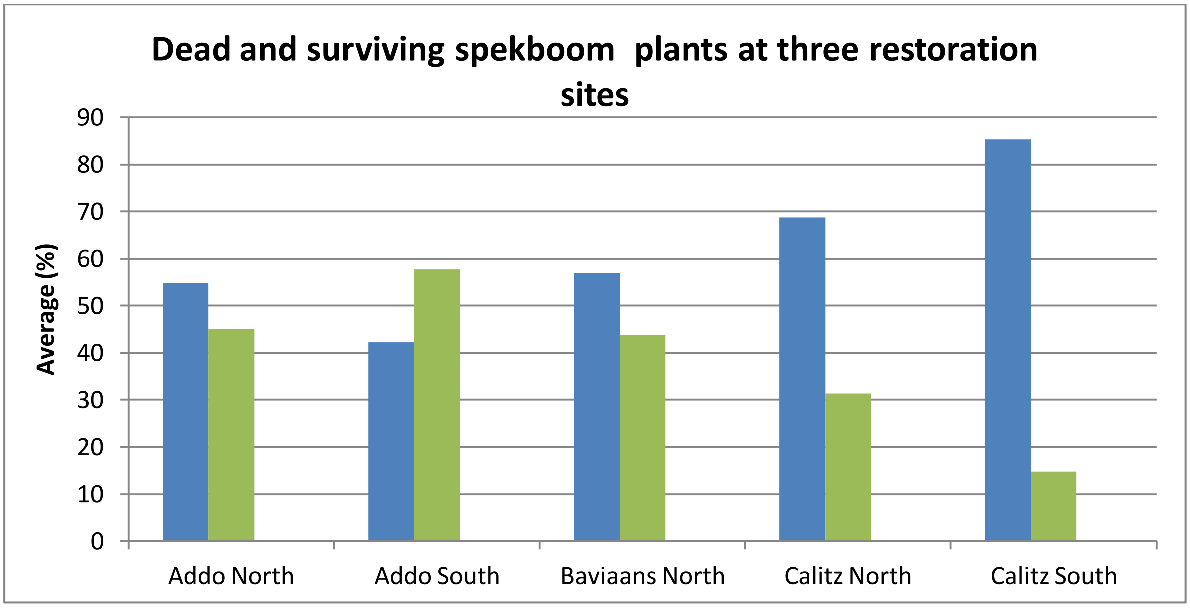

Figure 4.4: Average percentage of dead and surviving spekboom plants at the three restoration sites, on north and south facing slopes (note there were no south facing restoration plots in the Baviaanskloof). Blue bars denote average % mortality ; green bars denote average % survival. Surviving includes actively growing plants. Baviaans = Baviaanskloof, Calitz = Calitzdorp.

The influence of selected properties on the mortality of spekboom

1. The influence of all factors

When all the relevant explanatory variables were taken into account, the conditional inference tree analysis of mortality of spekboom across the three sites showed that site was very important in affecting mortality, with significantly more plants (on average 75 %) dying in the Baviaanskloof and at Calitzdorp than at Addo, with an average of 50 % ($p < 0.001$; Figure 4.4 and Figure 4.5). In the Baviaanskloof and at Calitzdorp, aspect and soil depth were also significant in affecting mortality ($p < 0.001$), but not at Addo. South facing slopes at Calitzdorp (there were no suitable south facing restoration plots slopes in the Baviaanskloof) had significantly higher mortality than the north facing slopes. The inference tree created a further split, where south facing slopes at Calitzdorp of more than 5 cm soil depth resulted in an average of 90% mortality, while shallower soils (less or equal to 5 cm) resulted in significantly ($p = 0.001$) lower mortality. To sum up, the lowest mortality of spekboom occurred at Addo, and the highest at Calitzdorp on south-facing, deeper soils.

2. The influence of soil and environmental characteristics

Once site was removed from the analysis, therefore considering only soil and topographical factors, clay and aspect emerged as predictors of spekboom mortality (see Figure 4.6). A clay content of less than 12 % resulted in significantly higher mortalities ($p = 0.01$), on average between 65 – 90 % dead, whereas a clay content higher than 12 % resulted in less than 60 % mortality. Where clay content was under 12 %, aspect emerged as a significant factor ($p = 0.008$), whereby south slopes resulted in higher mortality rates. To sum up, the highest mortality of spekboom occurred at relatively low clay contents on south-facing slopes.

3. The influence of soil characteristics

When only soil characteristics were considered as explanatory variables, P concentration and pH (Figure 4.7) emerged as significant factors affecting mortality. P concentration of more than 69 $mg.kg^{-1}$ resulted in significantly higher mortality rates ($p = 0.01$), and in these soils with higher P concentrations, a pH of more than 6.7 resulted in an average of 85 % mortality. Figure 4.7 indicates that even if the soil has a P concentration higher then 69 $mg.kg^{-1}$and a lower pH (pH of 6.7 or less) would lower the mortality slightly. To sum up, the highest mortality of spekboom occurs in soils with a pH higher than about 7 and with P concentrations higher than about 70 $mg.kg^{-1}$.

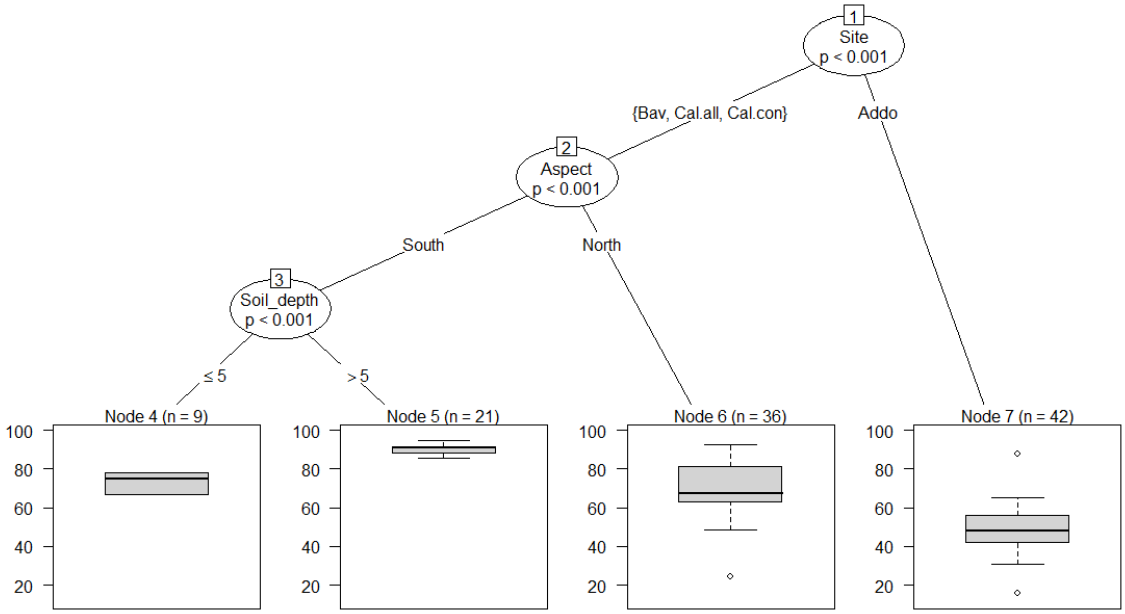

Figure 4.5: Results from the conditional inference tree analysis of spekboom mortality in restoration plots in Addo, Baviaanskloof and Calitzdorp, taking into account all explanatory variables. Addo, Bav, Cal.all and Cal.con are abbreviations for the different restoration sites, where Bav = Baviaanskloof, Cal = Calitzdorp, al = alluvium type soils, con = conglomerate type soils, the latter two seen in close proximity to each other at Calitzdorp. The bottom boxes/ nodes express the percentage of actively growing plants as box plots.

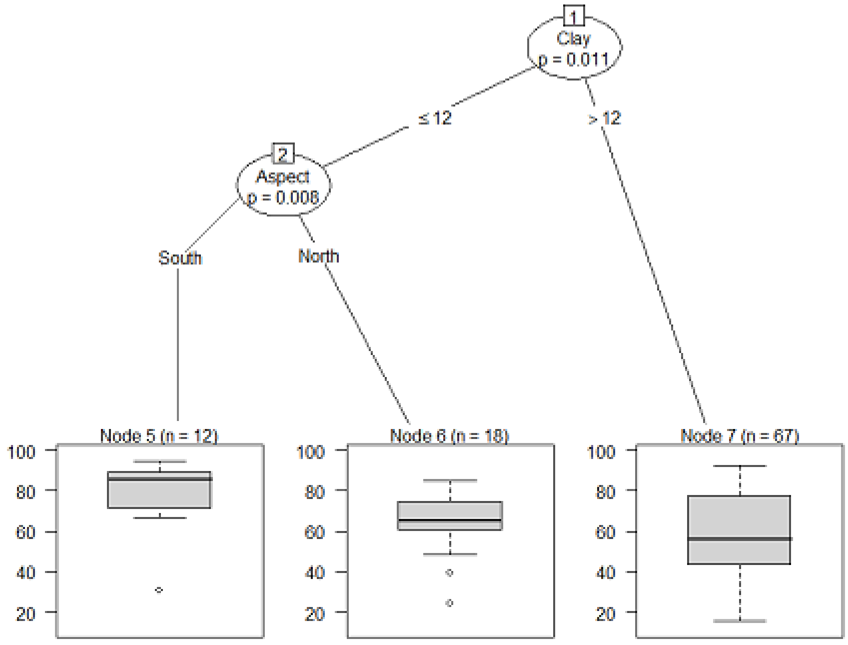

Figure 4.6: Results from the conditional inference tree analysis of spekboom mortality in restoration plots in Addo, Baviaanskloof and Calitzdorp, taking into account all explanatory variables, except 'site'. The bottom boxes/ nodes express the percentage of actively growing plants as box plots.

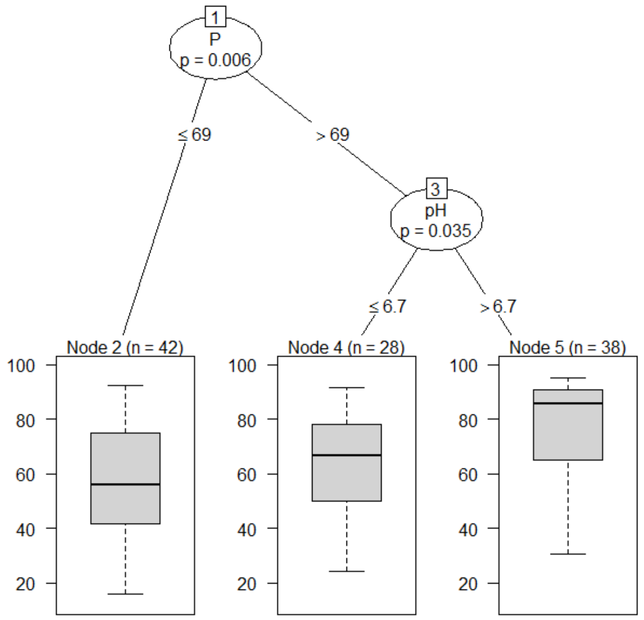

Figure 4.7: Results from the conditional inference tree analysis of spekboom mortality in restoration plots in Addo, Baviaanskloof and Calitzdorp, taking into account. pH and all the other soil elements sampled The bottom boxes/ nodes express the percentage of actively growing plants as box plots.

The influence of selected properties on actively growing spekboom

1. The influence of all factors

When all the relevant explanatory variables were taken into account, the conditional inference tree analysis of active growth of spekboom showed that site was very important in affecting where plants were actively growing, with significantly more plants growing in Addo and in the Baviaanskloof (on average between 20 – 60 %) than at Calitzdorp (on average between 0 – 20 %) ($p < 0.001$; Figure 4.4 Figure 4.8). At Addo and Baviaanskloof, aspect also significantly ($p < 0.001$) affected the percentage of actively growing plants, whereby south facing slopes in Addo (there were no appropriate restoration plots on south facing slopes in the Baviaanskloof), resulted in slightly more plants growing. Figure 4.8 indicates that spekboom growing on north facing slopes in Addo and Baviaanskloof grow significantly better on gentler slopes ($p = 0.01$) of less than 5.3°. At Calitzdorp there was a significant difference between conglomerate and alluvium soils ($p < 0.001$), where there was no spekboom growth on alluvium soils, and almost 20 % on conglomerate soils. To sum up, spekboom grows best at Addo (with up to 80% actively growing in certain plots) and on north-facing, gentle slopes in the Baviaanskloof. It also grows better on conglomerate soils in Calitzdorp than on alluvium soils.

2. The influence of soil and environmental characteristics

Once site was removed from the analysis, (therefore considering only soil and environmental elements), the results revealed similar trends to the previous analysis. Gradient and aspect emerged as significant factors affecting active growth again (Figure 4.9). Gradient followed a similar pattern to the previous analysis, the only difference was that the split occurred at 10° and not 5.3°, and the results expressed more clearly the higher numbers of actively growing plants on gentler slopes (on average 40 %) compared to steeper slopes (on average between 0 – 20%). If slopes were steep (more than 10°), then spekboom seemed to prefer north-facing slopes over south facing ($p = 0.02$). To sum up, spekboom grows best on gentler slopes, but if the slope is steeper than 10°, it grows better on north facing slopes.

3. The influence of soil characteristics

Once site and all other environmental variables were removed from the analysis, (therefore considering only soil characteristics), the conditional reference tree indicated that P concentration was an important factor determining whether spekboom grows (Figure 4.10). In Figure 4.10 a P concentration of 61 $mg.kg^{-1}$ or less resulted in significantly more active growth (on average 35 %; p = 0.04) than plants growing at more than 61 $mg.kg^{-1}$ (on average between 0 – 10 %).

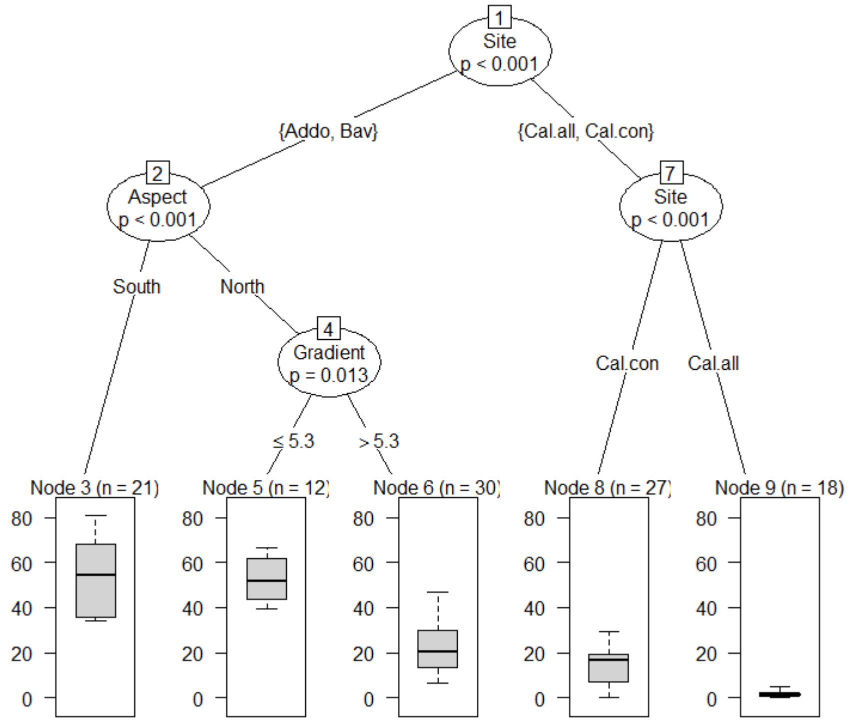

Figure 4.8: Results from the conditional inference tree analysis of active spekboom growth in restoration plots in Addo, Baviaanskloof and Calitzdorp, taking into account all explanatory variables. Addo, Bav, Cal.all and Cal.con are abbreviations for the different restoration sites, where Bav = Baviaanskloof, Cal = Calitzdorp, al = alluvium type soils, con = conglomerate type soils, the latter two seen in close proximity to each other at Calitzdorp. The bottom boxes/ nodes express the percentage of actively growing plants as box plots.

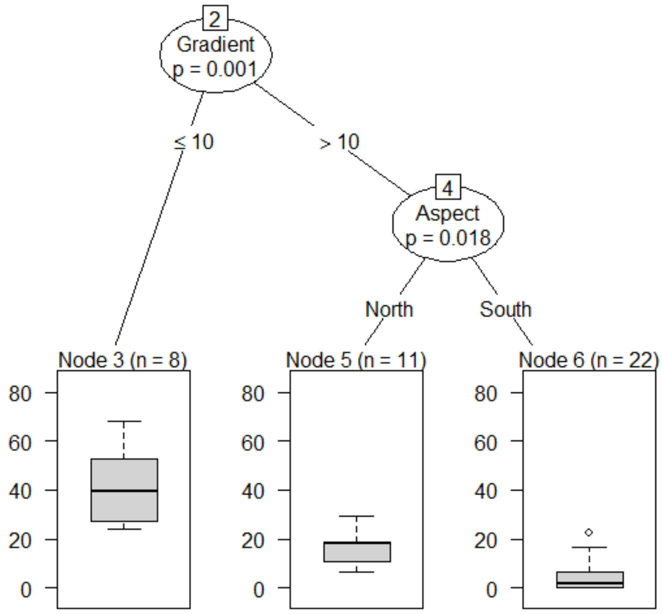

Figure 4.9: Results from the conditional inference tree analysis of active spekboom growth in restoration plots in Addo, Baviaanskloof and Calitzdorp, taking into account all explanatory variables apart from site. The bottom boxes/ nodes express the percentage of actively growing plants as box plots.

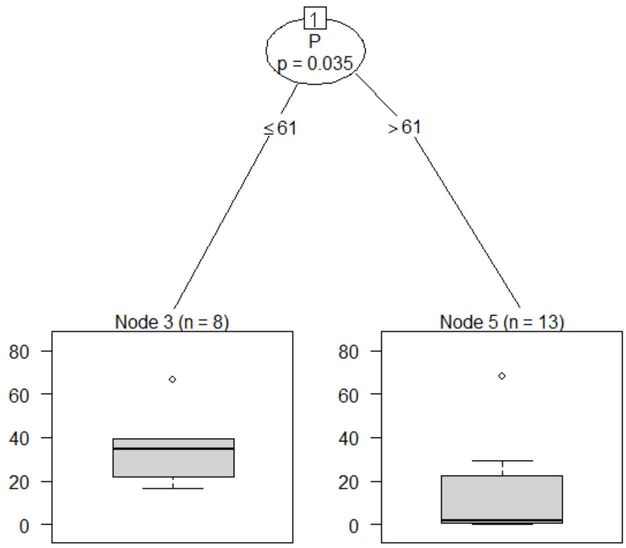

Figure 4.10: Results from the conditional inference tree analysis of active spekboom growth in restoration plots in Addo, Baviaanskloof and Calitzdorp, considering only soil characteristics. The bottom boxes/ nodes express active growth percentages as box plots.

Discussion

The focus of this chapter was to analyse the influence, or relationship, between selected soil and environmental properties and the numbers of dead and actively growing spekboom. I also measured spekboom survival, but as I could not be sure whether these spekboom were in a dormant phase and will eventually start growing, or whether they were in the process of dying, I removed survival from the analyses. Therefore it should be noted that the rates of mortality and actively growing plants are not the inverse of each other, as a portion of the percentage is 'surviving'. The only soil factors to emerge as having an influence on spekboom growth and mortality were clay content, pH, P content and soil depth. However, even though these variables indicated significant differences, in the majority of the analyses these differences were minimal. The most important factor affecting spekboom growth and mortality was location or site, where it was clear that the spekboom restoration plots perform better in the east.

The most important factors governing spekboom's active growth and mortality

There are many factors that I did not consider in my study that could affect the success of spekboom in different sites, but I would suggest that climatic variability and seasonal influences are very important, as shown by Powell (2009). Rainfall is extremely unreliable and varies greatly between the study areas, from a predominantly more summer rainfall area with a higher MAP in the east to the more winter rainfall area and lower MAP in the west. The season in which planting occurs could be a factor, because planting in the summer in Calitzdorp, which experiences hot, dry summers and planting in Addo, which is more likely to receive summer rain, will likely result in different survival rates. Calitzdorp is also more prone to frost, which negatively impacts spekboom (Baran, 2011, Oakes, 1973).

Apart from rainfall and temperature, the topography, altitude and geology of the landscape could account for differences among areas. The TWP's around Addo, and in particular Baviaanskloof, were located higher on mountain slopes. The site at Calitzdorp, on the other hand, was situated on small, undulating hills, on mostly alluvium type soils, which as the analysis indicated, resulted in low numbers of growing spekboom (and almost complete mortality). This generated very low percentages of growing plants for the Calitzdorp site in general.

Apart from ecological factors, the inconsistencies among planting teams also complicates comparisons of different sites. These inconsistencies include the time of year the spekboom was planted, how they were planted and by which contracting team, genotypes of spekboom used and planting density. In Addo for instance, the planting density in most of the plots was higher than the other plots, where there was less than 1m space between plants. Higher planting density (where plants are closer together), could have a significant impact on survival through increased infiltration of rain water (Mills and Cowling, 2006).

The first analysis indicated that at Calitzdorp aspect and soil depth further influenced the mortality rate, whereby south facing slopes resulted in higher mortality. This conforms to the current literature that spekboom prefers warm, north facing slopes (Mills et al., 2011, Oakes, 1973), and generally does not grow as readily on the cool, moist southern facing slopes. One explanation for better growth on northern slopes is that the amount of solar radiation a slope receives could influence a plant’s responses, because it affects surface energy budgets, temperatures and soil moisture balances; and could be regarded as one of the fundamental variables of the plant environment (Ciolkosz, 2009, Granger and Schulze, 1977, Zachar, 1982). In the middle latitudes (around 33°) solar radiation differences in aspects are greatest and south facing slopes show declining energy load with increasing slope angle (Holland and Steyn, 1975). This is especially prevalent in winter, where north facing slopes can receive up to three times the amount of solar radiation than those of south facing slopes (Schulze, 1975). Such contrasting and permanent differences in radiant energy may cause a variety of microenvironments that consequently affect vegetation development (Granger and Schulze, 1977). The considerably lower radiation loads on southern aspects in autumn through to spring, creates a more mesic soil moisture regime (Granger and Schulze, 1977). This results in the establishment of mesic thicket species to the detriment of spekboom, which is most competitive in arid environments (Mills et al., 2011).

On the south facing slopes at Calitzdorp, soils deeper than 5 cm resulted in almost 100 % mortality, and shallower soils of less than 5 cm were better for spekboom growth. The results were a bit unusual, as spekboomveld is generally reported as being confined to moderately deep soils (Kerley et al., 1995, Stuart-Hill, 1992, Vlok et al., 2003). However, regarding the two soils at Calitzdorp, conglomerate and alluvium, could account for this difference. Here, spekboom survived and grew much better on conglomerate soils than on alluvium soils. However, it is hard to know whether conglomerate soils were really shallower than alluvium soils as conglomerate soils are rockier than the fine textured alluvium soils, which could have influenced the ease with which the measuring pole was hammered into the ground.

The shallower soils could also be indicative of the location on the slope, where hill slopes consist of shallower (predominantly more conglomerate soils) and due to the movement of particles down slopes, the bottomland areas (predominantly alluvium soils) accumulate soil (Chapin et al., 2011, Fraser et al., 1987, Metternicht and Zinck, 1997, Ni and Zhang, 2007). One could argue that if this was the case then it should be the same for both north and south facing slopes, but there were no suitable lower slope positions with alluvium type soil to sample on the north facing side of the mountain, therefore the results purely represent the situation on the south facing side. However, it should still be noted that the differences between mortality on the shallower and deeper soils was fairly small, of ~ 15 %, and therefore depth probably does not play a large role in mortality.

It was unusual that on north facing slopes in Addo and Baviaanskloof more actively growing plants were found on flatter areas, because spekboom is generally associated with steep north facing slopes (Mills et al., 2011, Oakes, 1973, Rutherford et al., 2012, Vlok et al., 2003). Although it is unusual, it is not uncommon; for instance, in the Fish River Reserve, spekboom-dominated Short Succulent Thicket also grows on flat areas (Evans et al., 1997). Another possible explanation, especially regarding the plots in the Baviaanskloof, is that although the plot was located on the slopes, the plot was in a flatter midslope “plateau” area of the mountain (see Figure 4.11).

In Addo spekboom preferred south facing slopes and spekboom growth was much higher than on north-facing slopes (~ 55 % active growth on south facing slopes vs ~ 20 – 50 % on north facing slopes). This was also unusual, as the analysis for mortality indicated south-facing slopes generally result in higher mortality. However, it is also not uncommon, especially more towards the east, where spekboom is seen to be naturally growing on both slopes. Spekbooms presence on south facing slopes is probably due to function of climate, towards the east frost occurrence is lower and annual rainfall is higher than in the west, which may promote spekboom growth.

Figure 4.11: Typical restoration plot in the Baviaanskloof, located on a flatter area of the slope, near the crest of the mountain.

Soil factors affecting spekboom growth and mortality across all sites

When site was removed as a factor, therefore combining all three sites together, clay, aspect, P concentration and pH emerged as secondary factors important for spekboom mortality across all sites. The analysis indicated that mortality was lowest at a clay content of more than 12 % (~55 %), whereas clay contents of below 12 % resulted in mortality of 65 – 95 %. Thicket is generally described as being confined to clay rich soils derived from shale and mudstones (Cowling, 1984). The negative effect of lower clay contents seems to be increased on south facing slopes, where mortality is ~ 20 % higher than on north facing slopes of a low clay content. This could also be attributed to the effect of temperature or sunlight, where although clay content may be low, other conditions allow it to persist better than on south facing slopes.

P concentration and pH, and an interaction between them, were factors in determining mortality. P concentration seems to be a poorly understood soil nutrient in Thicket (Mills and Fey, 2004a), and was considered a possible factor promoting plant production, and “worthy of further research” by Mills and Cowling (2006). This nutrient is an important indicator of soil fertility, which is linked directly to plant and soil processes (Amezaga et al., 2004, Lechmere-

Oertel et al., 2005b). There have been conflicting reports on how P changes with degradation, some authors have found little evidence for changing P levels (Hoffman and Cowling, 1990, Lechmere-Oertel et al., 2005b) with degradation; some say that P increases significantly (Mills and Cowling, 2006, Mills and Fey, 2004a, Rutherford et al., 2012); while others have found that it decreases . Differences could be partially explained by landscape location, because P is also affected by gradient, where steeper slopes have lower values (Amezaga et al., 2004) and footslopes have higher concentrations (Ben-Shahar, 1990, Schimel et al., 1985, Yanagisawa and Fujita, 1999). My results indicate that P levels under 69 $mg.kg^{-1}$ resulted in the lowest mortality rates. Findings from intact spekboom-dominated Thicket generally indicates that P levels are low, such as Baviaanskloof (59 $mg.kg^{-1}$) (Mills and Cowling, 2010a) or near Uitenhage (59 – 76 $mg.kg^{-1}$) (Mills and Cowling, 2006). P concentration and availability are also related to soil texture, where fine textured soils have larger capacities to hold P than coarse textured soils. This results because of the inert character of sand particles as compared to clay particles (Busman et al., 2009), thus the alluvium type soils, especially of lower lying areas, may contain higher amounts of P than what spekboom can tolerate.

The pH of the soil influences P and micro-nutrient availability. P is most available at pH ranges 5.5 – 7.0 (Busman et al., 2009). Above a pH of 7.3, P becomes unavailable due to fixation (Lechmere-Oertel et al., 2005b, Medinski et al., 2010). pH is therefore also considered an indicator of fertility. In my analyses, a pH of 6.7 or lower resulted in a lower mortality than above 6.7. Research indicates that optimal growth in woody plant forms is in a pH range of 5.5 – 7 (Medinski et al., 2010, Mills and Cowling, 2006). Research of intact thicket indicates a pH range of 4.8 – 6.04 (Lechmere-Oertel et al., 2005b, Mills and Cowling, 2010a, Rutherford et al., 2012). An increased pH with degradation has been generally found in Thicket (Hoffman and Cowling, 1990, Lechmere-Oertel et al., 2005b, Mills and Cowling, 2010a, Mills and Fey, 2004a).

The pH level can also account for the differences in growth in Calitzdorp on the two different soils. More spekboom were actively growing on the “conglomerate” soils than the “alluvium” soils. This was also seen in the mortality data. Originally it was thought to be a function of soil texture, as alluvium soils are generally more clayey, but surprisingly, it was seen that they both have very similar clay contents, therefore differences between the two soils are not related to clay. Analysis indicated that the alluvium soil had a pH of 8, compared to the conglomerate soil, of pH 4. Therefore, as discussed above, the alluvium soil is too alkaline for spekboom growth. It could also be due to a salinity factor, as the alluvium soils had double the Na content of the conglomerate, and were dominated by salt tolerant species such as *Tetragonia fructicosa* and *Augea capensis.*

Conclusion

The STRP’s large scale restoration project spanning across 550 km of spekboom rich Thicket with degraded vegetation is possibly the largest ecological restoration experiment in the world (Mills et al., 2010b). Constant monitoring and evaluation of the restoration projects is a major function of the STRP, with the aim to improve survivorship and cost effectiveness.

There is no clear answer to the question whether spekboom growth and mortality is related to one or more soil factors as my results did not reveal very clear trends. This would support work by Mills et al. (2011) that spekboom is only constrained under extreme soil conditions and is tolerant of a wide range of soil conditions. Across all the sites mortality was high and the amount of actively growing plants very low. Site or location was the dominant governing factor of spekboom success, which is most likely due to climatic variability, especially with regards to rainfall, and seasonal influences. Unreliable rainfall, ambient temperature, solar radiation intensity, soil temperature and soil moisture will vary significantly between seasons. Key seasonal windows may exist with regards to optimising spekboom survivorship and ultimately good growth (Powell, 2009). It is clear that the plant performs better at the eastern end of its distribution, which is most likely due to the higher MAP. Therefore I recommend that the STRP focuses its efforts primarily around Addo and Baviaanskloof. In Addo aspect does not have a major influence on growth; therefore planting can take place on both north and south facing slopes. However, in general, north facing slopes would be a better option for planting sites, especially in the west near Calitzdorp. The results for the Baviaanskloof indicate that flatter areas are the best options for spekboom growth, which was also recorded by Powell (2009), who obtained 65 % survival in degraded flat areas.

In terms of soil factors, soils with a pH above 7 and P concentrations above 70 mg $P.kg^{-1}$ should preferably not be planted with spekboom. Planting on the lower lying, alkaline alluvium soils near Calitzdorp have resulted in complete mortality of spekboom and should not be considered for future planting sites. Soils with high clay content are beneficial for spekboom, as was also recorded by Powell (2009).

As Mills et al. (2011) concluded regarding the constraints of spekboom in the Fish River Reserve, it is probably a function of correlated factors related to position in the landscape (e.g. temperature or frost) and/or competition from other plants, and this could well be the case for the broader biome. The varied success rate of spekboom survival in the in the highly variable environments of degraded spekboomveld of the Eastern and Western Cape requires further investigation, especially regarding the influence of climate, planting methods and position in the landscape. I would recommend that the STRP analyses the influence of follow-up rainfall and planting season in the different areas. Also, as the factors being important for spekboom survival and growth were quite variable for different sites, I also recommend further soil related studies be done, in order to obtain more accurate, site-specific soil influences on spekboom.

Chapter 5 - General Discussion

Summary of major findings

The heavy levels of degradation in South African Thicket has been described as a "national tragedy" (Aucamp and Tainton, 1984). The high levels of degradation have stimulated research into protecting thicket against further transformation, as well as research into the processes that sustain this ecosystem. Most past work points towards the use of the ecosystem engineer *Portulacaria afra* (spekboom) to assist in the return of canopy plant biodiversity (Van der Vyver, 2011), and at the same time providing an income via carbon credits on international markets (Curran et al., 2012, Marais et al., 2009, Mills et al., 2010b, Mills and Cowling, 2006, Mills et al., 2007). Research on spekboom has focused on the future benefits obtained from planting spekboom, but very little has been done on the current and historical environmental influences on spekboom growth. This type of information has profound implications on the development of restoration protocols where success will only be achieved by planting spekboom in areas where it originally occurred, namely its original natural habitat (Mills et al., 2010b). The aim of this study was to further the understanding of the influence of selected soil properties on spekboom, with specific focus on the bearing it will have on the selection of future spekboom planting sites, by the Subtropical Thicket Restoration Programme (STRP) in South Africa.

In chapter 2 I investigated the influence that selected soil properties have on the landscape distribution of spekboom in natural, intact spekboom dominated Thicket. The idea was to see if soil properties, together with environmental features such as slope and aspect, could be responsible for the patchy distribution of spekboom in the landscape across the Thicket biome. The rationale is that an improved ecological understanding of factors influencing the plants natural site selection within the landscape (i.e. slope orientation and landscape position) will have a bearing on future restoration site selection (Mills et al., 2010b). The objectives is to determine if the presence of spekboom is related to soil factors and how these factors differ between different slope orientations as well as bottomland (valley) areas. Here I hypothesised that due to a catena effect, spekboom avoids bottomland areas that consist of fine textured, deep soils with high pH and nutrient levels, especially sodium (Na), and that these areas are more saline than the surrounding slopes. I further hypothesised that slopes of different aspects and bottomland areas differ in their soil and environmental composition. The results revealed four key findings: 1) I did not find a strong catena effect at the Thicket sites because all the factors, other than pH, did not show clear differences between the slopes and bottomland areas, especially regarding Na and salinity. 2) Spekboom prefers more acidic soils (pH range 4.4 – 5.1), 3) pH and slope are the only factors that appear to drive spekboom's preference for hill slopes and not valleys, and 4) there is a large degree of overlap in soil properties where spekboom does and does not occur. There is also an unambiguous trend in changing soil texture across the drainage basins from east to west. Although not considered in the study, it is recognised that slope angle, interlinked with aspect could be a significant environmental factor because it influences the amount of solar radiation a slope receives. The results confirmed previous observations on soils in Thicket which noted similar pH levels (Lechmere-Oertel et al., 2005b, Mills and Cowling, 2010a, Rutherford et al., 2012). It also confirms findings that spekboom can grow on a variety of geologies (Vlok et al., 2003), that it is tolerant of a wide range of soil conditions and is only constrained under extreme soil conditions (Mills et al., 2011). It also affirms Mills et al. (2011) argument that the catenas are not responsible for spekboom's distribution along slopes.

In chapter 3 I tested whether soil salinity (NaCl), Na or soil type could be affecting spekboom survivorship, growth, and overall plant condition in restoration sites. I hypothesised that plants subjected to high salinity conditions would most likely senesce or die, and if they do survive they would show little signs of above and below ground growth, as well as exhibit signs of poor plant condition. The rationale behind this hypothesis is that observations have indicated that spekboom does not grow well under saline conditions (Hobson et al., 1975), characteristic of lower lying, bottomland areas, where salts in the soil tend to accumulate after being washed down slope; or from evaporation in the soil. Information regarding spekboom's tolerance is generally extremely limited or 'unknown' (Dagar, 2000). The aim of this chapter is to increase the knowledge regarding spekboom's sensitivity to high salinity levels and to provide information to restoration managers of the STRP, who need to know where restoration work is likely to produce the best survival rates. The results indicated that: 1) soil type is not a significant factor, 2) spekboom plants grown under high saline conditions show signs of poor plant health, reduced root growth, reduced leaf numbers and little growth, while plants grown under low saline conditions grow better, increase in root growth and leaf numbers and have a general appearance of good plant health. 3) Although spekboom grown under high saline conditions displayed limited signs of growth, their high survival rate was un-expected, indicating a degree of tolerance to high salinity conditions. These findings affirmed observations that the plant is tolerant of a wide range of soil conditions (Mills et al., 2011). However, very high salinity will negatively affect spekboom growth.

Since 2004 the survival of spekboom at restoration sites has been extremely varied. Therefore, in chapter 4 I investigated relationships between spekboom cutting establishment and selected soil properties (macro-nutrients, pH, particle size, aspect, gradient, soil depth and infiltration) at three restoration sites, in Calitzdorp, Baviaanskloof Nature Reserve and around Addo National Park. Previous work has found that differences in soil characteristics, such as soil type, depth and degradation state, could manifest in different spekboom cutting survival, growth and carbon sequestration rates (Cowling and Mills, 2010, Mills et al., 2010b, Mills et al., 2011), all of which is of vital importance to the STRP. My results indicated three key findings: 1) site or location is the dominant governing factor of spekboom success, resulting in spekboom growing best in the east and mortality increasing westwards, 2) the selected soil properties do not have a large influence on spekboom's success rates. As soils play a limited role in the distribution of spekboom, I suggest that better spekboom performance in the east is most likely due to climatic variability, (especially regarding rainfall patterns) and seasonal influences. Although the soil data does not indicate strong correlations with growth or death, it does still indicate that north facing slopes result in more spekboom growth. Flatter areas are the best options for spekboom growth in the Baviaanskloof, which was also recorded by Powell (2009). Soils with a pH above 7 and P concentrations above 70 $mg.kg^{-1}$ should preferably not be planted with spekboom. Soils with a high clay content are beneficial for spekboom, as was also recorded by Powell (2009).

Research significance of this study

An understanding of the ecological requirements of a plant used for restoration is of vital importance. Most of the past Thicket research has been on the carbon sequestration aspect of spekboom and the effects of degradation. There is a gap in the understanding of the influence of soil and environmental factors on spekboom growth. My research has clearly indicated that soil is not a driving factor in spekboom distribution and growth. This is an important finding for botanists, restoration managers and landowners. My research has also generated a host of new questions and some that still remain un-answered. It is clear that pH is a limiting factor above 7, but it is not understood why. It is also not known why spekboom grows well on all aspects in some areas and not in others. My research supports the findings by Mills et al. (2011) that spekboom is not constrained by any specific soil factors. This tolerance to a wide variety of soil conditions promotes its importance and usefulness to the current and future restoration of Thicket landscapes. It is also significant to

know that a degree of soil salinity can be tolerated by spekboom, which is useful in restoring arid lands that are prone to salinisation.
It is however clear that other environmental factors and most likely climate, are largely responsible for spekboom's distribution. Mills et al. (2011) and Powell (2009) both noted that spekboom's position in the landscape is likely to be a function of factors relating to this, such as temperature or frost, to which I would agree. In my opinion, slope and aspect orientation are likely to further influence climate on different slopes, because of varying solar radiation loads. The differences in solar radiation loads and the possible effects on vegetation have been recorded in parts of South Africa (Schulze, 1975). This together with climate and rainfall would probably account for the patchy distribution of spekboom at the landscape scale. My results also indicate that towards the eastern end of spekboom distribution spekboom thrives, regardless of slope, both in the intact areas as well as the restoration sites. This also has important implications for the STRP, landowners and conservationists who may wish to restore the extent of Thicket. It should be recognised that towards the western end of spekboom distribution there may be more factors influencing spekboom's establishment and growth.

Limitations of this study

The key shortcomings in this study were a restricted sample size and a large degree of variability, due to influences beyond my control. In chapter 2 the sample size was limited to finding suitable valley areas, i.e. areas that were naturally free of spekboom and not due to livestock grazing. The major limitation in the nursery experiments in chapter 3 was a limited soil analysis. In order to determine a more accurate representation of the salinity levels in the soil, testing for chloride in the soil should have taken place, but this is a costly analysis performed by selected laboratories. On hindsight, a more economical method would have been to test for electrical conductivity and pH of the soil at the start and end of the experiment. This would have allowed me to observe the change in soil salinity in the two different soils over the course of the experiment and would have assisted in drawing more sound conclusions regarding spekboom's response to soil salinity.

Chapter 4, which focused on the restoration sites, also had limitations regarding the sample size, because most of the planting sites have been "blanked" by the planting teams, which is when the team removes dead spekboom plants and re-plants with new cuttings, creating a plot with different aged cuttings. The sample size was also reduced by there being no south facing plots in the Baviaanskloof, thus I could not compare north and south facing slopes in this area. There are many other factors that could influence survival in these plots (for example, time of year that planting took place, contractors, rainfall post planting) and the large range of environmental variability in the study area, all of which are beyond my control and cannot be standardised.

Recommendations

This study covered a large area, across which it was seen that spekboom grows on a variety of soil conditions, and my results, together with the findings from Mills et al. (2011), confirm that soil is not a driving factor for spekboom distribution. However, there are still areas that require investigation. On a smaller scale, within a given climate regime, research should focus on the unique set of conditions interacting on the soil and the vegetation. For example, at Calitzdorp, where within a small area of a few metres in extent, there was a change in soil which affected the survival of spekboom. Research is still needed to clarify why spekboom does not grow on south facing slopes around the Oudtshoorn area.

Considering climatic influences was not within the scope of this thesis, but it is recognised as a potentially important factor, and I would strongly recommend research into the influence of rainfall, temperature and/or frost on spekboom. Temperature could account for their absence in lower lying areas and from south facing slopes which are colder and receive less sunlight than north facing slopes. The use of relatively affordable Thermo Button Temperature Loggers within intact and degraded Thicket across the seasons would provide valuable information on how temperature differs within the landscape. Linked to temperature is also the influence of solar radiation. It would be worthwhile to know the amount of solar radiation the different slopes receive over the course of a year, as this affects surface energy budgets, temperatures and soil moisture balances; and could be regarded as one of the fundamental variables of the plant environment (Ciolkosz, 2009, Granger and Schulze, 1977, Zachar, 1982). I would also strongly recommend further research into the influence of rainfall seasonality and the time of year planting of cuttings takes place. For instance, if rainfall post planting could greatly increase survival of the cuttings, then planting just prior to the relevant rain season could be worthy avenue of action and research.

P concentrations and availability within the soil could be a limiting factor to spekboom growth. Although P has been noted as an important indicator in soil fertility, it is hard to explain why spekboom will grow less at higher levels of P. P is thus a nutrient whose influence in Thicket vegetation and degradation is poorly understood (Mills and Fey, 2004a). Mills and Cowling (2006) noted it as "worthy of research", and Van der Vyver (2011) emphasized its importance in soil fertility and consequently the carbon sequestration potential of the soil. I recommend further research into the role of P concentration in the soil and spekboom growth.

My research has indicated that pH levels in the soil to be a factor for spekboom growth and establishment. It would be useful to understand why and how pH affects spekboom. However, the information gained thus far could be useful to restoration managers when selecting sites for planting. There are a number of ways of quickly and cost effectively testing soil pH, to ensure that planting takes place in soils with a pH below 7. This could greatly reduce mortality of spekboom cuttings.

Chapter 6 - References

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