FACTORS INFLUENCING SURVIVORSHIP OF *PORTULACARIA AFRA* CUTTINGS IN RESTORATION OF DEGRADED LANDS

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ABSTRACT

Heavy over-browsing, over-grazing, and over-trampling has caused the degradation of vast areas of subtropical thicket, including parts of the Greater Addo Elephant National Park (GAENP). Severe degradation has resulted in the loss of vegetation cover and the deterioration of soils and soil functioning. The South African Department of Environmental Affairs (DEA), and specifically the Natural Resource Management Programme (NRM), have invested in restoration initiatives such as the Subtropical Thicket Restoration Programme (STRP), which has aimed to demonstrate the logistical and practical feasibility of restoring these degraded thickets by planting *en masse Portulacaria afra* (spekboom) cuttings. However, the planted *P. afra* cuttings often succumb to various abiotic and biotic stresses. This project aimed to identify various factors which may influence the survival of *P. afra* cuttings, including i) soil properties, ii) water (rainfall, infiltration, run-off, etc.), iii) browsing by mega-herbivores, iv) topographical features such as slope and aspect, or v) plant species or communities. Biodiversity and carbon baselines were carried out at 50 plots within the Main Camp, Darlington and Kabouga sections of the GAENP, providing pre-planting vegetation and soil data. The *en masse* planting of *P. afra* occurred following the completion of the baselines. Following a minimum rest period of three months after planting, survivorship counts were carried out at all plots. Infiltration rate had a significant positive relationship with planted *P. afra* survivorship across all of the sites. Positive trends between increases in litter and root biomass and planted *P. afra* cuttings survivorship in Kabouga were also evident. Magnesium, water-holding capacity and increasing soil clay percentage were found to have a significant negative relationship with planted *P. afra* survivorship in Kabouga. Aluminium, magnesium, and boron all had significant positive relationships with planted *P. afra* cuttings survivorship in Addo Main Camp. No soil variables had any significant relationship with survivorship of planted *P. afra* cuttings at Darlington. The presence of elephants (*Loxidonta africana*) had a significant negative relationship with planted *P. afra* survivorship. Plant communities in more 'moderately' degraded states, characterized by the retention of canopy dominant species, woody vegetation cover, limited bareground and higher cover of litter had higher survivorship of planted *P. afra* cuttings than those in more severely degraded states. The

grass *Panicum maximum*, and forb *Atriplex semibaccata* were associated with positive relationships with planted *P. afra* survivorship across all sites.

Future research should aim to develop matrices which plot likely survivorship percentages with parameters of measurable variables, such as infiltration, severity of soil capping, browsing densities, chemical indicators, and degradation severity, to identify suitable biophysical planting conditions for *P. afra* cuttings. Further research should assess whether the presence of elephants, in high densities, can reduce the economic feasibility of the *en masse* plantings of *P. afra* cuttings in attempts to restore degraded landscapes.

Keywords: Biodiversity, degradation, *Portulacaria afra,* restoration, subtropical thicket, survivorship

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LIST OF ACRONYMS AND ABBREVIATIONS

ABFRP	Addo, Baviaanskloof and Fish River Restoration Project
AENP	Addo Elephant National Park
ANOVA	analysis of variance
C	carbon
CAM	crassulacean acid metabolism
CDM	Clean Development Mechanism
CO_2	carbon dioxide
DEA	Department of Environmental Affairs
DistLM	Distance based linear modeling
DWAFF	Department of Water Affairs, Fisheries and Forestry
g	gram
g C m^{-2} yr^{-1}	grams of carbon per square meter per year
GAENP	Greater Addo Elephant National Park
GFRNR	Great Fish River Nature Reserve
GIB	Gamtoos Irrigation Board
ha	hectare
kg	kilogram
m^{-2}	square meter
MAR	mean annual rainfall (or MAP = precipitation)
MDS	Multi-Dimensional Scaling
mg	milligram
mm	millimeter
NAPs	National Action Programmes
NRM	Natural Resource Management Programme
PCA	principal component and classification analyses
PCoA	Principal Coordinate Ordination
SANParks	South African National Parks
SOM	soil organic matter
SOP	standard operating procedure
Spp.	species
STEP	Subtropical Thicket Ecosystem Planning Project
STRP	Subtropical Thicket Rehabilitation Programme
t C ha^{-1} yr^{-1}	tons of carbon per hectare per year
UNCCD	United Nations Convention to Combat Desertification
UNFCCC	United Nations Framework Convention on Climate Change
VCS	Verified Carbon Standard
WHC	water-holding capacity
yr	year

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1. INTRODUCTION

1.1 Degradation and climate change

The United Nations Convention to Combat Desertification (UNCCD) defines land degradation as the "reduction or loss of the biological or economic productivity and complexity of terrestrial ecosystems" (IPCC, 2001a). Degraded land has suffered a change relative to its previous state set by the climate, soil properties, topography and expectation of land managers (Prince *et al.*, 2009). Land degradation has effects at local, national, continental and global scales, progressively influencing social and environmental vulnerability; with desertification and degradation affecting more than 1.5 billion people globally (Nkonya *et al.*, 2011).

Negative regional effects of land degradation include: reduced biodiversity leading to lower ecosystem resilience (Mills *et al.*, 2007; Powell, 2009; Prince *et al.*, 2009; Lunderstedt, 2016), reductions in carbon sequestration and release of carbon through soil erosion (Powell, 2009; Prince *et al.*, 2009; van der Vywer, 2011); reductions in water and food security (Prince *et al.*, 2009); while regional climates are impacted through changes in evaporation ratios, roughness, albedo and increased atmospheric dust loads (Reynolds & Stafford Smith, 2002 cited in Prince *et al.*, 2009). Land degradation is typically associated with a continual loss of ecosystem efficiency (Scholes & Biggs, 2005), which incorporates transformation, resulting in a significant homogenization of landscapes, including reductions in their fertility (Lechmere-Oertel, 2003, Mills & Fey, 2004a). The loss of above ground vegetation and litter, and the associated deterioration of soils, results in a reduction in fertility of landscapes (Lal, 2001; Prince *et al.*, 2009). The removal of vegetation and the associated deterioration of soils results in carbon previously stored in soils and biomass being emitted into the atmosphere as CO_2 (Lal, 2001). Land-use change and over-grazing/over-browsing are pivotal drivers of land degradation (Kerley *et al.*, 1995; Scholes & Biggs, 2005), with land-use change being recognized as one of the major anthropogenic sources of atmospheric CO_2 globally (Watson *et al.*, 2000; Lal, 2001). The increased levels of atmospheric CO_2 impact climate change (Houghton *et al.*, 2000). The level of atmospheric CO_2 currently exceeds levels recorded over the past 800 000 years, with rates of change in CO_2 being the fastest in 150 years (World Meteorological Organization, 2017), which has focused worldwide attention on atmospheric CO_2 and associated concerns of global warming (Lal, 2001; Meadows & Hoffman, 2003). In 1992, the

Earth Summit and the United Nations Framework Convention on Climate Change (UNFCCC) directed increased attention towards anthropogenic climate change. This was followed by the Kyoto Protocol in 1997, which became the policy tool used to gauge the increasing rate of global climate change caused by greenhouse gases such as CO_2 (IPPC, 2007).

The African continent has been identified as particularly vulnerable to the effects of climate change, due to the low adaptive capacity and sensitivity of most of its populations (IPCC, 2007; Stringer *et al.*, 2009). Within Africa and developing countries worldwide, climate change takes place in tandem with and often exacerbates other stressors such as poverty, health, and water and food insecurity (Hoffman & Ashwell, 2001; Ziervogel *et al.*, 2014). The addition of these stressors to environmental change, drought and land degradation make addressing climate change and degradation within the developing world a challenging task (Adger *et al.*, 2005; Stinger *et al.*, 2009). Long-term regional climate change predictions typically show a warming and drying of southern Africa (Christensen *et al.*, 2007), along with increasing air temperatures, rainfall variability, and increases in extreme events, which will most likely accentuate land degradation across extensive areas of South Africa, especially those which have already been identified as severely degraded (Hoffman *et al.*, 1999; IPPC, 2001b). The forecasted climate change scenarios prioritize land degradation as one of the main environmental problems in the region (Darkoh, 2009; Rutherford & Powrie, 2013). Moreover, it is expected that land-use change and other forms of degradation will continue as the primary drivers of biodiversity loss in southern Africa over the next century (Scholes & Biggs, 2005; Biggs *et al.*, 2008). The predicted impacts of global climate change are thus likely to have detrimental consequences for South Africa's biodiversity, with range contractions, species compositional changes and even extinctions plausible (Van Jaarseveld & Chown, 2001). For developing nations such as South Africa, which are still coming to terms with the relationships of past and present social, political, economic and physical environmental constraints, it is critical that the issue of land degradation in the context of climate change be addressed, mitigated, and resolved where possible (Meadows & Hoffman, 2003).

A major step towards coming to terms with the global initiatives to combat climate change occurred when South Africa became a signatory of the UNCCD (Meadows & Hoffman, 2003). Under Agenda 21, National Action Programmes (NAPs) were developed to combat desertification

and degradation in South Africa, as a requirement for signatories of the UNCCD (Meadows & Hoffman, 2003). Desertification is land degradation in arid, semi-arid and sub-humid lands (IPCC, 2001a), and is largely influenced by prevailing regional scales of degradation (Kerley *et al.*, 1995; Reynolds *et al.*, 2007). According to the UNCCD definition of "affected drylands" more than 90 % of South Africa's land surface is considered affected. The Department of Environmental Affairs (DEA) coordinated the NAPs and embarked on a national review of land degradation and desertification (Hoffman *et al.*, 1999). The review was used as a basis to evaluate the potential impacts of various drivers of desertification, taking into account the implications of the nature and extent of the problem for a wide range of environmental and socio-economic concerns (Meadows & Hoffman, 2003). Key deliverables included national scale maps indicating the distribution and severity of degradation with reference to soil, vegetation, and surface and groundwater resources (Hoffman *et al.*, 1999; Meadows & Hoffman, 2003). The maps revealed several key areas of degradation in the country (Meadows & Hoffman, 2003), which included vast areas of the Eastern Cape province (Hoffman *et al.*, 1999; Meadows & Hoffman, 2003). Long-term outputs included the establishment of policies and plans to combat degradation, secure biodiversity and in turn mitigate against the predicted effects of a warmer and drier climate (Hoffman & Ashwell, 2001). Land-use practice was found to be the most direct human contribution to land degradation in South Africa (Hoffman *et al.*, 1999).

Transformed habitats, including subtropical thicket, were identified to be most susceptible to the impacts of climate change (van Jaarsveld & Chown, 2001), especially as they are currently one of the most extensively livestock-degraded habitats in the country (Kerley *et al.*, 1995; Lloyd *et al.*, 2002, Powell *et al.*, 2006). The Subtropical Thicket Ecosystem Planning Project (STEP) was started in July 2000, with the objective of identifying priority areas within the Thicket biome for conservation (Lloyd *et al.*, 2002). The STEP programme aimed at ensuring the incorporation of the conservation plan into land-use plans at the national, provincial and municipal levels (Pressley & Cowling, 2001 cited in Lloyd *et al.*, 2002). A key aim of the programme was to assess the extent of transformation of thicket types to develop an understanding of the threats to thicket ecosystems (Lloyd *et al.*, 2002). The programme revealed patterns of vast degradation and transformation across the majority of thicket types. All described vegetation types showed levels of severe

degradation, ranging between 32 % and 88 % (Lloyd *et al.*, 2002), and more than 70 % of all vegetation units explored were "moderately" or "severely" degraded (Lloyd *et al.*, 2002).

In January 2004, the Subtropical Thicket Rehabilitation Programme (STRP) was initiated, looking at ways to combat further degradation and restore large areas of severely degraded thicket (Powell *et al.* 2004; Mills *et al.*, 2007; Marais *et al.*, 2009). Under the Clean Development Mechanism (CDM), Article 12 of the Kyoto Protocol, an allowance was made to establish carbon sequestration projects in developing countries to facilitate an overall reduction in emissions (Stringer *et al.*, 2009). Initiated by the Department of Water Affairs Fisheries and Forestry (DWAFF), the STRP sought to test the feasibility of using *P. afra* to sequester carbon (Mills *et al.*, 2007; Marais *et al.*, 2009, Powell, 2009), using the recently emerging global carbon economy as an opportunity to finance the restoration of degraded thicket via carbon credits (Mills *et al.*, 2007; Mills & Cowling, 2010). Apart from mitigating against carbon lost through land degradation, the project also aimed to improve rural livelihoods, restore biodiversity, and replenish ecosystem services (Powell, 2009). The motivation for the project came from a study by Mills *et al.*, (2005a) which had shown that drier areas of subtropical thicket have high carbon stocks relative to the mean annual rainfall (MAR), therefore having potential for carbon farming and achieving subtropical thicket restoration goals simultaneously (Mills *et al.*, 2007). Increased awareness of the need for sustainable use and management of natural resources and the conservation of biodiversity underpins the necessity to restore degraded landscapes (Todkill *et al.*, 2006). Changes in land use and management practice to store and sequester carbon will not only assist in restoring degraded landscapes, but address global efforts to mitigate anthropogenic climate change and alleviate poverty (Stringer *et al.*, 2009). Aligned with other restoration initiatives, and the understanding of the necessity to invest in the restoration of natural capital, a bioregional restoration programme was deemed possible (Powell *et al.*, 2004, 2006; Mills *et al.*, 2007; Marais *et al.*, 2009).

1.2 Subtropical thicket and degradation

Subtropical thicket is a component of the Albany Thicket Biome (Hoare *et al.*, 2006), which covers approximately 17 % of the surface area of the Eastern Cape province of South Africa (Mucina & Rutherford, 2006; Powell *et al.*, 2006). When not severely degraded, the vegetation is typically short (3-5 m), evergreen, compact, spinescent, with a continuous canopy of woody trees and

shrubs, succulents, forbs, vines and bulbs (Vlok *et al.*, 2003; Hoare *et al.*, 2006). The 'thicketed' clustering of vegetation in turn supports a high species diversity of browsing mammals (Skead, 1987). Subtropical thickets are an ancient vegetation type, dating back to the Eocene and have been mooted as one of the initial biomes from which the rest of South African biomes evolved (Cowling *et al.*, 2005; Proche *et al.*, 2006). This suggests that subtropical thicket vegetation and the mammal species it supports have co-evolved over an extensive period of time (Kerley *et al.*, 1995). Intact subtropical thicket has substantial economic value (Sims-Castely, 2002), due to large stocks of carbon (Mills *et al.*, 2005a, 2005b; Mills & Cowling, 2006; Powell, 2009; van der Vyver, 2013). Intact subtropical thicket can store in excess of 245 t C ha^{-1}, which is unusually high for a semi-arid environment (Mills *et al.*, 2005a).

Over the past century, the semi-arid forms of subtropical thicket in the Eastern and Western Cape have undergone extensive transformation through over-grazing/over-browsing and land-use change (Acocks, 1988; Hoffman & Cowling, 1990; Stuart-Hill, 1992; Lloyd *et al.*, 2002). The thicket biome is not well suited to sustain domestic livestock due to the 'bottom-up' browsing habits of goats and sheep, resulting in degradation (Stuart-Hill, 1992; Lechmere-Oertel *et al.*, 2005a; Todkill *et al.*, 2006; van Luijk *et al.*, 2013). The over-stocking of small stock in *P. afra* dominated thickets dates back to the late 1800's (Lechmere-Oertel, 2003), with the degradation process being exacerbated in the 1960's to satisfy the highly successful mohair industry (Acocks, 1988). The severity of the over-grazing/over-browsing and subsequent degradation resulted in changes in species composition, vegetation structure and complexity, and the loss of canopy dominant species (Lechmere-Oertel, 2003; Lechmere-Oertel *et al.*, 2005a). Losses of 75 % of total dry biomass (Lechmere-Oertel, 2003; Lechmere-Oertel *et al.*, 2005a), 70 % canopy cover (Powell, 2009), and reductions of soil quality, soil carbon and nitrogen stocks (Mills & Fey, 2004b), as well as slower rates of water infiltration (van Luijk *et al.*, 2013), and decreased water use efficiency have been hypothesized (Powell, 2009) and recorded (Mills & Fey, 2004a). Nearly all forms of subtropical thicket experience moderate to severe levels of degradation (Lloyd *et al.*, 2002). Severely degraded thicket results in reduced ecosystem services and limited chances of recovery without active restoration or intervention (Stuart-Hill & Aucamp, 1993; Sigwela, 2004). In semi-arid or xeric forms of subtropical thickets, natural succession of severely degraded areas is extremely slow or non-existent (Stuart-Hill, 1992), but more mesic forms may have some self-

restoration capacity (Stickler & Shackleton, 2015). Pastoralism in subtropical thickets may be ecologically and economically unsustainable (Kerley *et al.*, 1999).

1.3 *P. afra* and subtropical thicket

P. afra (L.) Jacq., more commonly known as spekboom, is a dominant species within more arid subtropical thickets, playing a vital role in above and below ground carbon pools through its high carbon sequestration potential (Mills & Fey, 2004a, 2004b; Powell, 2009; van der Vyver, 2011, 2013). The species functions as a driver of soil nutrient status, strongly regulating soil organic matter through micro-climate, erosion control, high leaf litter production (Lechmere-Oertel, 2008), high rainfall interception capabilities (Cowling & Mills, 2011), and possibly soil chemistry (Mills & Fey, 2004b; Powell, 2009). The import role *P. afra* plays in the functioning of subtropical thicket could be due to *P. afra* having the ability to change between crassulacean acid metabolism (CAM) and C_3 photosynthetic pathways (Ting & Hanscom, 1977). This physiological ability has led to *P. afra* being described as a miracle plant (Vlok & Euston-Brown, 2002) and an ecosystem engineer (van der Vyver, 2013). Furthermore, *P. afra* can significantly lower beneath-canopy temperatures in relation to ambient temperatures (Lechmere-Oertel *et al.*, 2008), producing a microclimate which is thought to provide conditions favorable to a high sub-canopy species richness (Sigwela, 2004; Powell, 2009). The dominance of *P. afra* across large areas of subtropical thicket types (Vlok *et al.*, 2003) is thought to underpin why carbon storage in subtropical thicket is unusually high for a semi-arid environment (Mills *et al.*, 2005a). According to Mills & Cowling (2006), *P. afra* has the ability to sequester carbon rapidly in semi-arid environments, up to 0.42 kg C m^{-2} yr^{-1}. *P. afra* is a widespread species within the thicket biome, being found as a dominant canopy species within the majority of the 112 distinct subtropical thicket types (Vlok *et al.*, 2003; Powell *et al.*, 2006). However, due to heavy browsing by goats and the clearing of intact subtropical thicket for agriculture, *P. afra* is one of the dominant species that has been lost from most subtropical thickets (Lechmere-Oertel, 2003; Mills & Fey, 2004a; Powell, 2009). When exposed to high browsing pressure, recovery of *P. afra* plants is a long term process which can take up to 18 months to recover from 50 % defoliation by goats (Aucamp, 1976, 1979 cited in Lechmere-Oertel, 2003). Patterns and causes of degradation on *P. afra* dominated thickets have been well documented (Hoffman & Cowling, 1990; Stuart-Hill, 1992; Moolman & Cowling, 1994; Kerley *et al.*, 1995; Mills & Fey, 2004a; Lechmere-Oertel *et al.*, 2008; Sigwela *et al.*, 2009).

Findings suggest that the transformation of *P. afra* dominated thicket involves a negative feedback cycle with the loss of the woody and succulent shrub components causing a reduction in nutrient cycling (Lechmere-Oertel, 2003), including homogenization of the spatial distribution of soil properties and the processes which maintain that pattern (Lechmere-Oertel, 2003). Therefore, the loss of *P. afra* from the landscape results in a transformation from subtropical thicket into open savanna dominated by annual grasses and forbs (Mills & Fey, 2004a). At a certain level of degradation, an abiotic threshold will most likely be crossed which will cause changes in soil properties, thus creating a barrier that will limit successful regeneration of *P. afra* and other thicket canopy species (Mills & Fey, 2004a).

1.4 *P. afra* and restoration

In most areas of degraded subtropical thicket where *P. afra* has been removed completely, natural regeneration via seedling recruitment is non-existent (Powell, 2009). Regeneration in open patches between thicket 'clumps' is also highly unlikely (Sigwela, 2004), as *P. afra* has constraints which inhibit the species from colonizing highly degraded areas (Powell, 2009). Therefore, in degraded subtropical thicket, especially drier forms, active restoration is required to restore landscapes and return keystones species (such as *Euclea undulata*, *Schotia afra*, and *Pappea capensis*) by planting *P. afra* cuttings (Powell *et al.*, 2004; Sigwela *et al.*, 2009; Mills *et al.*, 2011). It has been hypothesized that if *P. afra* can be re-established on degraded landscapes, it has the ability to supply the conditions required for the landscape to naturally restore dominant canopy species (van der Vyver *et al.*, 2013) and other plant biodiversity which otherwise would have no natural recruitment under degraded conditions (Lechmere-Oertel *et al.*, 2005a; Mills & Cowling, 2006; Sigwela *et al.*, 2009).

Due to the ease of *P. afra* propagation (Swart *et al.*, 1994) and high carbon accrual rates in both soils and biomass at the landscape scale (Lechmere-Oertel, 2003; Mills & Cowling, 2006; van der Vyver *et al.*, 2013), *P. afra* planting can drive restoration through carbon credits in the formal and informal carbon markets (Mills & Cowling, 2006; Powell *et al.*, 2006; Marais *et al.*, 2009; Powell, 2009). Furthermore, planting *P. afra* cuttings could be the most cost effective method of restoring large areas of the subtropical thicket biome (Swart *et al.*, 1994; van der Vyver *et al.*, 2013). Therefore, the restoration of degraded thicket landscapes is being tested at large scales across the

Eastern Cape and Western Cape by planting *P. afra* cuttings (Powell *et al.*, 2004; Mills & Cowling, 2006; Mills *et al.*, 2007; Sigwela *et al.*, 2009; Mills *et al.*, 2011), with the belief that 'carbon farming' as a land use could become a more profitable farming practice than pastoralism (Mills *et al.*, 2007).

1.5 Soils and degradation

Soil is the dynamic layer of materials and biota covering the land surface that differs from the underlying geological "parent" material with respect to chemical, physical, biological and morphological properties (Perkins *et al.*, 2013). Soil degradation relates to the long-term deterioration of soil productivity and its environmental moderating capacity (Lal, 2001). The degradation of soils is a problem which has been exacerbated by increases in human and animal populations, cultivation, and the adoption of extensive, resource-based farming methods (Hazell & Wood, 2008). Soil degradation has negative environmental and economic impacts (Ananda & Herath, 2003; Hazell & Wood, 2008). Soil degradation also affects water quality and emission of radioactively-active gases to the atmosphere (Lal, 2001). Although soil holds the largest terrestrial store of organic C, estimates of soil organic C for many countries or continents are either unavailable or mostly uncertain as they are derived from sparse data, with large gaps throughout most regions (Viscarra Rossel *et al.*, 2014). However, using accurate baseline data, it is possible to effectively monitor soil conditions and develop effective policies to offset the emissions of greenhouse gases and, in turn, combat climate change (Viscarra Rossel *et al.*, 2014). Restoring degraded soils and ecosystems has a potential to sequester C, reducing the rate of accumulation of atmospheric CO_2 and other gases (Lal, 2001), as well as restore degraded landscapes (Todkill *et al.*, 2006; Powell, 2009).

1.6 Soil properties and plant performance

Land-use history and associated past disturbances can greatly influence soil properties and plant performance, with some effects lasting for decades (Evans & Belnap, 1999; Kulmatiski *et al.*, 2006). Soils can have species-specific effects on plant growth, and plants can have species-specific effects on soil nutrient availability, soil microbial communities, and therefore the performance of plants in following generations (Aerts, 1999; Perkins *et al.*, 2013). Therefore, it is important to incorporate soil properties into ecological studies, allowing for the acknowledgement of

aboveground impacts on belowground conditions (Perkins *et al.*, 2013). Such plant-soil feedbacks are a dynamic part of aboveground - belowground linkages, which influence plant coexistence, invasion and restoration (Perkins & Nowak, 2013). Soil properties such as soil texture, pH, fertility and organic matter content are physical and chemical indicators of soil health (Arias *et al.*, 2005), and all influence plant growth and performance (Perkins & Nowak, 2013). Such soil factors determine the outcome of plant performance, plant-plant interactions, and plant–soil interactions (Aerts, 1999; Perkins *et al.*, 2013).

Soil texture, pH, and organic matter are fundamental soil properties which have influences throughout the soil system (Perkins *et al.*, 2013). Soil texture is the proportion of the various sizes of soil particles such as sand, silt and clay, and influences plant growth, water infiltration, and nutrient holding capacity (Perkins *et al.*, 2013; van Luijk *et al.*, 2013). Soil pH affects nutrient availability, the solubility of soil minerals, the activity of microorganisms, and therefore plant growth (Arias *et al.*, 2005; Perkins *et al.*, 2013). Soil organic matter (SOM) is a mixture of biogenic constituents that include non-decomposed plant materials and microorganisms (Arias *et al.*, 2005). SOM influences the chemical and physical properties of soil (Arias *et al.*, 2005), and provides nutrients and habitat to organisms living in the soil which are necessary for biological activity in the soil (Perkins *et al.*, 2013). SOM improves soil structure which promotes drainage and root penetration (Sollins *et al.*, 1999 cited in Perkins *et al.*, 2013). Higher SOM generally results in greater plant productivity (Perkins *et al.*, 2013). Nitrogen (N) and phosphorus (P) are important nutrients for plant growth. Mineral N is formed by the mineralization on SOM, and is the form of N which is available for plant uptake (Aerts, 1999; Perkins *et al.*, 2013). P is the second most limiting nutrient for plant production after N (Lajtha *et al.*, 1999 cited in Perkins *et al.*, 2013). Potassium (K) is another macronutrient which influences plant performance (Perkins *et al.*, 2013). K levels in soil positively influence primary production and growth of trees (Tripler *et al.*, 2006), competitive relationships between plants (Perkins *et al.*, 2013), and plant-soil feedbacks (Perkins & Nowak, 2013).

Micronutrients also have critical roles to play in plant–soil relationships and plant performance. Although micronutrients are only required in small amounts, their balance and availability is vital for optimal plant performance (Perkins *et al.*, 2013). Such micronutrients include boron (B),

copper (Cu), iron (Fe), and manganese (Mn). Boron plays a unique physiological role in plants. It is involved in the synthesis of plant cell walls which is required for normal plant growth and development to occur (Camacho-Cristobal *et al.*, 2008). Although it is not required in high amounts, if it is not supplied at the appropriate levels it can cause severe plant growth problems.

1.7 Soils, subtropical thicket and *P. afra*

P. afra plays an important role in facilitating carbon integration into the soil, assisting in the maintenance of ecosystem functioning (Mills & Fey, 2004a; Lechmere-Oertel *et al.*, 2008). Bushclumps in a matrix of *P. afra* thicket have a distinct spatial pattern of soil fertility where nutrients and C are concentrated under the patches of perennial shrubs, compared to under canopy trees and open spaces (Lechmere-Oertel, 2005b). When loss of vegetation intactness occurs due to degradation, landscapes become dysfunctional, losing the spatial organization of vegetated fertile patches, and much of their reserves of organic matter and nutrients (Lechmere-Oertel, 2003). The loss of SOM and nutrients hinders natural recovery within thicket types, due to the lack of recovery of soil processes (Todkill *et al.*, 2006). *P. afra* is tolerant of a wide range of soil conditions (Mills *et al.*, 2011), even in degraded areas which have experienced severe losses of soil fertility (Mills & Cowling, 2006: Mills *et al.*, 2007; Sigwela *et al.*, 2009; Mills *et al.*, 2011). However, restoration initiatives using *P. afra* cuttings are not always successful, with high mortality rates in certain areas (Swart *et al.*, 1994; Lagerwall 2010; Powell, 2009).

1.8 Water-holding capacity, infiltration and crusting

The key driver of primary production in semi-arid landscapes is water (Lechmere-Oertel, 2003). Each rainfall event produces water that either infiltrates into the soil, which is captured by the soil surface or canopy, or runs off the soil surface (Lechmere-Oertel, 2003). Therefore, water availability to plants depends on rainfall, evaporation, soil depth, and the water-holding capacity of soils (Mills *et al.*, 2009), with growing evidence that dew and mist could play significant roles, especially in semi-arid landscapes (Sharma, 1976; Nikolayev *et al.*, 1996; Xiao *et al.*, 2009). Slope, texture and structure of the soil affect the division of precipitation between infiltration and run-off (Mills *et al.*, 2009). The primary interest in surface features is to understand the way in which precipitation behaves once it reaches the soil surface (Lechmere-Oertel, 2003).

Overstocking with small stock in semi-arid thickets results in a severe loss of above ground biomass and the crucial litter layer, disrupted nutrient cycles, slower rates of water infiltration, decreased water use efficiency and can ultimately lead to a state of desertification (Powell *et al.*, 2006). Overgrazing forms a patchy vegetation pattern within subtropical thickets which leads to a decreased density of plants and species richness (Mills & Fey, 2004a), resulting in crusting of soils, decreased infiltration, and changes in soil properties in transformed lands (Lechmere-Oertel, 2003; Mills & Fey, 2004b). In semi-arid areas, small differences in soil properties have a major effect on soil erodibility (Martinez-Mena *et al.*, 1998 cited in Lechmere-Oertel, 2003), thus effecting surface water responses. Furthermore, the loss of intactness of vegetation can also be correlated with litter loss, which also reduces infiltrability (Lechmere-Oertel, 2003; Mills & Fey, 2004c), as crusting is correlated with litter cover loss (Belnap & Lange, 2001; Lechmere-Oertel, 2005b). With the homogenization of landscape pattern, soil moisture retention (matric potential) decreases along with water infiltration which can decrease from 62 – 0.6 % (Lechmere-Oertel, 2005b). The reduction of vegetative density can also influence soil pH, electrolyte concentration and organic matter concentration which all affect clay dispersion (Mills & Fey, 2004a; Mills & Fey, 2004c), which in turn increases the chances of crusting.

Crusting can occur on most soils including the loamy sands and clays found in many degraded, semi-arid, subtropical thickets (Mills & Fey, 2004c). Soils that have a tendency to crust often lead to low infiltration rates (Mills *et al.*, 2009), reducing the availability of water for plants (Mills & Fey, 2004a). Iron (Fe) is considered a stabilizing constituent which reduces the tendency of soils to crust and therefore improve soil infiltration (Mills *et al.*, 2009). Aluminum (Al) tends to be correlated to clay content (Perkins *et al.*, 2013). Crusting can be used as a potentially useful index for assessing soil degradation on certain soil types in South Africa (Mills & Fey, 2004c; Mills *et al.*, 2009).

P. afra thickets, like most plant communities in arid and semi-arid systems, illustrate opportunistic responses to rainfall, with increases in growth of dominant species following significant rainfall events (Hoffman & Cowling, 1991). However, decreased landscape fertility can lead to a decoupling of rainfall events and net primary production (Holm *et al.*, 2002 cited in Lechmere-Oertel, 2005b), as well as a reduction in time that water remains in the soil or does not infiltrate to

the effective root depth, resulting in plants being unable to respond to rainfall events due to the limiting of nutrients (Lechmere-Oertel, 2003). Soil crusting and reduced soil infiltration are consequences of land degradation, which subsequently result in the inability of soils to capture rainfall (van Luijk *et al*, 2013). Therefore, a reduction in infiltration could be a major contributor to high mortality of planted cuttings. Powell (2009) suggests that degraded soils with high clay content and soil crusting could increase mortality of planted *P. afra* cuttings. Lechmere-Oertel (2003) found that the transformation of landscapes significantly reduces the ability of the landscape to retain moisture. Therefore, the restoration of species richness, biomass, and vegetation structure in degraded lands may require chemical or physical modification of soil to increase infiltration and increase survivorship (Beukes & Cowling, 2003).

1.9 Plant species combinations as indicators of suitable biophysical restoration conditions.

The transformation of *P. afra* dominated thicket involves a positive feedback cycle with the loss of the woody and succulent shrub components causing a breakdown in nutrient cycling (Lechmere-Oertel, 2003). At a certain level of degradation, an abiotic threshold will most likely be crossed which will cause changes in soil properties, thus creating a barrier that will limit successful regeneration of *P. afra* and other thicket canopy species (Mills & Fey, 2004a). However, the transformation of intact thickets is not always homogenous throughout the landscape. Often degradation results in isolated thicket patches, which occur within a matrix of karroid-like grasses, woody shrubs, and bare ground (Lechmere-Oertel, 2003; Lechmere-Oertel *et al*., 2005b). The changes in vegetation structure and functions associated with such transformations result in reductions in soil organic matter and fertility, as well as the loss of above-ground biomass in the transformed areas (Lechmere-Oertel *et al*., 2005b). However, vegetation patches, or thicket 'patches', retain soil nutrients and create micro-climates for natural recovery processes (Lunderstedt, 2016). It has been found within savannas that these vegetation patches play an important role in nutrient cycling, especially in more arid gradients (Wang *et al*., 2009).

No evidence of regeneration has been found within the open patches in degraded spekboomveld (Sigwela *et al*., 2009). In many degraded thickets, the karroid like grass and shrub matrix may have passed a system threshold, making it resilient to recovery processes (Lunderstedt, 2016). However, it is plausible that a regeneration gradient exists moving away from the thicket patches

towards the open patches, which could be driven by the diffusion of soil nutrients from the thicket patches. This gradient could potentially be characterized by certain plant species and communities which may be tolerable of intermediate soil characteristics between degraded and intact states, and may be significant in identifying suitable areas for restoration efforts.

Rutherford *et al.* (2012) found that the woody shrub *Rhigozum obovatum* decreases in abundance as degradation increases in spekboomveld, whilst the woody shrub *Lycium ferocissimum* increases in abundance with increased browsing pressures. The shrubs *Aizoon glinoides, Atriplex lindleyi* subsp. *inflata, Pentzia incana,* and *Solanum tomentosum* increase in both abundance and cover in transformed or degraded thickets (Vlok & Euston-Brown, 2002; Rutherford *et al.*, 2012). *E. undulata* and *Grewia robusta,* which are not considered dominant tree species in intact semi-arid thickets, are residually dominant in numerous degraded semi-arid thicket types (Lloyd *et al.*, 2002), acting as degradation indicator species. The loss of *P. afra* from most degraded thicket types results in a transformation from subtropical thicket into open savanna dominated by annual grasses and forbs (Mills & Fey, 2004a). *Cynodon dactylon, Enneapogon desvauxii* and *Aristida congesta* are grass species which increase in degraded spekboom (Vlok & Euston-Brown, 2002). In certain areas, the loss of *P. afra* has resulted in increases in the woody shrub *Putterlickia pyracantha* and the invasive *Opuntia ficus-indica* (Hoffman & Cowling, 1990).

It is yet to be shown that individual plant species or compositions influence the survivorship of planted *P. afra* cuttings, although this question is being investigated. However, Lagerwall (2010) found that survivorship of planted *P. afra* cuttings in degraded sites surrounding certain thicket types, namely Spekboom thicket and Pentziaveld, was significantly higher than Noorsveld thicket. Certain guilds and/or species could potentially act as indicators of suitable biophysical environment to plant *P. afra* cuttings. This could be of great benefit to decision-makers and planners with regard to future planting efforts.

1.10 Herbivory

Subtropical thicket has historically supported a high diversity of vertebrate browsers (Skead, 1987), including black rhinoceros (*Bicornis biocornis* subsp. *bicornis*), kudu (*Tragelaphus strepsiceros*), and elephant (*Loxadonta africana*), which are found in high densities (Cowling & Kerley, 2002). Indigenous animals are an integral component in the ecology of subtropical

thickets, specifically due to zoochory (Kerley *et al.*, 2004). Historical densities of these mammals have led to the hypothesis of co-evolution between browsers and the vegetation type (Kerley *et al.*, 1995). Indigenous ungulates, primates, and birds play a vital role in the dispersal of most thicket canopy plant species (Cowling *et al.*, 1997; Sigwela, 2004; Sigwela *et al.*, 2009). Areas protected from mega-herbivores such as black rhinoceros and elephant may experience altered browsing pressures which could result in plant and animal communities developing differently (Cowling & Kerley, 2002). This is a major concern as subtropical thickets are vulnerable to desertification if herbivore management is not sound (Wilson, 2002 cited in Kerley & Landman, 2006). The management of elephants in conservation areas has caused much interest in conservation, policy, and decision making circles due to the loss of biodiversity (Lombard *et al.*, 2002), which has led to the so-called 'elephant problem' (Kerley & Landman, 2006).

Significant changes to landscape patchiness occur due to the widening of paths and opening of habitats with increasing elephant density (Kerley & Landman, 2006). Kerley & Landman (2006) postulate that path formation has important knock-on effects due to changes in microclimate associated with a change in vegetation density. Stuart-Hill (1992) hypothesized that thicket containing *P. afra* is adapted to browsing from the 'top-down' by elephants, unlike the destructive 'bottom-up' browsing by goats which has been such a significant driver of degradation in subtropical thickets historically. 'Top-down' browsing is thought to promote asexual recruitment of *P. afra* by protecting cover at ground level, facilitating coppicing and the development of a 'skirt' (Stuart-Hill, 1992; Sigwela *et al.*, 2009; Powell, 2009). Therefore, a lack of mega-herbivores could negatively affect the growth rate of *P. afra* cuttings as high densities of smaller indigenous herbivores could lead to a 'bonsai' growth form of *P. afra* developing (Powell, 2009).

Elephants could increase the diversity of the endemic-rich fauna as they are less likely to browse on low succulents and geophytes (Moolman & Cowling, 1994), especially in the mosaic open thicket that emerges under elephant browse pressures (Stuart-Hill, 1992; Kerley & Landman, 2006). Browse pressure on established *P. afra* is optimal within the 25 – 50 % range of leaf material removal (Aucamp, 1979 cited in Lechmere-Oertel, 2003), when matched with the required resting period. However, this browse pressure will be different for newly planted cuttings, and must take regional variation in soil and rainfall into account (Powell, 2009). It is vitally important to

understand the browsing densities planted *P. afra* can withstand to determine the thresholds or carry capacities which need to be preserved to achieve successful restoration.

The Greater Addo Elephant National Park (GAENP) treats elephants together with other forms of biodiversity and recognizes the need to maintain elephant populations as an integral part of the patterns and processes required to minimize the loss of biodiversity (SANParks, 2006). Therefore, to achieve both indigenous mammal and vegetation recovery, restoration goals need to be aligned and function together at the landscape scale.

1.11 Survivorship of planted *P. afra*

Mills & Robson (2017) collected planted *P. afra* survivorship data in the Darlington section of the GAENP and the Great Fish River Nature Reserve (GFRNR). The study found a mean survivorship of 28 % between the two study sites, with large variations ranging from 0 to 93 %. None of the investigated geographical variables were found to be related to survivorship (Mills & Robson, 2017). Lagerwall (2010) also collected survivorship data in the Darlington section of the GAENP, finding a mean survivorship of 26 %. Lagerwall (2010) found that the survivorship of planted *P. afra* cuttings in degraded sites surrounding Spekboom thicket (43.5 %) and Pentziaveld (31.0 %) vegetation types is higher than Noorsveld (15.1 %). Powell (2009) found that impacts from both kudu and baboons (*Papio ursinus*) following planting in unfenced plots can lead to extremely high mortality rates before roots are secured within the soil. Furthermore, it was found that planting posture played a significant role in *P. afra* survivorship, with cuttings planted upright (53.2 ± 1.7 %) being higher than flat cuttings (33.6 ± 1.6 %). Powell (2009) also showed planting density to have a significant difference in survivorship, with low density planted cuttings experiencing better survivorship. Swart *et al.*, (1994) found that planting time or season, planting depth or water regimes had no influence on mortality, with leaf stripping significantly adding to mortality. Van der Vywer (2011) found otherwise, noting that the survival of planted cuttings co-insides with rainfall events, finding 100 % survivorship rates within fenced off plots during productive rainfall periods. Aspect may also influence survivorship, as La Cock (1992) found seedling germination and sapling survival of thicket shrub species was higher on south facing slopes in arid thickets. Duker *et al.* (2015) found that frost plays a vital role in determining the boundaries between thicket and nama-karoo vegetation, based on freezing tolerances of succulent species (Duker *et al.*, 2015).

Powell (2009) further suggests that frost events result in increased mortality of newly planted cuttings, along with: desiccation prior to root establishment, fires, rodents ring-barking stems, grass competition, and fungal attack (Powell, 2009). Norman (2016) found that the season during which *P. afra* cuttings are planted plays a significant role in root biomass production.

Although a number of previous studies investigated the survivorship of *P. afra*, restoration initiatives using *P. afra* cuttings have generally been unsuccessful at large scales, with high mortality rates being recorded across a number of sites (Swart *et al.*, 1994; Lagerwall 2010; Powell, 2009). Many previous have studies have explored site and treatment specific variables, and have therefore reported large variations in survivorship, and variables which influence survivorship. However, there is a paucity of research that has investigated these findings over large spatial and temporal scales with varying climatic, ecological, and biophysical contexts. A matrix of conducive environmental conditions in which to plant *P. afra* cuttings in attempts to restore degraded landscapes has yet to be developed.

1.12 Objectives & key questions

This thesis sought to i) determine the underlying ecological factors that influence the survivorship of planted *P. afra* cuttings, and ii) to identify indicators of suitable biophysical environments for planting *P. afra* which can be used to forecast planted *P. afra* survival rates, for future management and planning in the GAENP. The following key questions were addressed:

1. What soil physical and chemical attributes influence the survivorship of planted *P. afra* cuttings?
2. Do biotic variables have an effect on *P. afra* cuttings survivorship in transformed landscapes?
3. Do combinations of specific plant species indicate suitable biophysical environment for the *en masse* planting of *P. afra* cuttings?
4. To what extent does herbivory play a role in the survivorship of planted *P. afra* cuttings?

2. STUDY SITES

2.1 Greater Addo Elephant National Park

In 1931, the Addo Elephant National Park (AENP) was proclaimed to protect the remaining 11 Addo elephants, following the decimation of the population through hunting and competition with farmers for agricultural resources (Hoffman, 1993). The GAENP was formed in the late 1990's, as part of an expansion project which aimed to incorporate a variety of land and seascapes, biodiversity and socio-economic opportunities (SANParks, 2006). The formation of the GAENP extended the conservation focus of the AENP, incorporating the protection of threatened Thicket vegetation types into the original goal of conserving a threatened elephant population. Aligned with this vision was the restoration of Thicket vegetation types which had been severely degraded due to heavy over-browsing, over-grazing, and over-trampling by small livestock in the late 1800's (Lechmere-Oertel, 2003), and in the 1960's to satisfy the highly successful mohair industry (Acocks, 1988). The success of the expansion project has resulted in the GAENP incorporating five terrestrial biomes (Fynbos, Thicket, Forest, Grassland, Nama-Karoo), as well as marine protected areas (SANParks, 2006). Aligned with the socio-economic objectives of the expansion, the eco-tourism industry in areas surrounding the Park has expanded, contributing significantly to the regional economy (SANParks, 2006). However, old agricultural lands and degraded landscapes within the GAENP still remain.

The GAENP is located within the Sundays River Valley and falls within the Subtropical Thicket Biome in the Eastern Cape province of South Africa (33°30' S; 25°45' E). The reserve lies within the Algoa drainage basin with the Indian Ocean to the south and the Zuurberg mountain range to the north (Figure 1). The GAENP spans approximately 178 900 ha which is divided into five fenced-off sections, namely: Woody Cape Coastal section, Addo Main Camp, Zuurberg, Kabouga, and Darlington sections, and includes three contractual partners. The study sites only included the Addo Main Camp (and neighbouring Kleinvlakte Camp), Kabouga, and Darlington sections of the GAENP, where *P. afra* plantings have occurred. Citrus, dairy, livestock and game farming are other main industries surrounding the GAENP.

2.1.1 Addo Main Camp

Addo Main Camp, also known as AENP, is the most southerly of the study sites, with its southern boundary falling within five kilometers of the Indian Ocean, close to the mouth of the Sundays River in the town of Colchester. The Woody Cape Coastal section lies to the south-west of Addo Main Camp. The town of Paterson is found to the east of Main Camp along the N10, with the town of Addo lying to the West on the R335 which runs towards Port Elizabeth, the closest city to the GAENP. The R400 road runs from just outside Grahamstown to Jansenville. The R400 runs from Paterson through to Addo town separating Addo Main Camp (approximately 42 000 ha) with private land (approximately 16 000 ha) to the north. The private Riverbend and Kuzuko sections are managed by SANParks and are incorporated into the GAENP.

2.1.2 Kabouga

To the north-west of Addo Main Camp, out of the Sundays River Valley and over the Zuurberg Mountain range, the park stretches to the Kabouga (33°17’ S 25°14’ E) and Darlington sections of the GAENP. The Kabouga section joined the GAENP in 2006. Kabouga is located to the north-west of the town of Kirkwood, directly west of the Zuurberg Mountains. Access to Kabouga is limited to 4x4 vehicles from either Kirkwood or Darlington. Kabouga incorporates a number of land parcels (approximately 50 000 ha) which run alongside the Sundays River right up to the Darlington Dam which is at the north-western corner of Kabouga.

2.1.3 Darlington

The Darlington section (33°10’ S 25°8’ E) was the most recent expansion to the GAENP. It is approximately 38 200 ha with the Darlington Dam covering approximately 3 500 ha. The Sundays River flows south from Darlington Dam through the Zuurberg and Kabouga mountains. The Darlington section is located in between the towns of Jansenville and Riebeeck-East, approximately 50 km from Jansenville. The Darlington section can be accessed from the R400 provincial road, or via a 4x4 vehicle that runs north over the Zuurberg mountain range from Kabouga. Commercial small stock, game farming, and eco-tourism ventures are the most prominent land-use practices surrounding the Darlington section of the GAENP.

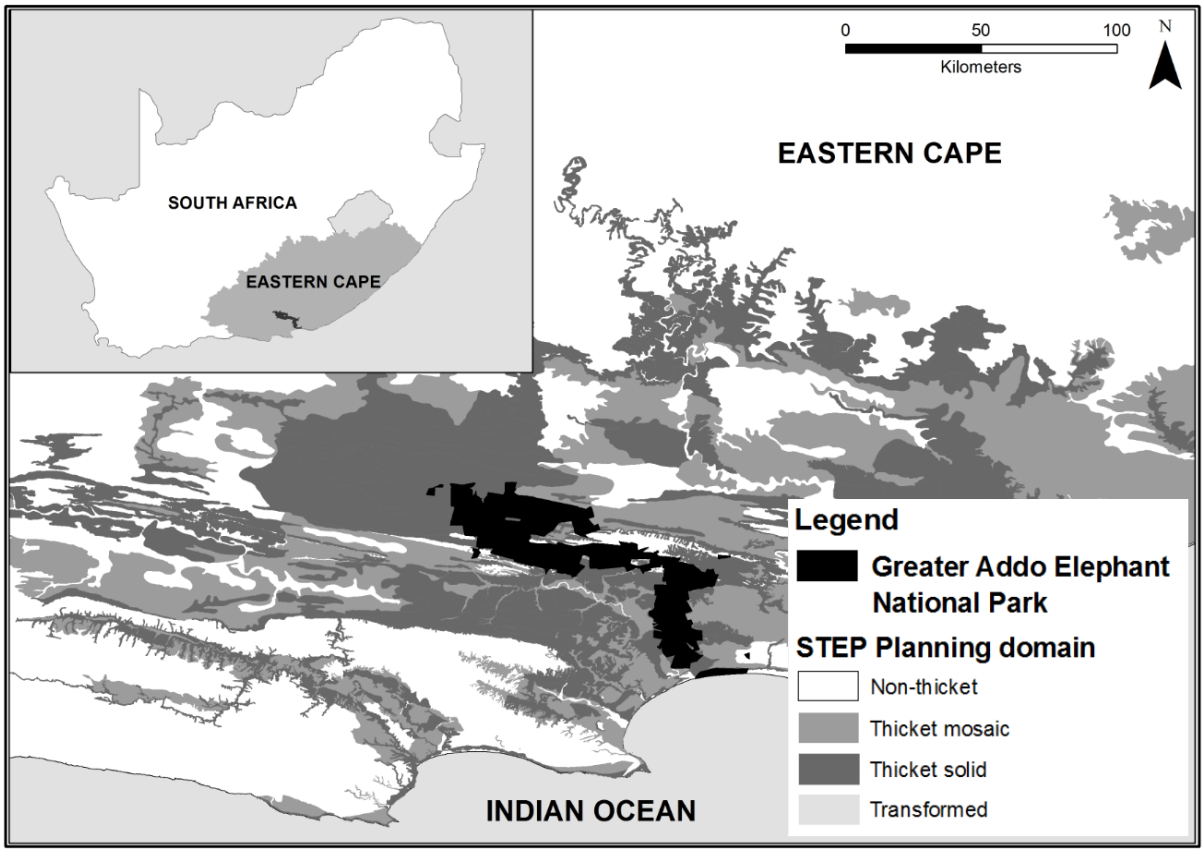

Figure 1: Locality map of the GAENP adapted from the STEP planning domain (Vlok & Euston-Brown, 2002).

2.2 Climate

The GAENP's climate is best described as warm temperate. The GAENP experiences mixtures between winter, summer and all-year round rainfall due to altitudinal variations along a gradient from the coast moving inland (SANParks, 2015). Mean annual rainfall (MAP) varies from 900 mm in the coastal Alexandria forests to the south-east of Addo Main Camp, to 250 mm in the rain-shadow areas of Darlington Dam (SANParks, 2015). Daily temperatures range from 15 °C to 45 °C in summer and 5 °C to 18 °C in winter (SANParks, 2015).

Addo Main Camp is an all-year rainfall area, receiving an annual rainfall of between 430 and 530 mm (South African Weather Services, 2014). The mean summer temperature is 27 °C and the mean winter temperature is 11 °C (SAWS, 2014). The Kabouga and Darlington sections experience summer rainfall, with Darlington receiving a low annual rainfall of between 250 mm

and 280 mm. Kabouga receives slightly more annual rainfall, between 280 mm and 300 mm. In Darlington, the mean summer temperature is 26 °C, and the mean winter temperature is 11 °C, with maximum temperatures in summer reaching 48 °C and minimum temperatures reaching freezing (0 °C) in winter (Lagerwall, 2010). In Kabouga, the mean summer temperature is 24 °C, and the mean winter temperature is 13.4 °C.

2.3 Topography

The GAENP extends over a vast area and traverses a number of different landscape types from coastal dune forests to the deeply incised mountain ranges. The GAENP ranges from 0 masl at the Woody Cape Coastal section to 951 masl in the Zuurberg Mountain section. The Zuurberg Mountain range is part of the Cape Fold Belt, which is an east-west trending mountain range which characterizes the northern parts of the GAENP. In the south, Addo Main Camp is characterized by a generally flat terrain with gently sloping hills and a few pronounced 'koppies', which are found within a mosaic of thickets and old agricultural lands. Elevation increases gradually from 60 masl in the south of Addo Main Camp to about 150 masl at the Riverbend section which lies at the foothills of the Zuurberg Mountain range (SANParks, 2015). Kabouga is found to the east of Zuurberg and consists of steep mountainous areas with highly heterogeneous topographies, which are dissected by the Sundays River. Elevations in Kabouga range from approximately 150 masl in the Sundays River valley to over 450 masl on the peaks of many of the steep mountains. The Sundays River meets the Darlington Dam which is located on a plateau at 230 masl. The Darlington section is dominated by steep mountains to the south (which link Darlington to Kabouga), with smaller east-west trending ridges which become less pronounced moving north. The ridges rise to between 300 and 600 masl from the plateau (230 masl).

2.4 Geology and soils

The GAENP is characterized by a complex mixture of geology and geomorphological terrains (SANParks, 2015), mostly within the Witteberg Group of the Cape Geological Supergroup, which consist of both mudstone and sandstone deposits. The coastal areas of the GAENP are dominated by limestone soils which feed into the southern section of Addo Main Camp. Ancient wave-cut platforms in the north of Addo Main Camp are derived from the Uitenhage Group, and made up

of a mixture of arenite, mudstones, conglomerates, and sedimentary rocks which are formed on the Sundays River, Algoa, Kirkwood, Enon, and Quatenary geological formations (Figure 2). Soils in Addo Main Camp are generally deep, red, sandy clay loams, loams, and sandy loams (Moolman & Cowling, 1994). Seventeen (17) plots were surveyed during this study (see plots number A2-01 to A2-20 in Figure 2).

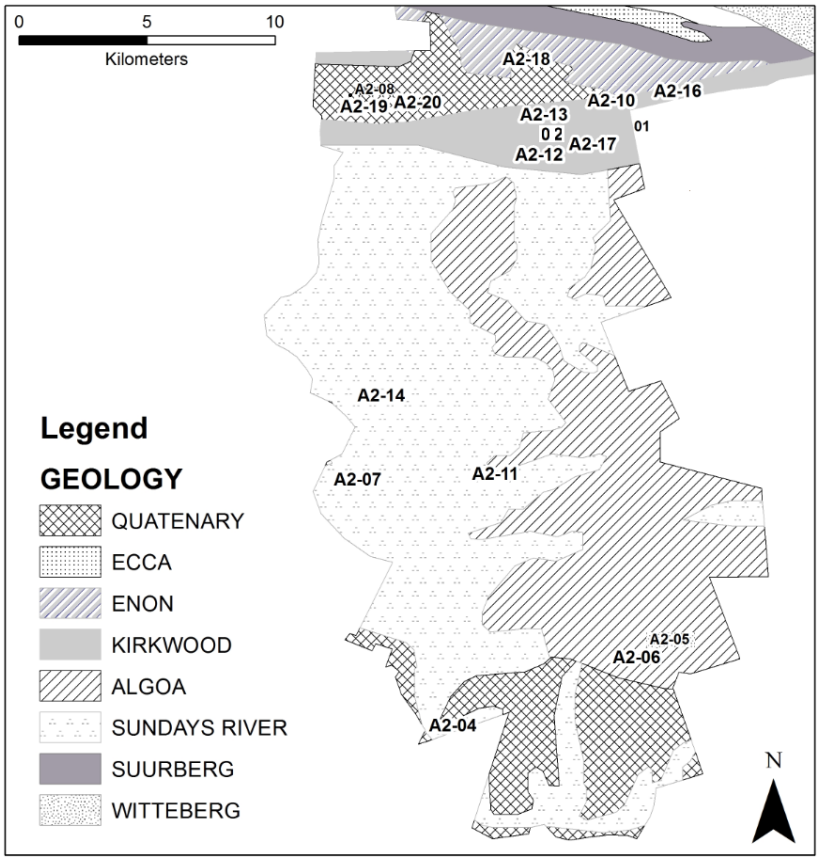

Figure 2: Addo Main Camp geology in relations to the location of the sample plot sites (n = 17).

Moving further north into the Zuurberg Mountain range, quartzite and sandstone become dominant (SANParks, 2015). Moving west, the Witteberg formation is found within the mountainous areas of Kabouga, with the Dwyka formations dominating the lower areas within the Sundays River valley (Figure 3). The soils in these mountains are less fertile than the sedimentary deposits found to the south of the mountain range. The area is dominated by lithic soils on the steep slopes, with sandy loams and clays occurring on the more gradual topography. Nineteen (19) plots were surveyed during this study (see plots numbered A3-03 to A3-35 in Figure 3).

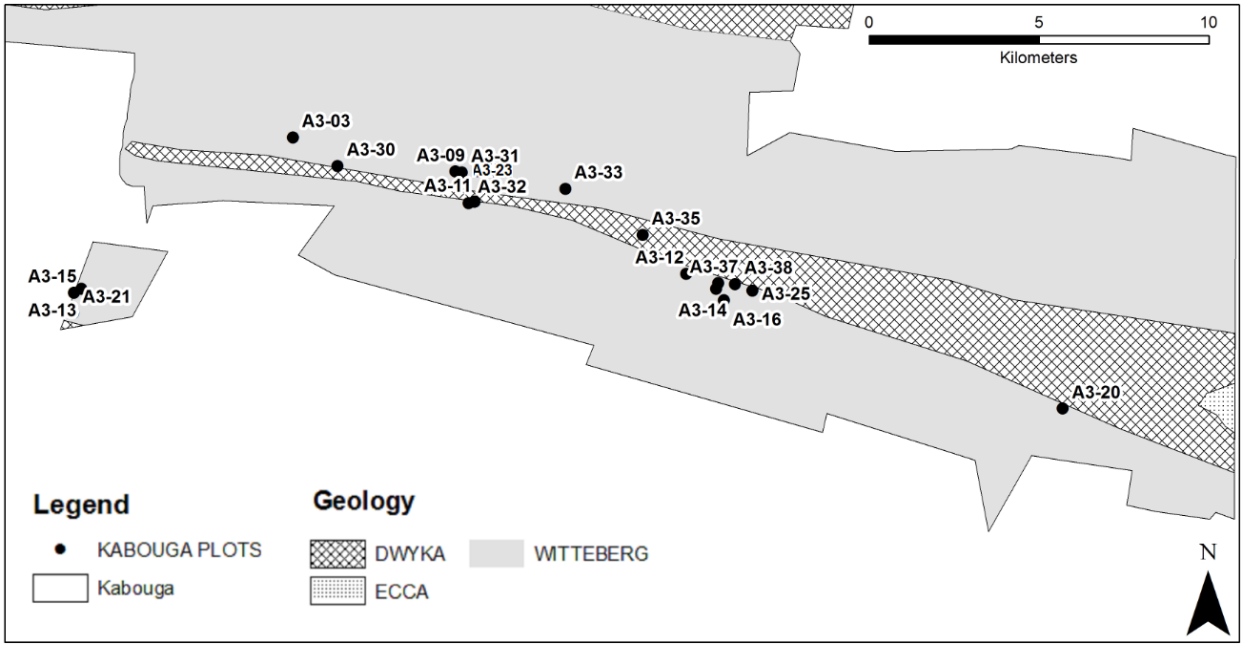

Figure 3: Kabouga geology in relation to the location of the sample plot locations (n = 19).

Darlington is underlain by lithologies from the Cape and Karoo Supergoups, and is dominated by Witteberg and Dwyka geologies with the addition of Ecca and Beaufort groups (Figure 4). The majority of the sample plots occur in the Ecca group. The shales of the Ecca Group are highly erodible, whereas the shales of the Beaufort Group are more stable (Mills & Cowling, 2006). Darlington contains arenite, tillite, shale and mudstone lithologies, but unlike the geology to the south of the mountain range, does not include any limestone deposits (SANParks, 2015). Fourteen (19) plots were surveyed during this study (see plots numbered A1-01 to A1-22 in Figure 4).

2.5 Vegetation

Vlok *et al.* (2003) identified and described subtropical thicket vegetation types for the Subtropical Thicket Ecosystem Planning (STEP) project. A typological hierarchy was used to classify thicket vegetation types, based on geography and biogeography, structure and grain. Vlok *et al.* (2003) recognized four main thicket types, namely i) Dune Thicket, and Mainland Thicket, comprising ii) Thicket, iii) Valley Thicket, and iv) Arid Thicket. The Mainland Thicket types are separated along an aridity gradient which is responsible for the compositional shifts in plant species and guilds (Hoffman & Cowling, 1990). Within these four main thicket types, 112 unique thicket vegetation types, 78 of which included thicket clumps in a matrix of non-thicket vegetation (hereafter referred

to as 'mosaics') were described (Vlok *et al.*, 2003). These vegetation types support 1 558 plant species, of which 20 % are endemic to the thicket biome (Vlok *et al.*, 2003).

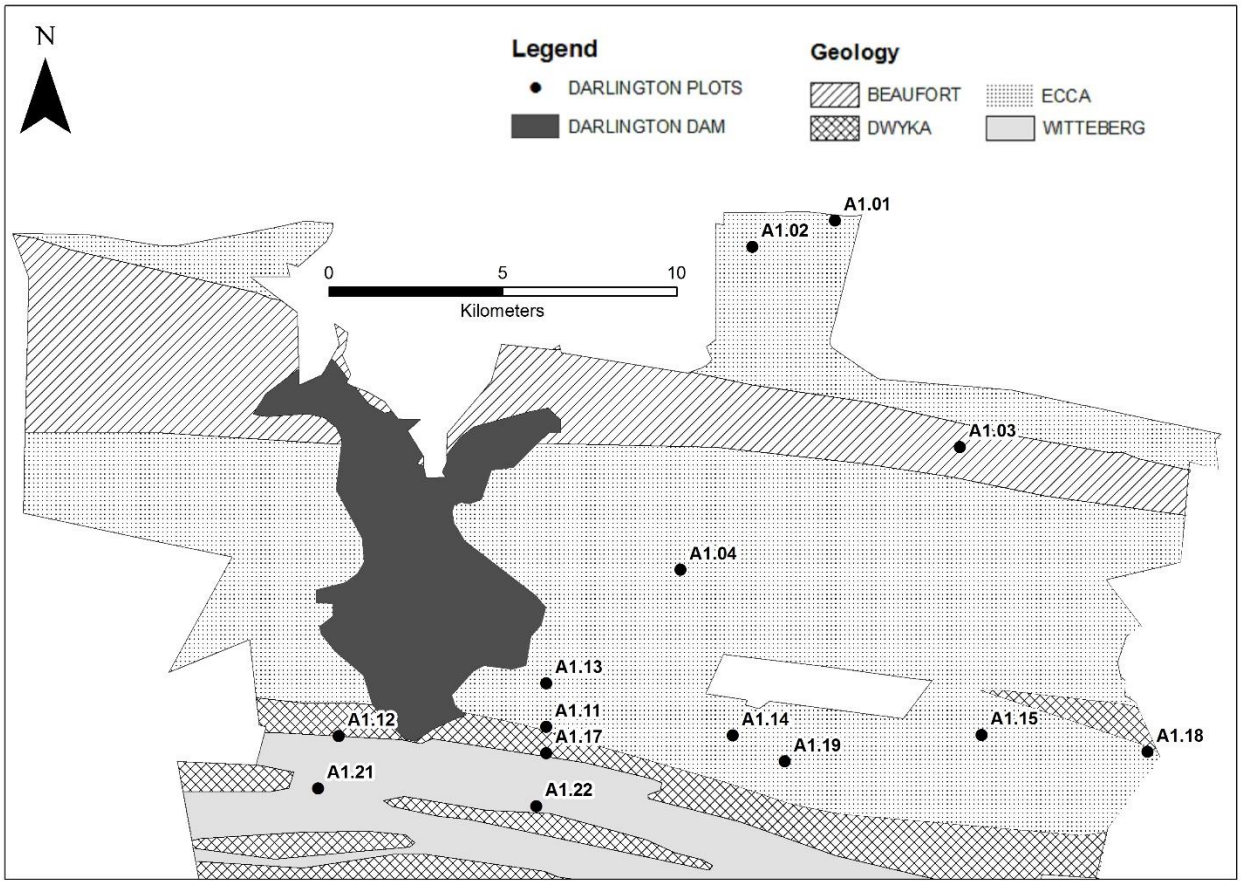

Figure 4: Darlington geology in relation to the sample plot locations (n = 14).

Addo Main Camp consists of Sundays Spekboom Thicket, Sundays Thicket and Grass Ridge Bontveld (Figure 5). Sundays Thickets are found in the valleys towards the southern section of Addo Main Camp, and are characterized by tall, woody trees such as tree *Euphorbia* species that tower above canopies exceeding five meters tall (Vlok & Euston-Brown, 2002). Woody tree species which dominate the canopy include: *Cussonia spicata, Searsia chirendensis, Scutia myrtina, Schotia latifolia,* and *Ptaeroxylon obliquum* (Vlok & Euston-Brown, 2002). Sundays Spekboom Thicket is the main vegetation type in Addo Main Camp, and is dominated by *P. capensis, Putterlickia verrucosa, R. obovatum, Searsia pterota, Searsia longispina* and *S. afra* (Vlok & Euston-Brown, 2002), Tree *Euphorbia spp.* characteristic of Sundays thickets are absent, with *P. afra* now present in the species composition matrix. Grass Ridge Bontveld is characterized by thicket clumps (or mosaics) which are distributed non-randomly, and are associated with

termitaria or fractures in hardpans (Vlok *et al.*, 2003). Grass Ridge Bontveld is found in the central and eastern parts of Addo Main Camp and is dominated by *Acmadenia obtusata, Euryops ericifolius, Themeda triandra,* and *Aloe ferox* (Vlok *et al.*, 2003).

Kabouga contains Paardepoort Spekboom Thicket, Sundays Spekboom Thicket and Sundays Thicket (Figure 5). In its intact form, Paardepoort Spekboom Thicket is characterized by *Euphorbia tetragona* and *Ozoroa mucronata,* and is dominated by *P. afra* and *P. capensis* (Vlok *et al.*, 2003). The abundance of woody tree species decreases as aridity increases, with *E. undulata* and *P. capensis* occurring in lower abundance in the Spekboom Thicket found in Kabouga when compared to Addo Main Camp (Vlok & Euston-Brown, 2002; Lunderstedt, 2016). The Sundays Thicket found in Kabouga has a similar composition to those of Addo Main Camp.

Darlington contains Sundays Noorsveld, Sundays Spekboomveld, and Sundays Spekboom Thicket. Overall, the vegetation typically becomes shorter, with more succulents and spinescent species (Vlok & Euston-Brown, 2002) moving north along the aridity gradient from the coast (Vlok *et al*, 2003). Sundays Noorsveld is characterized by *Euphorbia coerulescens,* commonly known as 'noors', which is a dominant succulent species in the more arid regions. The woody shrub, *R. obovatum,* and the tree *Boscia oleoides* also dominate Sundays Noorsveld (Vlok *et al.*, 2003). Spekboomveld found in Darlington is dominated by the tree species *P. capensis* and *S. afra* (Vlok *et al*, 2003), which appear in a "pseudo-savanna" landscape when in a degraded state. Spekboomveld is found in the semi-arid areas of the thicket biome, and is the most affected thicket type by historical overgrazing. *P. capensis* and *E. undulata* are the dominant trees, still evident in the majority of spekboomveld (Vlok & Euston-Brown, 2002). The presence of *P. afra* in previously farmed spekboomveld and spekboom thickets is very rare. The thicket types of the GAENP are illustrated in Figure 5.

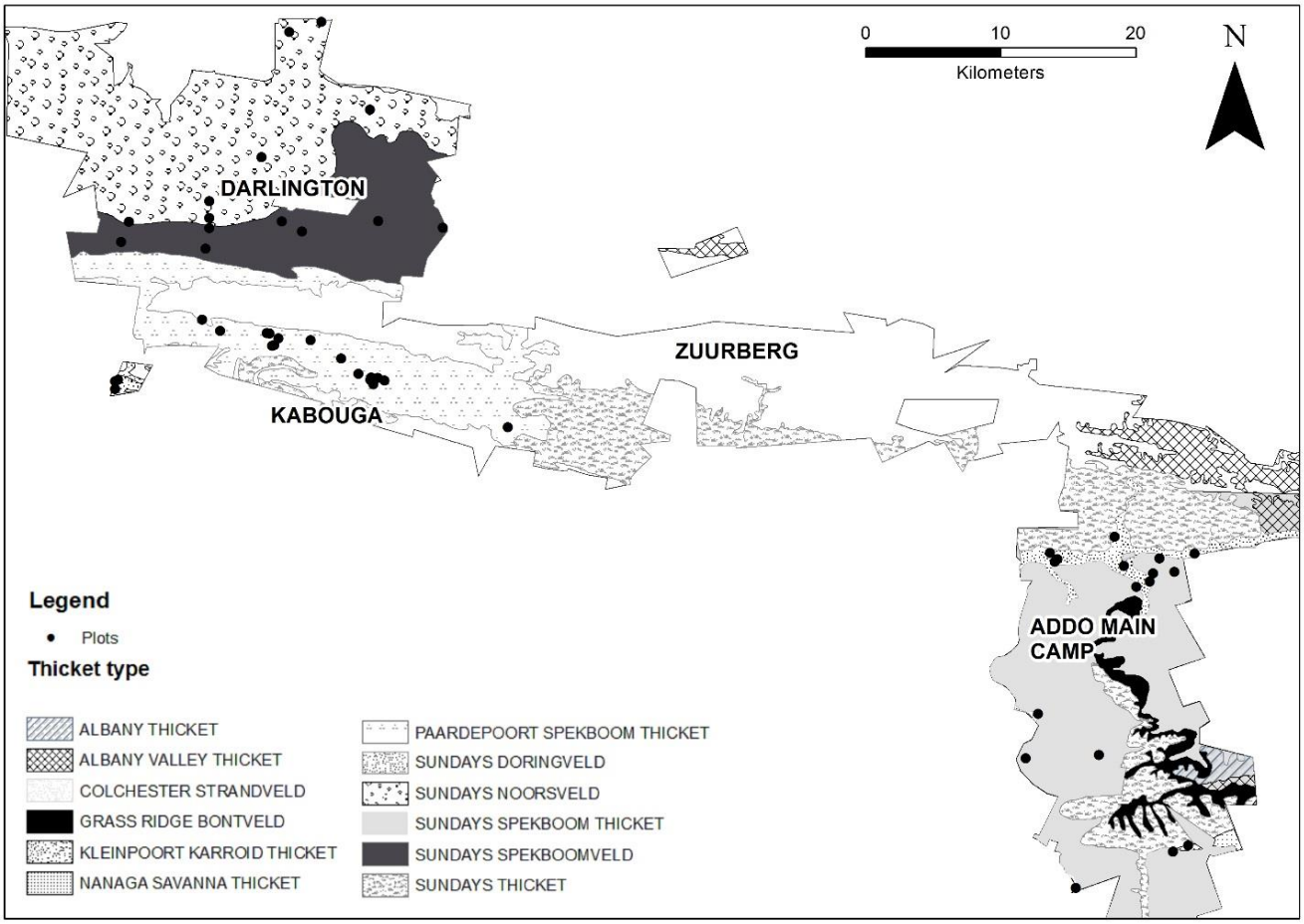

Figure 5: Thicket types (adapted from Vlok et al., 2003) of the GAENP in relation to the location of the sample plots (n = 50).

2.6 Terrestrial fauna

The GAENP is home to numerous species of fauna, with each section supporting different species assemblages which are managed separately in fenced-off areas. Addo Main Camp has all of the 'Big Five', namely: black rhinoceros, elephant, buffalo, lion (*Panthera leo*) and leopard (*Panthera pardus*). A successful re-introduced population of spotted hyena (*Crocuta crocuta*) has also taken place at Addo Main Camp. The only mega-herbivore species found in Darlington are the black rhinoceros and buffalo. No mega-herbivores are found in Kabouga.

All sections of the GAENP are home to a high diversity of meso and small carnivores, including: caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristata*), bat-eared fox (*Otocyon megalotis*), cape fox (*Vulpes chama*), and the vulnerable honey badger

(*Mellivora capensis*). Numerous ungulates such as kudu, bushbuck (*Tragelaphus scriptus*), eland (*Taurotragus oryx*), Burchell's zebra (*Equus quagga burchelli*), Klipspringer (*Oreotragus oreotragus*), Cape grysbok (*Raphicerus melanotis*) and warthog (*Phacochoerus africanus*) are abundant throughout the GAENP. Two species of primate, namely baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus pygerythus*), eight species of shrew, one species of mole, and 17 species of bat are other mammals which also occur within the GAENP.

The GAENP supports a great avifaunal diversity, of over 420 species (South African Bird Atlassing Project, 2015). Many are on IUCN and South African Red Data Lists, including: the ground hornbill (*Bucorvus leadbeateri*), Cape vulture (*Gyps coprotheres*), martial eagle (*Polemaetus bellicosus*), Stanley's bustard (*Neotis denhami*), kori bustard (*Ardeotis kori*), grass owl (*Tyto capensis*) and the African cuckoo hawk (*Aviceda cuculoides*) (SANParks, 2015).

The GAENP is home to a large diversity of herpetofauna, including 16 amphibians, 14 lizards, 15 snakes (Branch, 1998) and five species of land tortoise (SANParks, 2015). Mason (2010) found that tortoises represent approximately 12 % of the biomass of mammalian herbivores in thickets, having an influential role as herbivores. Thirteen of these reptile species are classified as endemic, two of which are restricted to the Eastern Cape, namely the Tasman's girdled lizard (*Cordylus tasmani*) and the Cape legless burrowing skink (*Scelotes anguina*) (SANParks, 2015). Due to the large number of mega herbivores in Addo Main Camp, this area supports a large population of the endemic flightless dung beetle (*Circellium bacchus*).

3. MATERIALS AND METHODS

3.1 Soil baselines

Severely degraded thickets within the study area were mapped as part of the STEP and STRP programmes (Lloyd *et al.*, 2002). Within the mapped areas, randomly allocated GPS co-ordinates were derived using ARCMAP software. Navigation in the field to each co-ordinate was undertaken using a Trimble PROXRS sub-meter, real-time GPS. The collection of soil data in each plot was based on the Standard Operating Procedure (SOP) for carbon baselines of the Addo, Baviaanskloof and Fish River Restoration Project (ABFRP), which was developed from the CDM methodology AR-AM0002 v3. Eighty plots were allocated, 30 each for the Darlington and Kabouga sections, and 20 plots for the Addo Main section.

A 10 x 10 m quadrat was oriented facing magnetic north at each plot. The height and diameter of all *P. afra* and *E. coerulescens* (noors) stems were recorded within each 10 x 10 m plot to calculate above-ground biomass. Soils were sampled at six points in each plot, holes H1 to H5 refer to holes dug for soil carbon, and H6 refers to the hole dug for bulk density estimates (Figure 6). This involved digging 10 x 10 x 30 cm holes, removing the soil, rocks and roots, and documenting the dimensions of the holes. Surface litter was collected at each of the four corners of each plot in 50 x 50 cm quadrats. All detached litter was collected from holes H1 to H4. Sampling took place in Darlington from November 2011 to March 2012, in Addo Main Camp in October 2011 and again in February and March 2013, and in Kabouga between April and June 2013.

The soil and litter samples were transported from the field to the Gamtoos Irrigation Board (GIB) warehouse in Grahamstown. Wet soil samples for bulk density were sieved, using a 2 mm industrial sieve, and separated into gravel, rocks, roots and soil. The volumes of the roots and gravel were measured using a volume displacement technique. The bulk density of the soil, the percentage of coarse fragments such as rocks, stones and gravel, and the depth of the soil samples, were all calculated to estimate the soil mass. Bulk density is the dry mass of intact soil in a given volume (Perkins *et al.*, 2013).

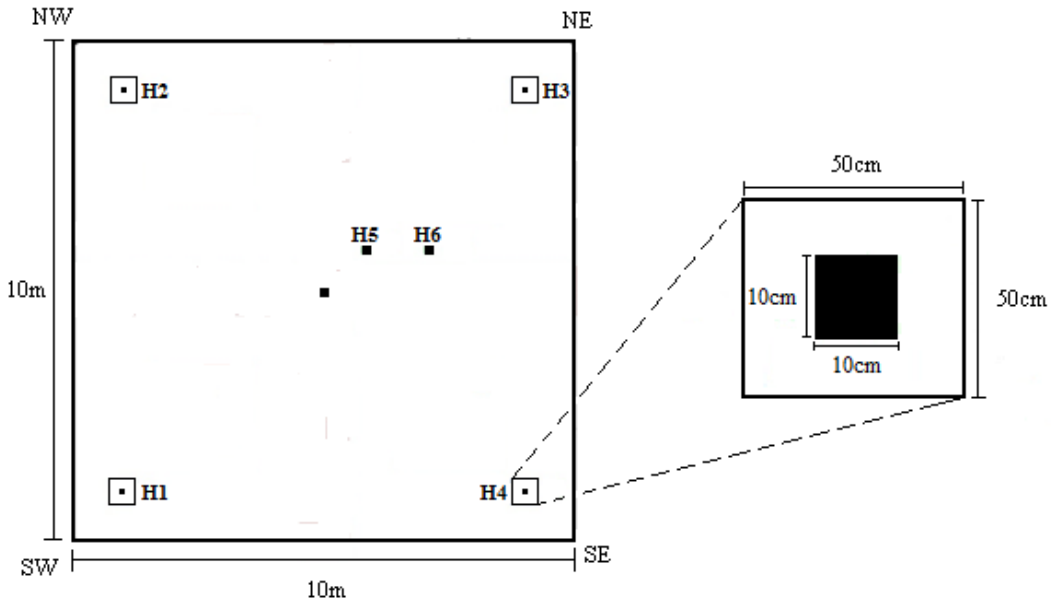

Figure 6: The typical schematic plot design (Adapted from DEA NRM SOP, 2011).
**Holes H1 to H5 dug for soil carbon, H6 refers to the hole dug for bulk density estimates*

The soil samples were then oven dried (60 °C) to a constant mass (0.01 %), to prevent excessive alterations of soil properties and activity over time (Perkins *et al.*, 2013). Litter was oven dried (60 °C) to a constant mass using the Verified Carbon Standard (VCS) methodology (VCS, 2016), and weighed. The dried soils from each quadrat (H1 to H5) were mixed together to prevent pseudo-replication. Approximately 350 g of soil from each of the mixed samples was transferred into individually marked containers and sent for lab analysis at the Dohne Agricultural Institute. Fifteen chemical and physical soil variables were tested. These variables as well as the methods that were used are indicated in Table 1.

Table 1: Soil variables tested and methods used

Variable	Method	Variable	Method
C (%)	Walkey-Black	**Mn (mg/kg)**	Ambic-1
P (mg/kg)	Bray-2	**B (mg/kg)**	$CaCl_2$ (0.02 $mol.dm^{-3}$)
K (mg/kg)	Ambic-1	**pH (KCL)**	KCL
Na (cmol(+)/kg)	Electrical Conductivity	**Resistance (Ω-m)**	Electrical Paste Resistance
Ca (cmol(+)/kg)	Electrical Conductivity	**Fe (mg/kg)**	Ambic-1
Mg (cmol(+)/kg)	Electrical Conductivity	**Al (mg/kg)**	KCL (1 $mol.dm^{-3}$)
Cu (mg/kg)	Ambic-1	**WHC (100 kPa %)**	Stress Point Capacity
Zn (mg/kg)	Ambic-1		

Levels of organic C and available P were tested, as they are soil fertility indicators which are directly linked to plant and soil processes (Perkins *et al.*, 2013). C analysis also provide insight into the tendency of soils to crust (Mills & Fey, 2004c). Organic matter content was calculated from organic carbon values by multiplying organic C by 1.72 as SOM contains approximately 58 % C (Nelson & Sommers, 1996 cited in Perkins *et al.*, 2013). Extractible acidity, resistance and pH were analyzed because salinity and acidity play vital roles in controlling the mobility of P and micronutrients in the soil solution (Lechmere-Oertel, 2003), and therefore could influence soil functioning and ultimately restrict the establishment of planted cuttings. pH and electrical conductivity (EC) were also analyzed to investigate the tendency of soils to crust. Basic cations (K, Ca, Mg, Na, Zn), texture and Al were analyzed as they have been reported to constrain the growth of adult *P. afra* at extreme levels (Mills *et al.*, 2011).

Water-holding capacity and soil texture were determined as they influence infiltration and crusting probabilities. Soil infiltration was determined by leaching a water solution through a soil column (Mills & Fey, 2004a), using an infiltrometer. At each plot, three infiltration tests were done at each of the four corners of the 10 x 10 m quadrat. Aspect and slope were determined using a compass and inclinometer, respectively. Rainfall data for the GAENP were obtained to investigate correlations between rainfall and survivorship. On site data for Addo Main Camp and the Darlington sections were obtained, rainfall data for Kirkmans Town, which is located 2.5 km from Kabouga was used for the Kabouga rainfall as on site rainfall data was unobtainable.

3.2 Plant biodiversity baselines

Plant biodiversity data were based on the Standard Operating Procedure (SOP) for plant biodiversity baselines of the Addo, Baviaanskloof and Fish River Restoration Project (ABFRP). The biodiversity baselines were conducted at each of the 80 plot locations used for the soil baselines.

View (a) of Figure 7 illustrates the positioning of the four biodiversity quadrats within the 10 x 10 m plot. The biodiversity quadrats are located 2.121 m from each corner of the 10 x 10 m plot as can be seen in view (b). In each quadrat all plant species and bare ground percentages were visually assessed. The process was repeated for all four quadrats (Q1, Q2, Q3 and Q4) as can be seen in

view (a). Any plants which were not identifiable during the fieldwork were pressed for later identification in the Selmar Schonland herbarium in Grahamstown.

Two 1 x 50 m belt transects were completed at each plot, to record the larger plants such as shrubs and trees (d). The transects were positioned south to north and east to west, bisecting the centre point of the plot (c). The tape measure was anchored at the south point ending at the north point. A 1 m measuring rule was placed above the tape measure at the 50 cm mark, and used to record the canopy cover of all woody species encountered within the 1 m belt along the 50 m transects (e). The schematic plot layout for plant biodiversity sampling is illustrated in Figure 7.

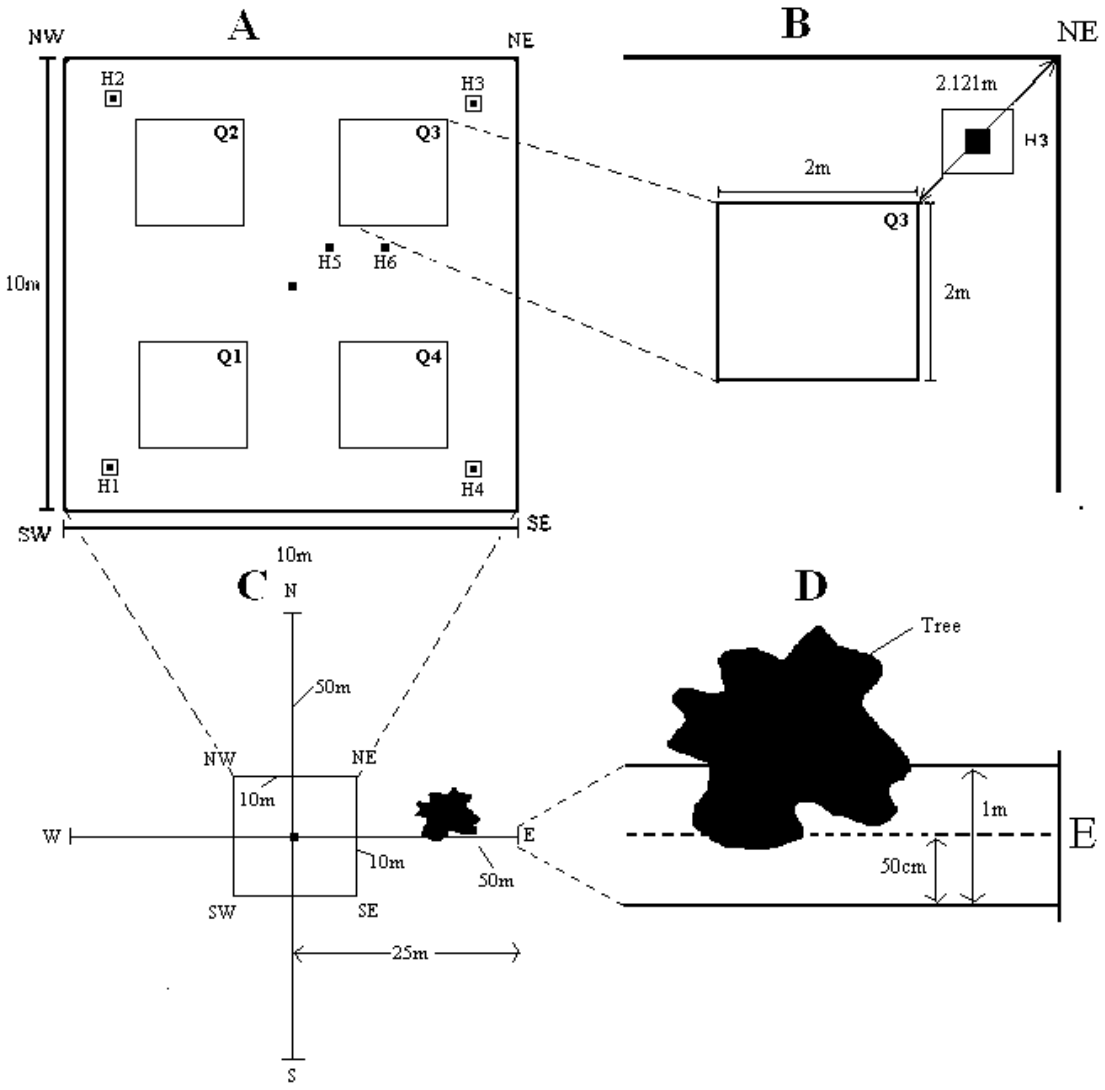

Figure 7: Schematic plot layout for plant biodiversity sampling (Adapted from DEA NRM SOP, 2011).

3.3 Herbivory

The effects of mega-herbivores on planted *P. afra* survivorship was measured using exclusion plots in the Kleinvlakte section of Addo Main Camp. The Kleinvlakte section (33°26'26.91"S; 25°48'49.91"E) is adjacent to the Addo Main Camp; however it does not contain any mega-herbivores. The baseline techniques described above were carried out on five plots within the Kleinvlakte section, as well as five plots immediately adjacent to Kleinvlakte within Addo Main Camp. The comparison between the two areas provided insight into the effects of mega-herbivores on newly planted *P. afra* cuttings. Furthermore, the Darlington and Kabouga sections do not contain elephant populations which aided in comparing the effects of different mega-herbivore species. The Darlington section contains both black rhinoceros and buffalo, while the Kabouga section does not contain any mega-herbivores. Dung was collected and identified to species level to verify the presence of various browsing herbivores within each plot. The distance to the nearest intact thicket was calculated using Geographic Information Systems (GIS) at all plots, to assess if it plays a significant role in establishing species survivorship (Mills *et al.*, 2011).

3.4 Survivorship counts

All 80 plots were revisited at least three months after planting of *P. afra* to conduct mortality counts. Based on personal communications with experts, three months was established as the minimum amount of time necessary for the cuttings to establish or succumb to abiotic or biotic pressures. However, numerous plots had not been planted within the contractual timeframes which reduced the total number of plots to 50. A total of 14 plots in Darlington, 17 in Addo Main Camp, and 19 in Kabouga.

The planting of *P. afra* cuttings took place over a three year period starting early January 2011. Due to the vast differences between the time of planting and the time of survivorship assessments, it was anticipated that the data would need to be retrofitted to a survivorship curve. Furthermore, due to the variable weather conditions over the extended planting period, it was also anticipated that the survivorship models would have to take the seasonal variability into consideration.

The mortality counts were done by surveying planted cuttings in a 50 x 50 m area surrounding each plot. Treatment information such as: cuttings diameter, planting posture, clumping, and density (appropriate planting density) was documented. The mortality counts included classes i) alive, ii) dead (lying), iii) dead (standing), iv) coppicing, v) leaf-stripped, vi) other (browsing evidence, e.g. ring-barking by rodents).

3.5 Data analyses

Sixteen soil chemical variables, twelve soil physical variables, and seven surface feature variables were explored to identify correlations with survivorship of *P. afra*. Principal component (PCA) and classification analyses using Statistica 13 were run to identify relationships between survivorship and soil and surface variables. Multiple regressions were run between survivorship and variables which displayed potential correlations in the PCAs. Correlation and ordination testing between variables and across samples was conducted using R software and PRIMER 6 +PERMANOVA (Plymouth Routines in Multivariate Ecological Research, Anderson *et al.*, 2008). Primer was used to perform a hierarchical cluster analysis of soil chemical properties across sites (SIMPROF Cluster Analysis was run at a significance level of 5%). The means and standard deviations of groups defined by the cluster analysis were compared using a one-way ANOVA.

PRIMER 6 +PERMANOVA was used to perform species composition analyses. The plant cover data by species was used as the biological abundance data and survivorship data was added as an environmental variable. The plant species cover data were pre-treated using a square root transformation before conducting a resemblance matrix using Bray-Curtis similarity. The survivorship data were normalized before being added to the biological data as a vector. A non-metric Multi-Dimensional Scaling (MDS) was run to group communities based on species rankings. Percentage *P. afra* survivorship was then visualized on the MDS plots using bubble plots which represent the values of the variable as a symbol of differing sizes and superimposing these symbols on the plant species ordination of the samples. The MDS was followed by a Principal Coordinate Ordination (PCO) which was used to relate species compositions taking numerical data, distances and similarities into account. A SIMPROF Cluster Analysis was run at a significance level of 5% to statistically separate the plant species communities. The survivorship trends between the different communities were then investigated. A one-way SIMPER test was

used to tabulate the most abundant species within each community. A Random Forest was run in R software to model and rank individual plant species based on their likeliness of correlation with survivorship of planted *P. afra*.

Distance based linear modeling (DistLM) in +PERMANOVA was used to relate and correlate the trends in the plant species community data with the soil and environmental data. The model was built using a BEST analysis to describe the plant species resemblance using ranked individual environmental variables based on level of significance. The DistLM was then performed which incorporated the significant variables into a step-wise BVSTEP model which explained the level of significance variables had on the separation of plant communities, as well as the percentage that each of these variables described the difference in communities. This model was run across all sites as well as for each site independently.

Principal component (PCA) and classification analyses (CA) were run to explore potential relationships between dung counts of browsing species and *P. afra* survivorship across all sites. As with the soil data, regressions were run between survivorship data and all dung counts which displayed potential relationships following the PCAs. A two sample t-test was used to compare the means and standard deviations of plots frequented by elephants with those excluded by elephants in GAENP.

3.6 Limitations

The reduction in sample size from 80 plots to 50 plots due to a number of contractual planting areas not being planted within the stipulated timeframes was a limitation to the study. Additionally, insufficient short-term climatic data was obtained to determine if climatic events such as low rainfall, heavy frost, or short-term extremes in temperatures potentially result in mortalities in periodic events before, during, or following planting. This is particularly relevant to frost events, as Darlington and certain parts of Kabouga are more prone to frost than Addo Main Camp. Although it would seem that this is not the case as Addo Main Camp had the lowest mean survivorship of *P. afra*, the impact of elephants needs to be factored in. Data could be heavily influenced by the impact of elephants on the survivorship of *P. afra*, and therefore trends and correlations with other variables which were explored across the three sites may have been masked

by the effect of elephants in Addo Main Camp. This could also explain the variations in findings between the sites, and reiterates the importance of analyzing the sites individually to seek trends independently of large mammal species compositions, particularly elephants.

4. RESULTS

4.1 Survivorship

The time since planting ($p = 0.121$), rainfall ($p = 0.943$), and the mean low ($p = 0.239$) and high ($p = 0.340$) temperatures (°C) during planting seasons did not have an influence on the survivorship of *P. afra* (Figure 8a). Therefore, it was assumed that it was not immediate planting conditions or time since planting that influenced subsequent survival. Survivorship counts for all following results were based on the surveyed survivorship data irrespective of time since planting or seasonal climatic variability.

Mean survivorship across the three sites was 42.0 ± 23.2 % (n = 50), varying from 35.1 ± 29.1 % (n = 17) at Addo Main Camp to 48.2 ± 22.9 % (n = 19) in the Kabouga section. The Darlington section of the GAENP had a survivorship of 42.1 ± 11.7 % (n = 14) (Figure 9). A single factor ANOVA found no significant variation between the sites ($F = 1.46$; $p = 0.24$).

4.2 Soil characteristics

Table 2 summarizes the soil data used for the analyses which follow. The relationships between soil and surface attributes and the survivorship of planted *P. afra* were explored across all sites (n=50), and within each site independently (Addo, Kabouga, Darlington). Addo Main Camp (n = 17) had the highest levels of K and resistance, and the lowest infiltration rate. It also had the lowest stone volume (amount of below ground stone) and highest levels of fine sand, of the three sites. Kabouga (n = 19) had the highest C, Mn, B, Fe, Al, gravel density, silt, and infiltration rate of the sites. Darlington (n = 14) had the highest Na, Mg, stone volume, and soil compactness. The Ca levels at Darlington were four times higher than the other sites, with levels of K and Fe significantly lower than the other sites. Levels of P, Cu, Zn, pH, clay, and water holding capacity were similar across sites.

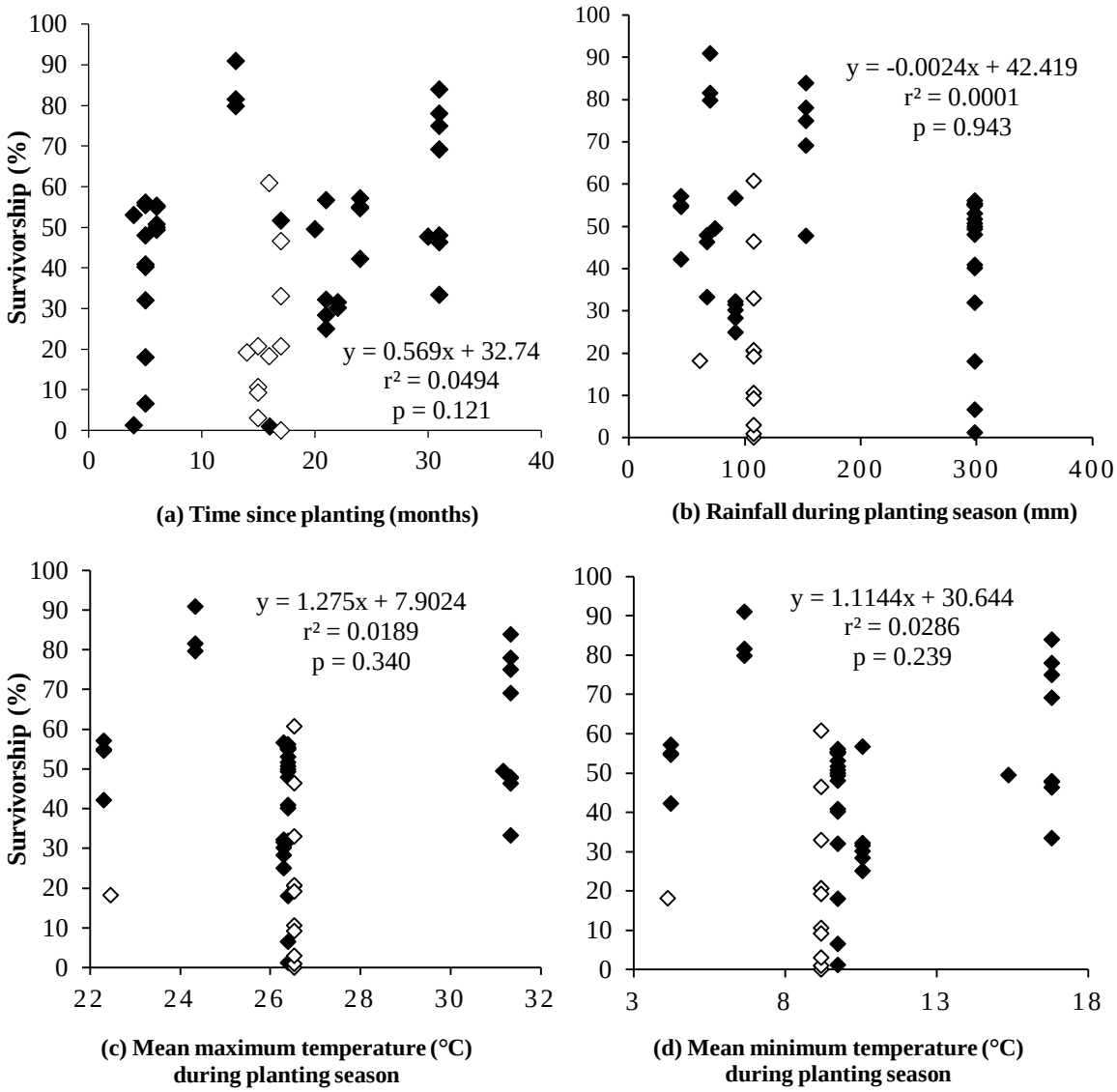

Figure 8: Regressions of survivorship of planted *P. afra* cuttings with (a) time since planting, (b) rainfall during planting season, (c) mean maximum temperature during planting season, and (d) mean minimum temperature during planting season (n = 50).

**Hollowed-out data points indicate sites which were exposed to elephant herbivory.*

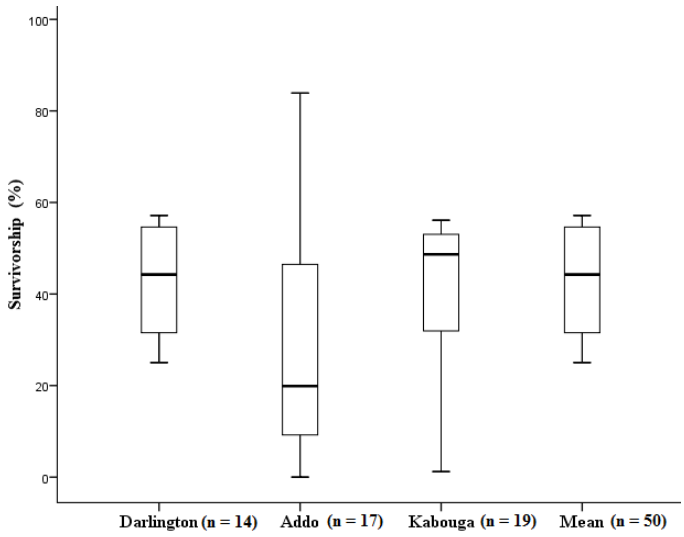

Figure 9: Mean (± SE) *P. afra* cuttings survivorship % across sites.

Table 2: Mean (± SE) soil data of the sites

Variable	Addo	Kabouga	Darlington	All sites pooled
C (%)	0.9 ± 0.3	1.4 ± 0.5	0.9 ± 0.4	1.1 ± 0.5
P (mg/kg)	17.3 ± 12.8	23.8 ± 31.2	24.6 ± 23.0	21.8 ± 23.7
K (mg/kg)	390.1 ± 165.3	310.7 ± 284.3	206.8 ± 112.4	308.6 ± 217.4
Na (cmol(+)/kg)	0.4 ± 0.3	0.4 ± 0.3	0.9 ± 2.2	0.5 ± 1.2
Ca (cmol(+)/kg)	10.6 ± 6.8	11.5 ± 5.8	45.6 ± 62.2	20.7 ± 36.0
Mg (cmol(+)/kg)	2.0 ± 0.9	2.7 ± 1.2	3.2 ± 1.3	2.6 ± 1.2
Cu (mg/kg)	2.1 ± 0.8	1.9 ± 0.7	1.4 ± 0.8	1.8 ± 0.8
Zn (mg/kg)	2.2 ± 1.2	2.2 ± 0.9	1.5 ± 0.7	2.0 ± 1.0
Mn (mg/kg)	168.2 ± 86.8	186.6 ± 98.5	154.2 ± 88.9	171.3 ± 91.1
B (mg/kg)	0.5 ± 0.3	0.8 ± 0.5	0.5 ± 0.3	0.6 ± 0.4
Fe (mg/kg)	130.3 ± 130.5	184.2 ± 205.6	39.1 ± 22.4	125.2 ± 157.2
Al (mg/kg)	3 111 ± 1 350	5 430 ± 1 628	4 061 ± 1 481	4 258 ± 1 775
T-Value (cmol/kg)	14.1 ± 7.9	15.5 ± 7.3	17.6 ± 8.0	15.6 ± 7.7
pH (KCL)	6.9 ± 0.7	6.7 ± 0.5	6.6 ± 0.7	6.7 ± 0.6
Resistance (Ω-m)	1144 ± 734	790 ± 276	722 ± 310	891 ± 513
Soil density (g/cm^3)	1.4 ± 0.17	1.2 ± 0.10	1.2 ± 0.16	1.26 ± 0.17
Gravel density	1.15 ± 1.54	3.75 ± 4.7	2.35 ± 0.28	2.47 ± 3.23
Clay (%)	29.1 ± 9.6	30.3 ± 7.9	26.3 ± 8.7	28.7 ± 9.0
Silt (%)	10.7 ± 6.5	16.2 ± 5.0	11.0 ± 3.8	12.9 ± 5.9
Fine sand (%)	54.5 ± 12.8	39.9 ± 12.3	42.6 ± 7.4	45.6 ± 13.1
Medium sand (%)	5.1 ± 2.9	6.5± 3.0	7.7 ± 3.7	6.4 ± 3.4
Coarse sand (%)	0.7 ± 0.6	7.2 ± 4.5	12.5 ± 4.3	6.5 ± 5.9
Stone volume (v/v)	0.3 ± 0.5	2.5 ± 1.8	3.9 ± 0.7	2.1 ± 1.9
WHC (100 kPa %)	20.1 ± 4.2	21.8 ± 3.1	19.0 ± 3.0	20.4 ± 3.7
Infiltration (mm/m)	13.2 ± 13.9	24.4 ± 12.5	20.9 ± 13.3	19.6 ± 14.1
Compactness (t m^{-2})	29.5 ± 8.7	37.1 ± 6.6	41.6 ± 5.4	36.1 ± 8.7

**WHC = Water Holding Capacity*

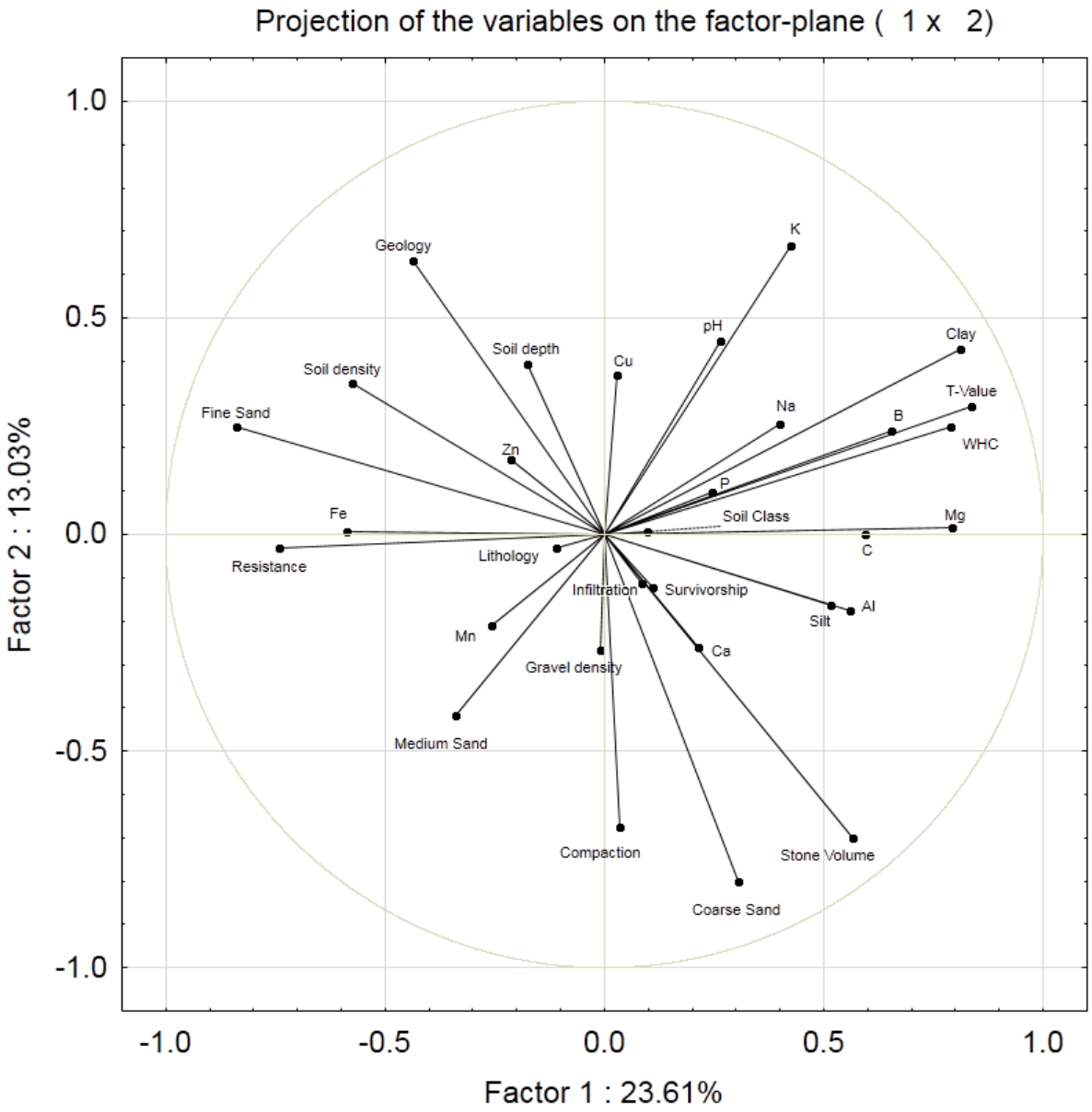

Figure 10: Principal Component Analysis (PCA) of soil properties across all sites (n = 50) relative to mean survivorship.

Figure 11 illustrates the degree of similarity between the tested variables. Infiltration is the most closely associated variable to survivorship, with gravel density, soil class, lithology, and Ca found slightly further away. These variables are the most likely to have relationships with survivorship among the investigated attributes.

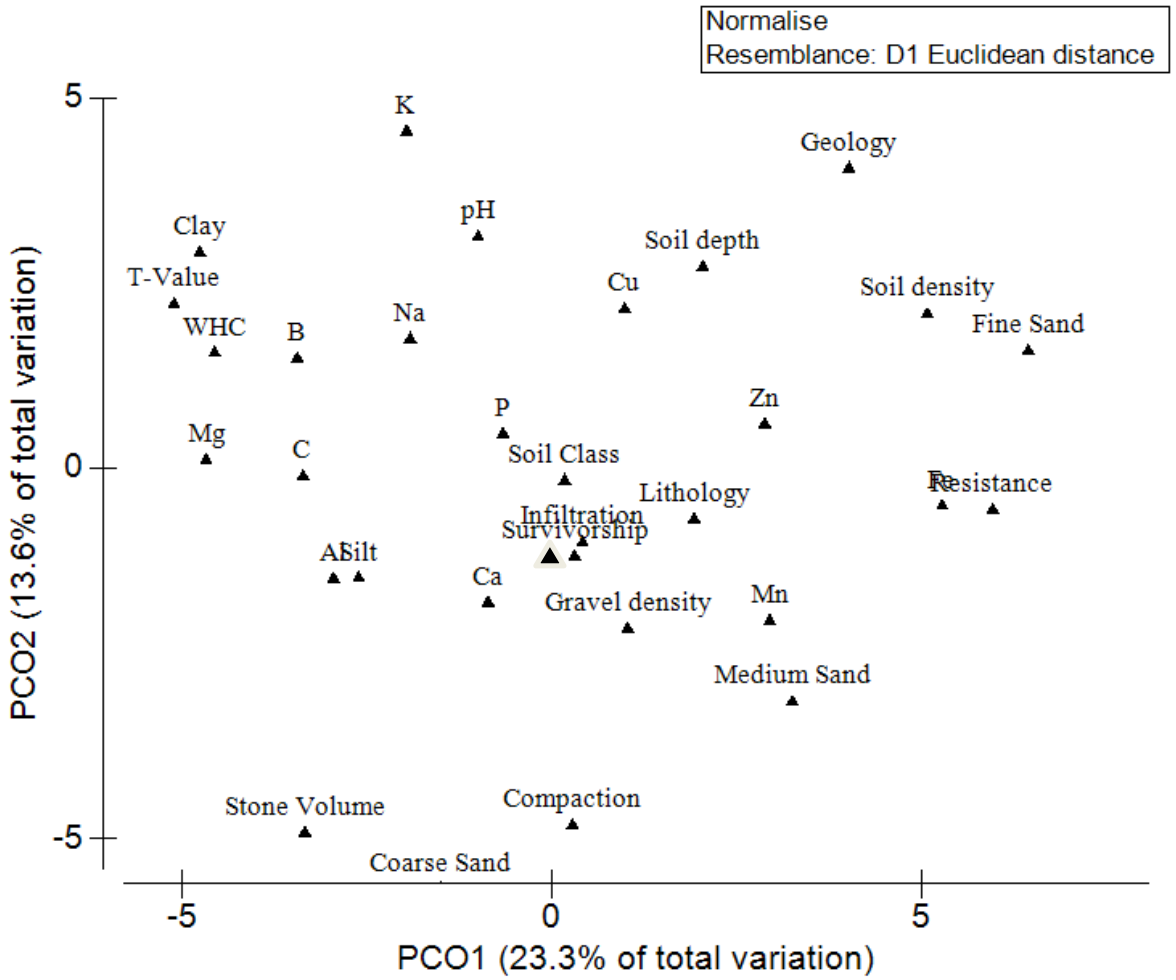

Figure 11: Principal Coordinate Analysis (PCoA) illustrating the similarities between soil variables.

Direct Analysis Indicates that infiltration rate has a significant ($r^2 = 0.173$; $p < 0.002$), positive relationship with *P. afra* survivorship across all of the plots (Figure 12). A regression between gravel density and survivorship of planted *P. afra* cuttings also found a weak positive relationship ($r^2 = 0.091$; $p < 0.034$). However, this was largely due to an outlier and therefore statistically not viable as a significant relationship. There was no significant relationship between Ca and survivorship of planted *P. afra* cuttings ($r^2 = 0.004$; $p < 0.638$).

Planted *P. afra* survivorship on the sedimentary (19.4 % ± 1.0 %) and conglomerate (3.0 %) lithological groups was low. As the sample sizes of these groups are low (sedimentary– $n = 3$; conglomerate – $n = 1$) assumptions regarding the relationship between the lithological groups and planted *P. afra* survivorship cannot be made across the three sites (Figure 13). No significant

differences between the rest of the groups and *P. afra* survivorship were evident (F = 1.62; p = 0.18). Soil type did not have a significant relationship with planted *P. afra*, with the survivorship for sandy soils equating to 16.2 ± 14.6 %, loamy soils 50.9 ± 25.3 %, and clay soils 35.7 ± 24.9 % (Figure 14). A single factor ANOVA found no significant variation between the soil types (F = 0.38; p = 0.86).

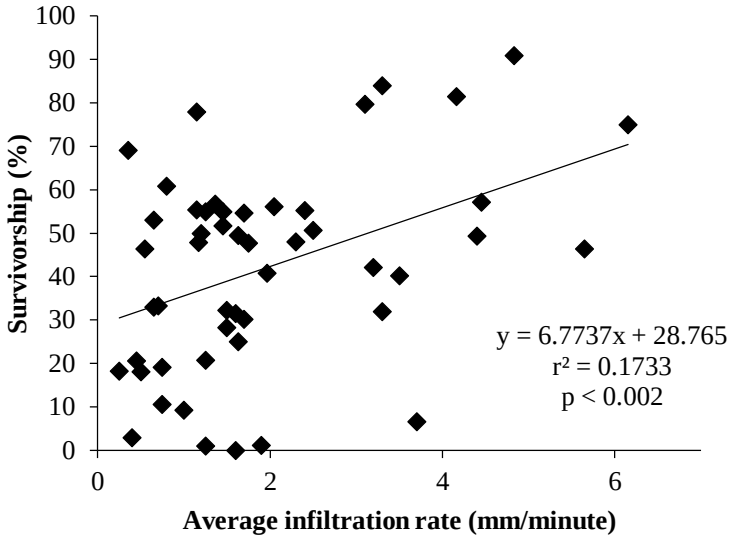

Figure 12: The relationship between infiltration (mm/minute) and *P. afra* survivorship across sites (n = 50).

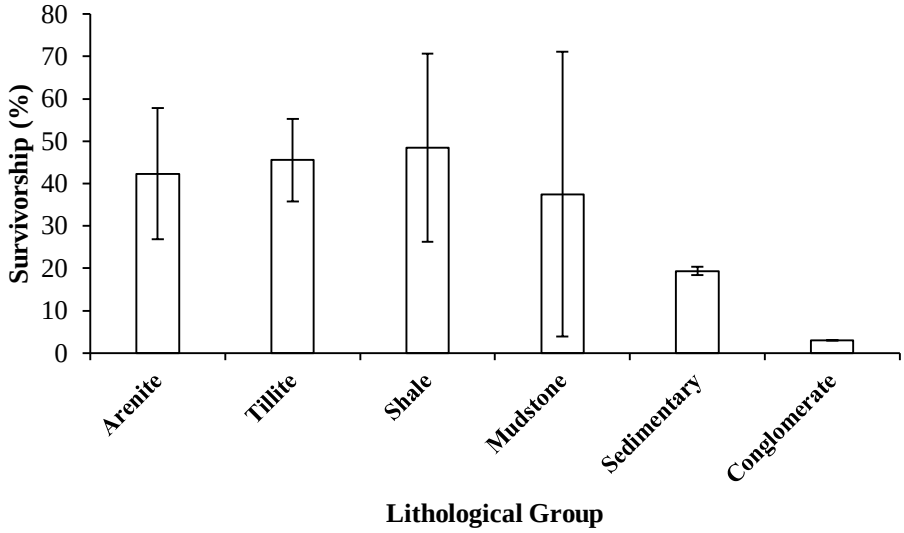

Figure 13: Planted *P. afra* survivorship on different lithological groups of the GAENP.
**Arenite (n = 14), Tilite (n = 5), Shale (n = 19), Mudstone (n = 8), Sedimentary (n = 3), Conglomerate (n = 1).*

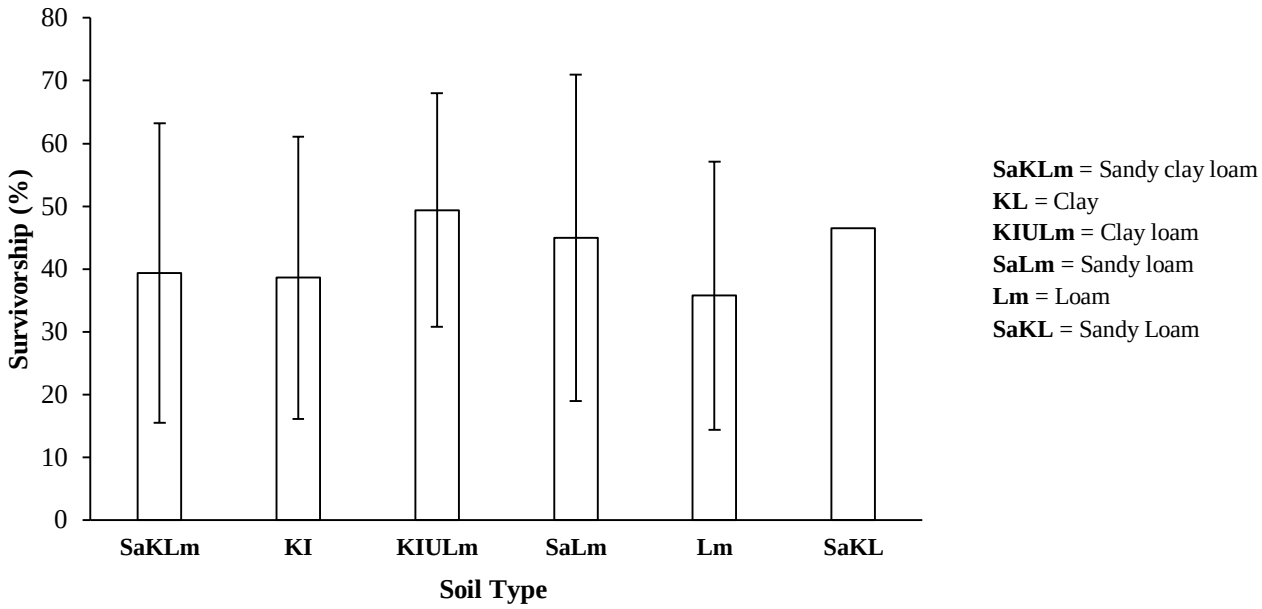

Figure 14: Planted *P. afra* survivorship on different soil groups of the GAENP.
**SaKLm (n = 20), KI (n = 6), KIULm (n = 11), SaLm (n = 7), Lm (n = 5), SaKL (n = 1)*

The hierarchical cluster analysis in Figure 15 highlights defined groups based on all soil properties (listed in Table 1) between all plots across the three sites (n = 50). The clusters are defined by the level of similarity of properties between the plots, as opposed to Figure 11 which illustrates the similarities between the variables. Although site (Addo Main Camp, Kabouga, and Darlington) plays a significant role in the clustering of plots by soil properties, the hierarchical cluster groups each contain plots from other sites with similar soil characteristics.

Survival of *P. afra* cuttings was significantly different ($F_{(3, 44)} = 4.52$; $p = 0.007$) between these different soil classes, ranging from 20.8 ± 17.27 % in Group 1 to 49.7 ± 27.51 % in Group 3. Post-hoc testing showed a significant difference in survivorship between soil properties of Groups 1 and 3.

Aluminium content was significantly different ($F = 31.92$; $p < 0.005$) between group 1 and groups 2, 3 and 4 (Figure 16), which were defined by the hierarchical cluster analysis. A significant difference also existed between soils groups 2 and 3. Group 1 has significantly lower aluminium than group 3, as well as a significantly lower survivorship (20.8 ± 17.27 %) compared to group 3 (49.7 ± 27.51 %). This suggests that lower levels of aluminium could have a negative impact on the survivorship of planted *P. afra* cuttings.

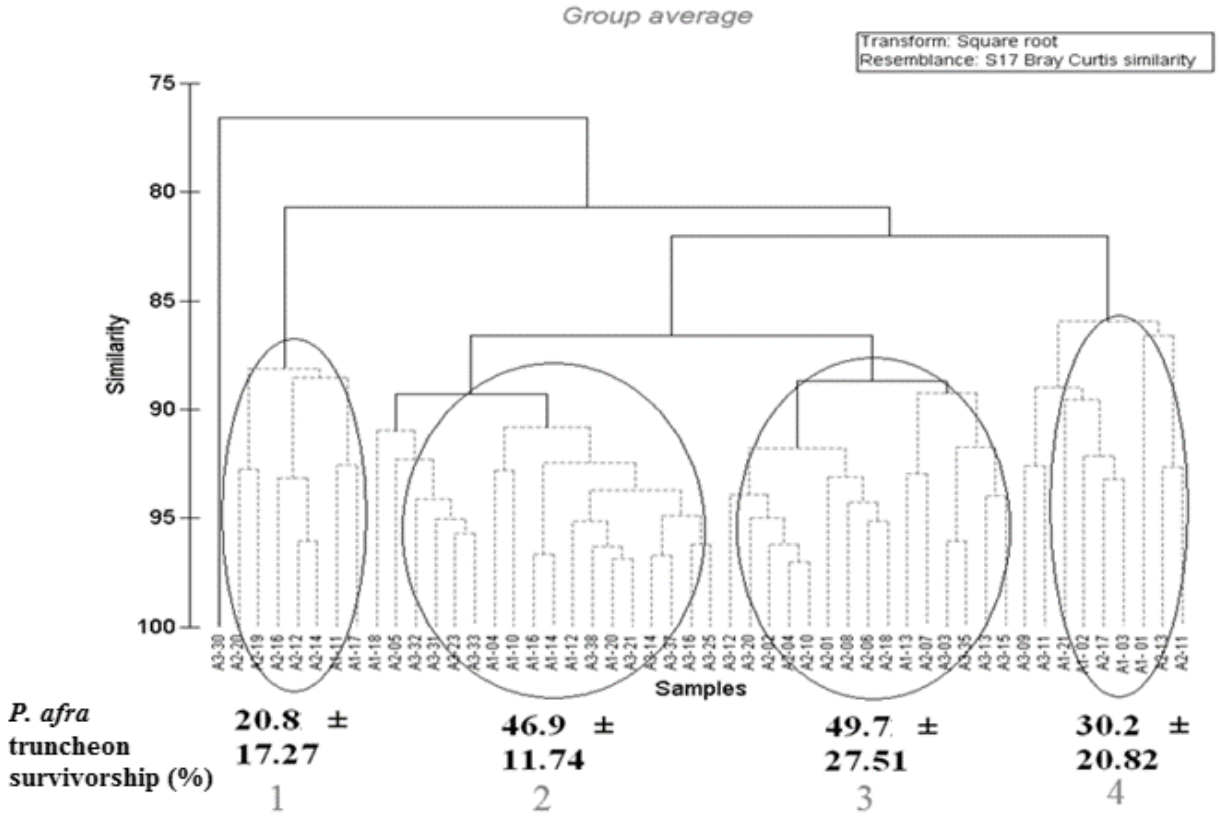

Figure 15: Hierarchical cluster of soil properties across sites (n = 50).

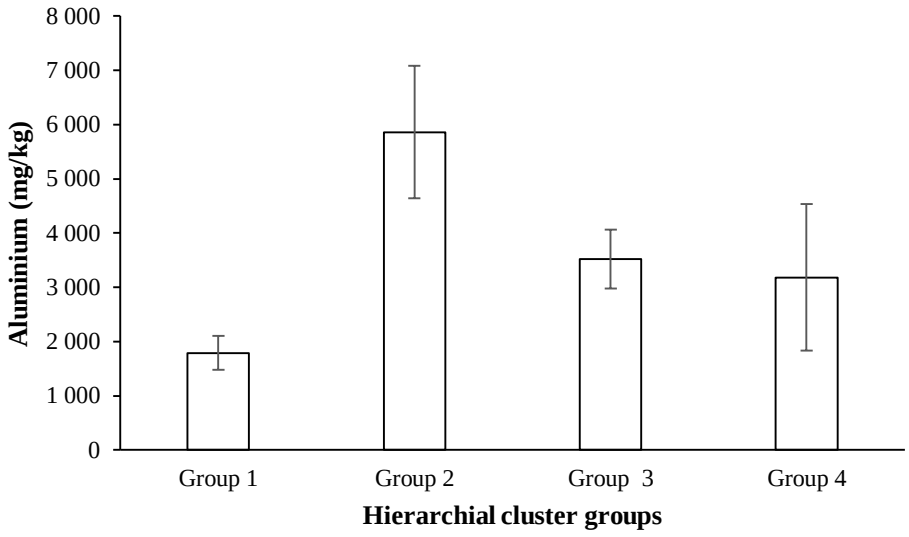

Figure 16: The level of aluminium (mg/kg) in the four soil groups.

A Principal Coordinate Ordination (PCoA) in Figure 17 illustrates that the soil and surface attributes separate the plots into sites, as the majority of plots from Darlington (D), Addo Main Camp (A), and Kabouga (K) are clustered independently, with some overlap between some of the Darlington and Kabouga plots. The line indicating the direction of increasing survivorship does not indicate any significant relationships with any plot clusters. Therefore, soil attributes are largely site specific and need to be individually investigated.

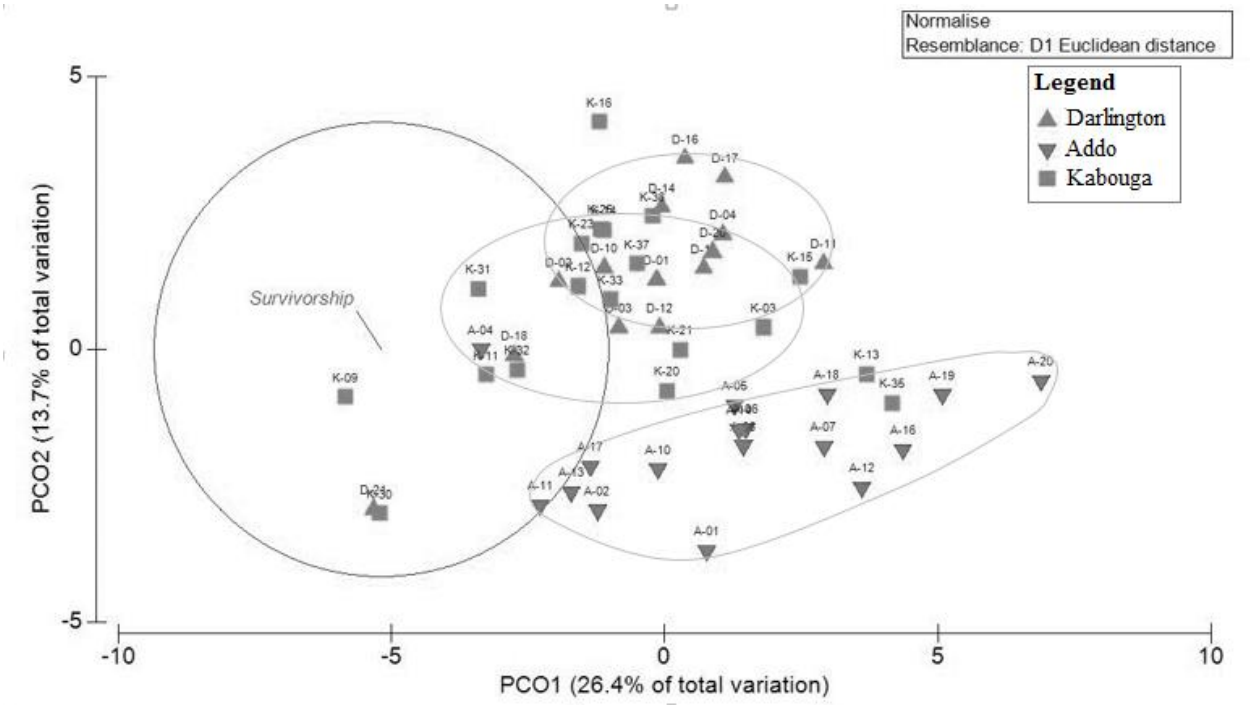

Figure 17: PCoA illustrating plot clusters based on percentage of total variation between soil variables, and the directional trend of survivorship of planted *P. afra* cuttings.

Site specific soil characteristics

Correlations and similarities between variables were explored using principal component (PCA) and ordination (PCoA) analyses for each site independently (Addo Main Camp, Kabouga, Darlington), resembling those illustrated in Figures 10 and 11. The outputs from these analyses can be seen in Appendix A.

Boron ($r^2 = 0.26$; $p < 0.026$), Al ($r^2 = 0.29$; $p < 0.026$), and Mg ($r^2 = 0.31$; $p < 0.02$) have significant positive relationships with survivorship in Addo Main Camp (Figure 18). However, K ($r^2 = 0.15$;

p < 0.13) which was flagged as a potential correlate in the PCA analysis did not have a significant relationship with survivorship. A single factor ANOVA found no significant variation between geology (F = 0.64; p = 0.64) and lithology (F = 0.91; p = 0.46), and survivorship in Addo Main Camp.

Water holding capacity (r^2 = 0.34; p < 0.008), Mg (r^2 = 0.370; p < 0.005), and soil clay percentage (r^2 = 0.41; p < 0.003) have significantly negative relationships with survivorship in Kabouga. Medium sand percentage has a significant (r^2 = 0.27; p < 0.022) positive relationship with survivorship of planted *P. afra* cuttings in Kabouga (Figure 19). However, Fe (r^2 = 0.12; p < 0.15), stone volume (r^2 = 0.14; p < 0.11), and Al (r^2 = 0.05; p < 0.36), which were identified as potential correlates using exploratory statistics, did not have any significant relationships with survivorships in Kabouga. No soil variables had any significant relationship with survivorship of planted *P. afra* cuttings at Darlington.

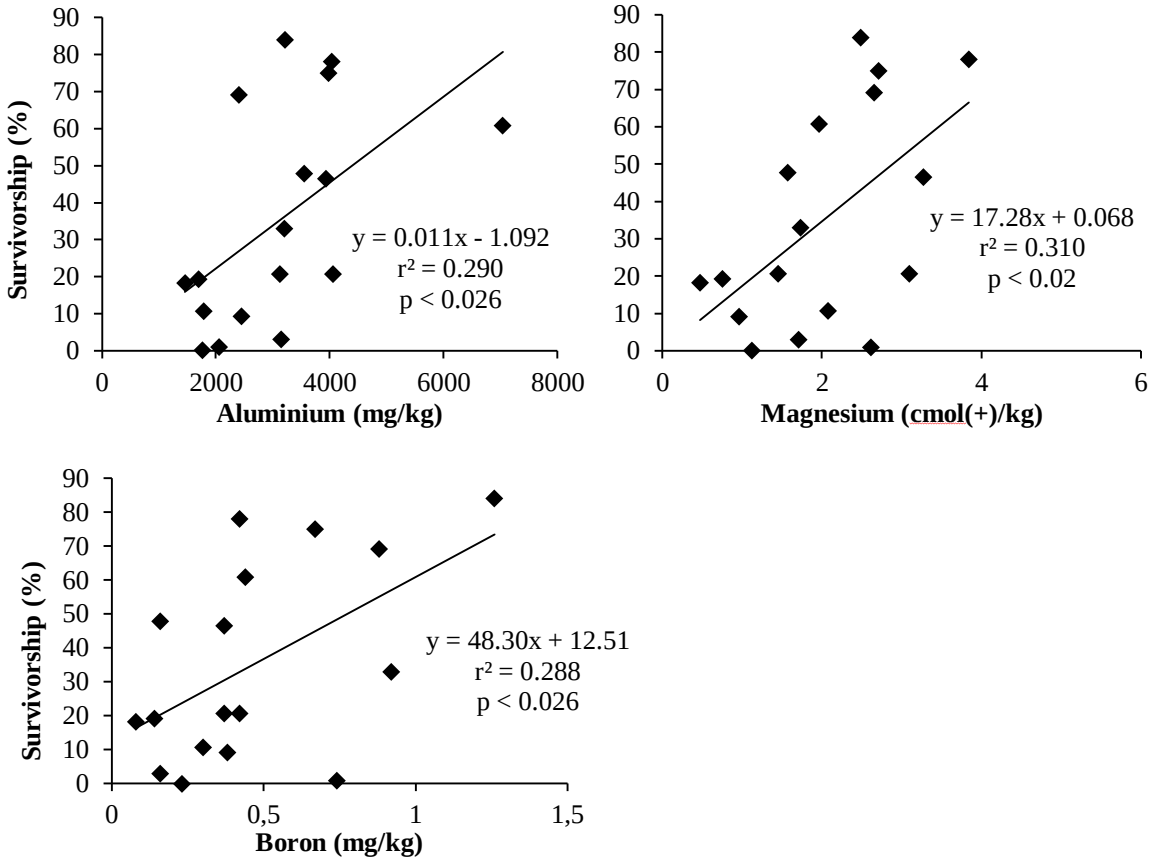

Figure 18: The relationship between soil Al, Mg and B, and *P. afra* cuttings survivorship in Addo Main Camp (n = 17).

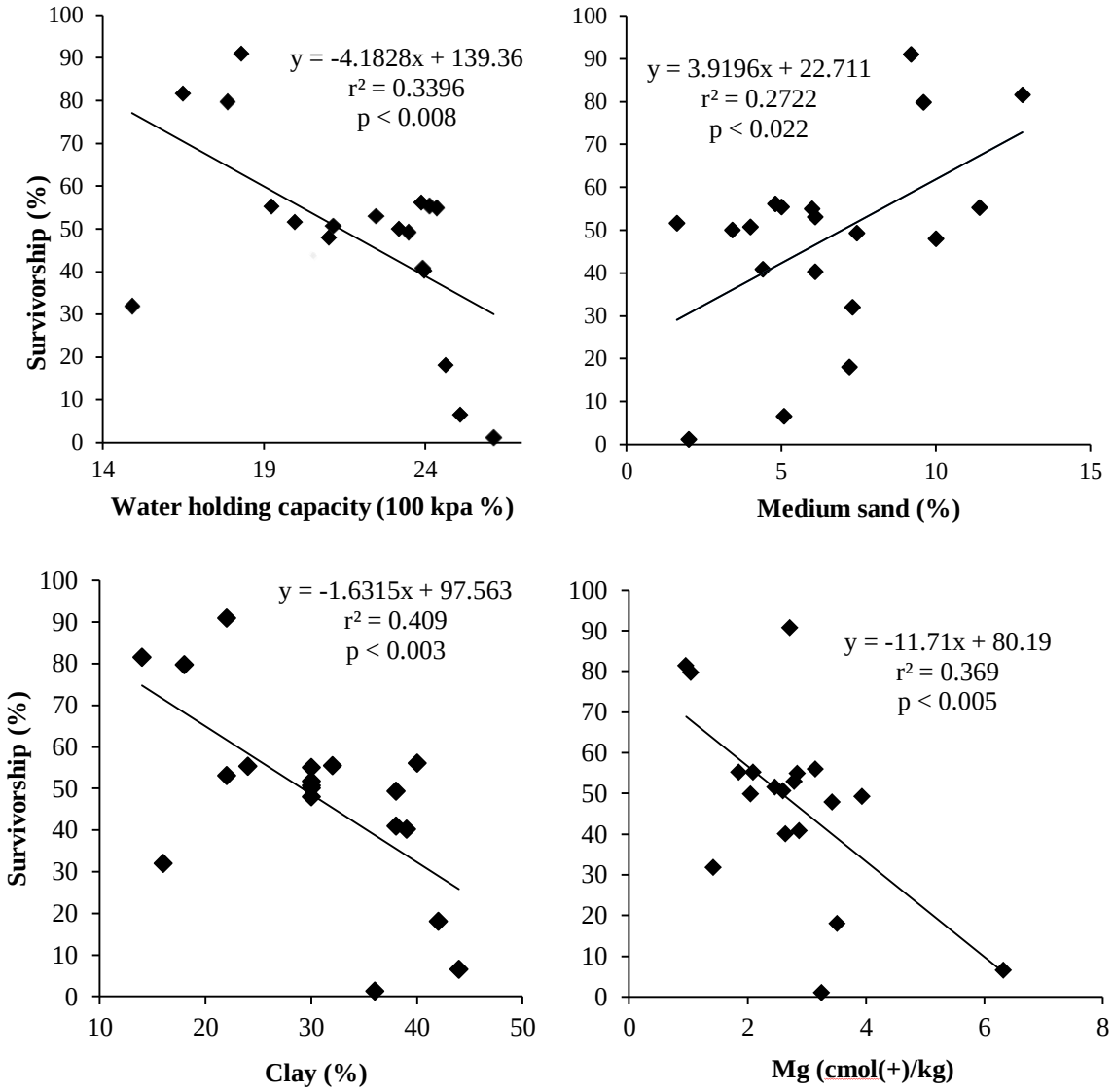

Figure 19: Significant relationships between soil variables and survivorship of *P. afra* in Kabouga (n = 19)

4.3 Plant species and community compositions

A total of 260 plant species were identified in the 50 plots across all sites. One-hundred and fifteen (115) species were identified in Darlington, 136 species in Addo Main Camp, and 112 species in Kabouga (a full plant species list can be found in Appendix B).

The non-metric Multi-Dimensional Scaling (MDS) illustrated in Figure 20 highlights the communities based on species resemblance rankings of individual plant species. The size of the

bubble plot is proportionate to the survivorship within that plot. Site appears to have the greatest influence on communities as the majority of plots from Darlington (D), Addo Main Camp (A), and Kabouga (K) are clustered independently, barring outliers which are found beyond cluster borders. Therefore, plant communities are largely site specific and need to be individually investigated.

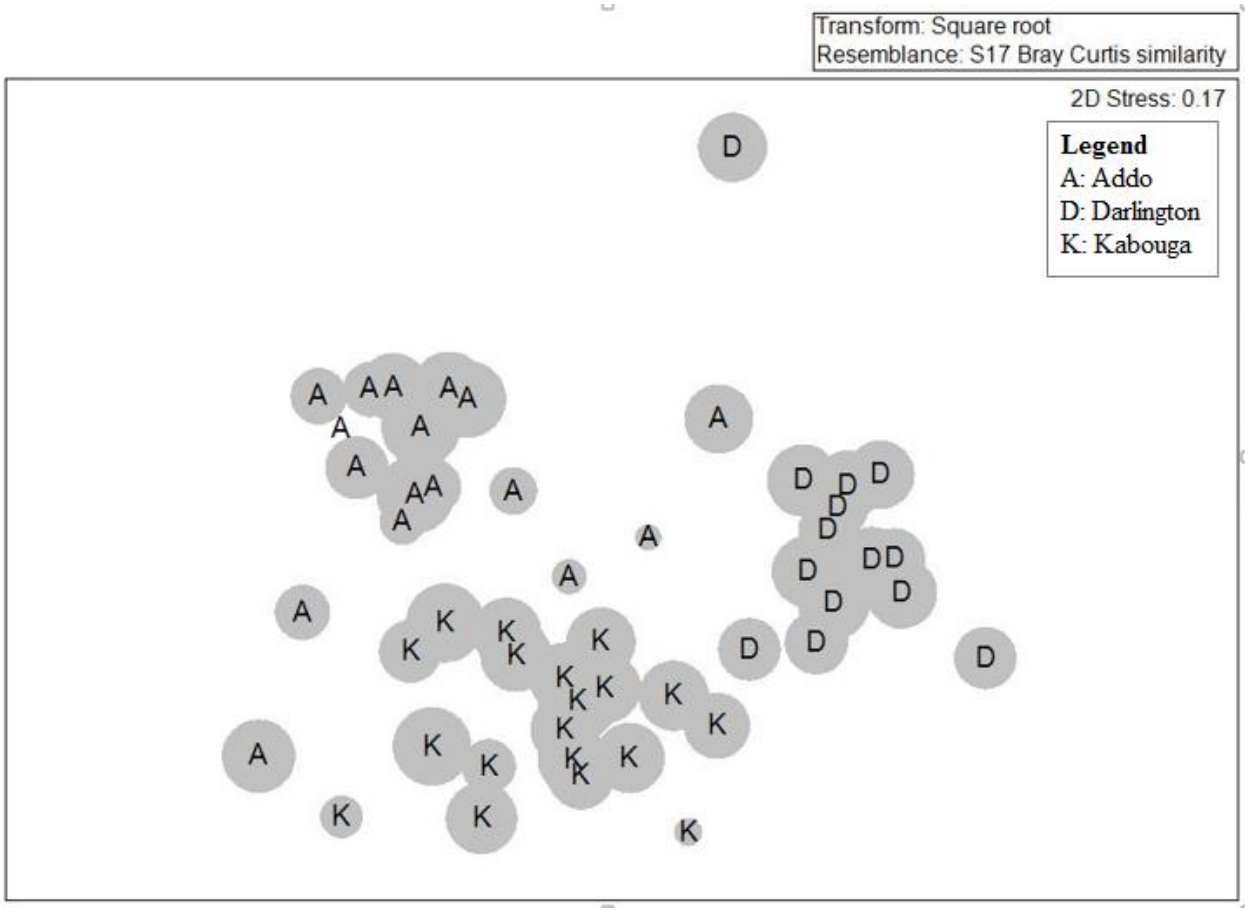

Figure 20: MDS illustrating plant communities, with survivorship displayed in bubble plots (n=50).

A Principal Coordinate Ordination (PCoA) was used to group plant communities based on the level of similarity between the plots (Figure 21) instead of the resemblance of species as was the case in Figure 20. The PCoA illustrates a very similar trend to the MDS, with site appearing to have the greatest influence on communities.

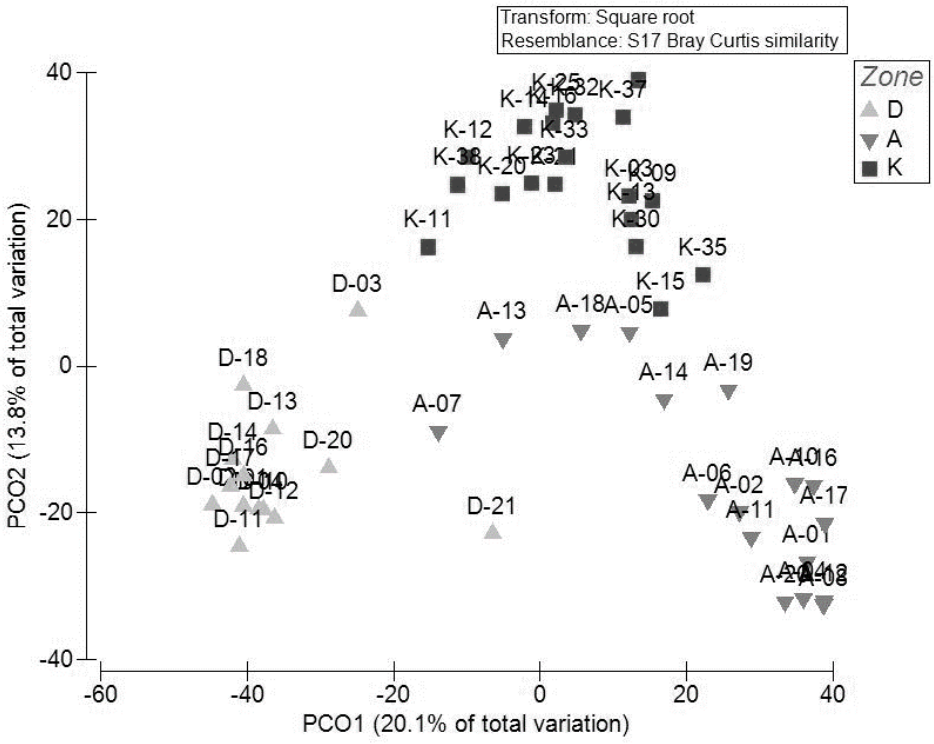

Figure 21: PCoA illustrating plant communities based on correlations between species.

A SIMPROF Cluster Analysis was run at a significance level of 5% to statistically categorize the plant communities. Nine plant communities were identified, based on the similarity of composition being greater than 25% (Figure 22). The survivorship trends between planted *P. afra* cuttings and the different communities are illustrated in Figure 24.

Plant community 4 has a significantly higher survivorship of *P. afra* (80.7 ± 1.27 %) than all of the other communities. A one-way SIMPER test revealed that community 4 is dominated by succulent shrub *Delosperma subincanum*, dwarf shrubs *Selago geniculata* and *Galenia pubescens*, the grass species *P. maximum*, the geophyte *Bulbine narcissifolia*, and the herb *Lotononis pungens* (Table 3). The survivorship of planted *P. afra* cuttings in community 8 is significantly lower than communities 1, 2, 4 and 9. Community 8 is dominated by the dwarf shrubs *Helichrysum rosum* var. *asculata* and *Hermannia althaeoides*, succulent shrub *Drosanthemum hispidum*, herbs *Conyza bonariensis* and *Sutera campanulata*, and the grass species *C. dactylon.*

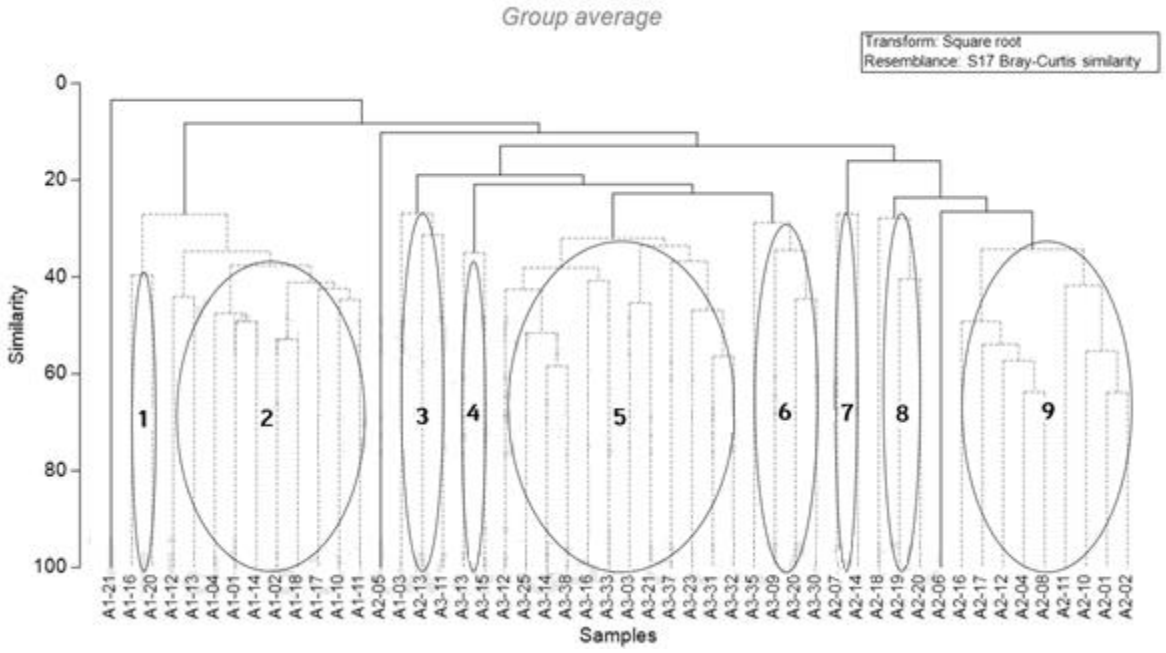

Figure 22: SIMPROF Cluster analysis illustrating plant communities separated by percentage similarity of plant species (n=50).

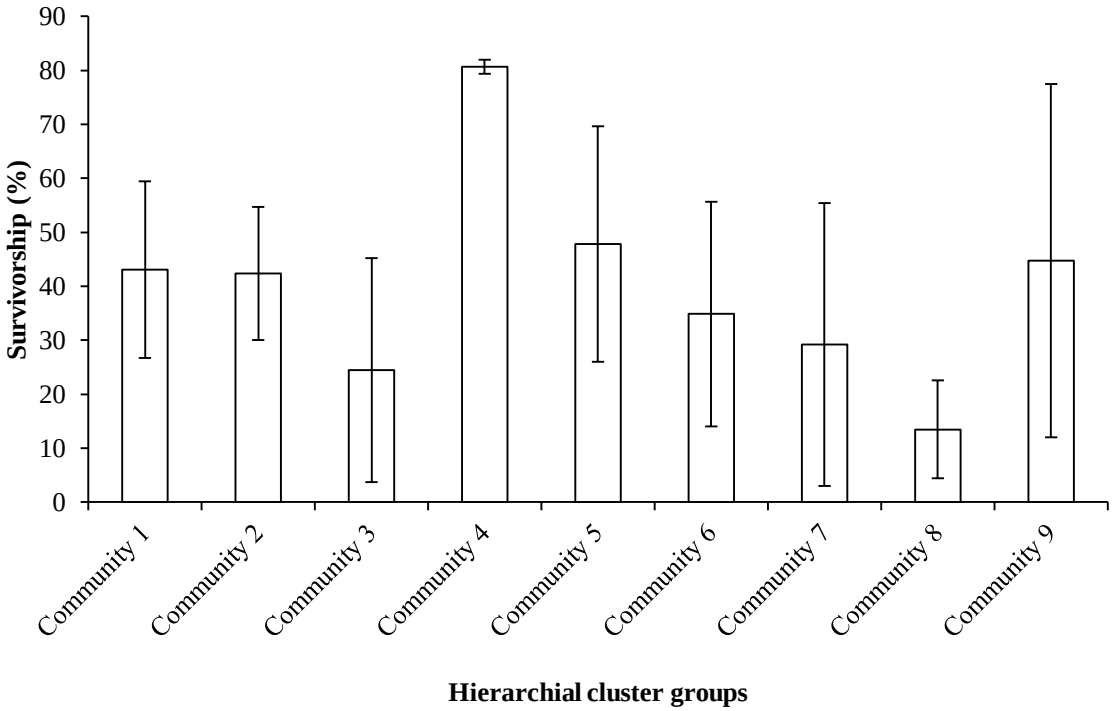

Figure 23: Survivorship (%) of planted *P. afra* cuttings per plant community.
**Community 1 (n = 2), 2 (n = 10), 3 (n = 3), 4 (n = 4), 5 (n = 12), 6 (n = 4), 7 (n = 2), 8 (n = 3), 9 (n = 9)*

Table 3: SIMPER test highlighting the dominant species within each community.

Community	Similarity (%)	Survivorship (%)	Dominant plant species
1 (n = 2)	39.6	43.1 ± 16.3	*R. obovatum, Rosenia humilis, P. incanca, Felicia filifolia , Eberlanzia ferox*
2 (n = 10)	38.6	42.4 ± 12.4	*E. coerulescens, P. incana, Panicum deustum, R. obovatum, Mesembryanthemum aitonis, Felicia hirsute*
3 (n = 3)	28.3	24.4 ± 20.8	*P. incana, Leucas capensis, Asparagus suavolens, Enneapogon scoparius*
4 (n = 4)	35.0	80.7 ± 1.3	*D. subincanum, S. geniculata, G. pubescens, P. maximum, B. narcissifolia, L. pungens*
5 (n = 12)	35.8	47.9 ± 21.8	*G. robusta,, G. pubescens, P. incana, P. pyracantha, P. maximum, C. dactylon, S. geniculata*
6 (n = 4)	33.3	34.9 ± 20.8	*C. dactylon, G. pubescens, Lycium horridum*
7 (n = 2)	27.0	29.2 ± 26.2	*Helichrysum rosum* var. *arcuatum, Senecio radicans, Cynodon incompletus, S. geniculata, Mestoklema elatum*
8 (n = 3)	32.1	13.5 ± 9.1	*H. rosum* var. *asculata, D. hispidum, H. althaeoides, C. bonariensis, S. campanulata, C. dactylon*
9 (n = 9)	42.3	44.8 ± 32.7	*C. incompletus, D. hispidum, G. pubescens, Atriplex semibaccata*

H. althaeoides, C. dactylon, A. semibaccata, P. maximum, C. incompletus, and G. robusta were identified as species which may have relationships with *P. afra* survivorship based on a random forest model analysis (Figure 24), which ranks species most likely to be correlated to the

survivorship of planted *P. afra*. *A. semibacata* ($r^2 = 0.070$; $p = 0.037$) and *P. maximum* ($r^2 = 0.174$; $p < 0.003$) percentage cover both have a significant positive relationship on the survivorship of planted *P. afra* cuttings. Although having a higher weighted importance according to the random forest model, *H. althaeoides* ($r^2 = 0.032$; $p = 0.216$) and *C. dactylon* ($r^2 = 0.003$; $p = 0.701$) did not have significant associations with planted *P. afra* survivorship. None of the other species have significant relationships with the survivorship of planted *P. afra* cuttings.

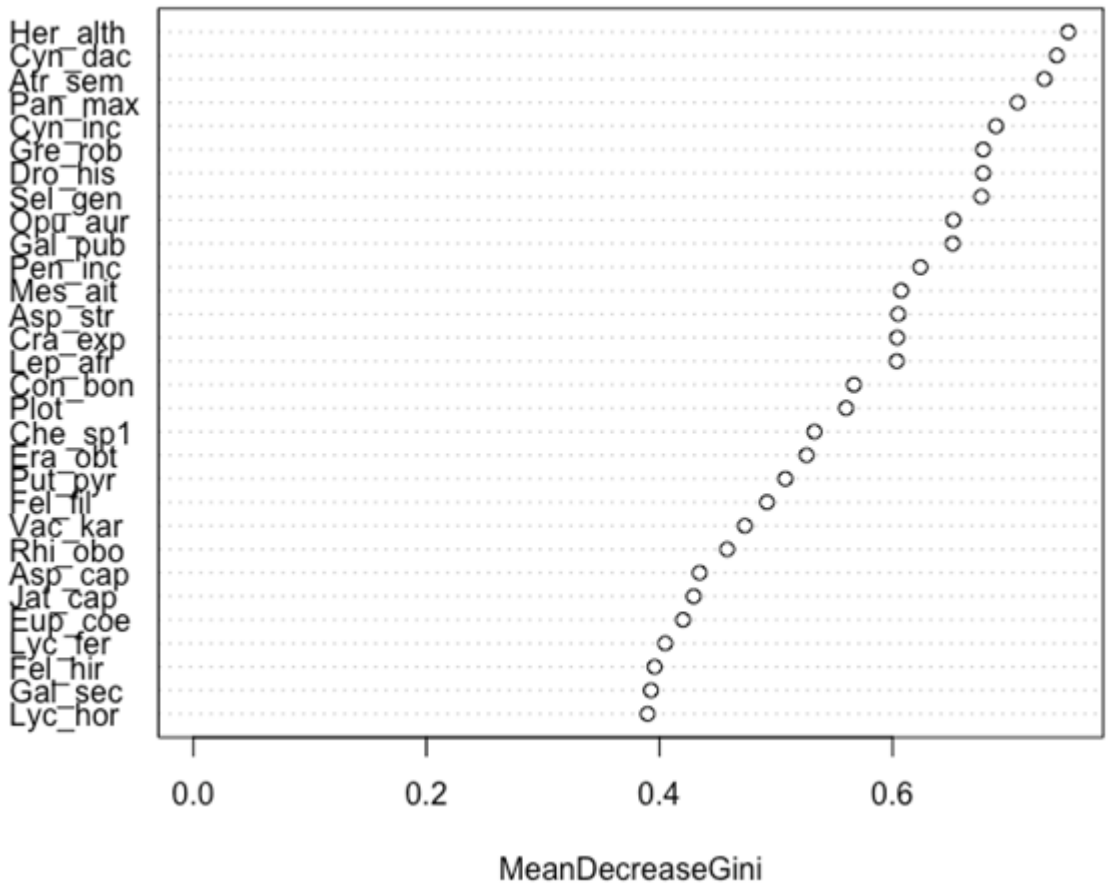

Figure 24: Random forest model ranking species most likely to be correlated to the survivorship of planted *P. afra*.

4.4 Plant-related abiotic indicators

The relationship between the aboveground abiotic variables; woody vegetation cover, bareground, litter, distance to *P. afra*; distance to intact thicket; and species richness, as well as root mass, and survivorship of planted *P. afra* were explored using Principal Component Analyses. No strong

associations between *P. afra* survival and the tested abiotic variables were found across all sites, in Darlington, and in GAENP (Figure 25). However, strong associations between *P. afra* survival and litter and root mass at Kabouga were identified (Figure 26). Subsequent regressions indicated an increase in litter mass ($r^2 = 0.32$; $p < 0.012$) and root mass ($r^2 = 0.32$; $p < 0.012$) has a positive significant relationship on survival of planted *P. afra* cuttings in Kabouga (Figure 26).

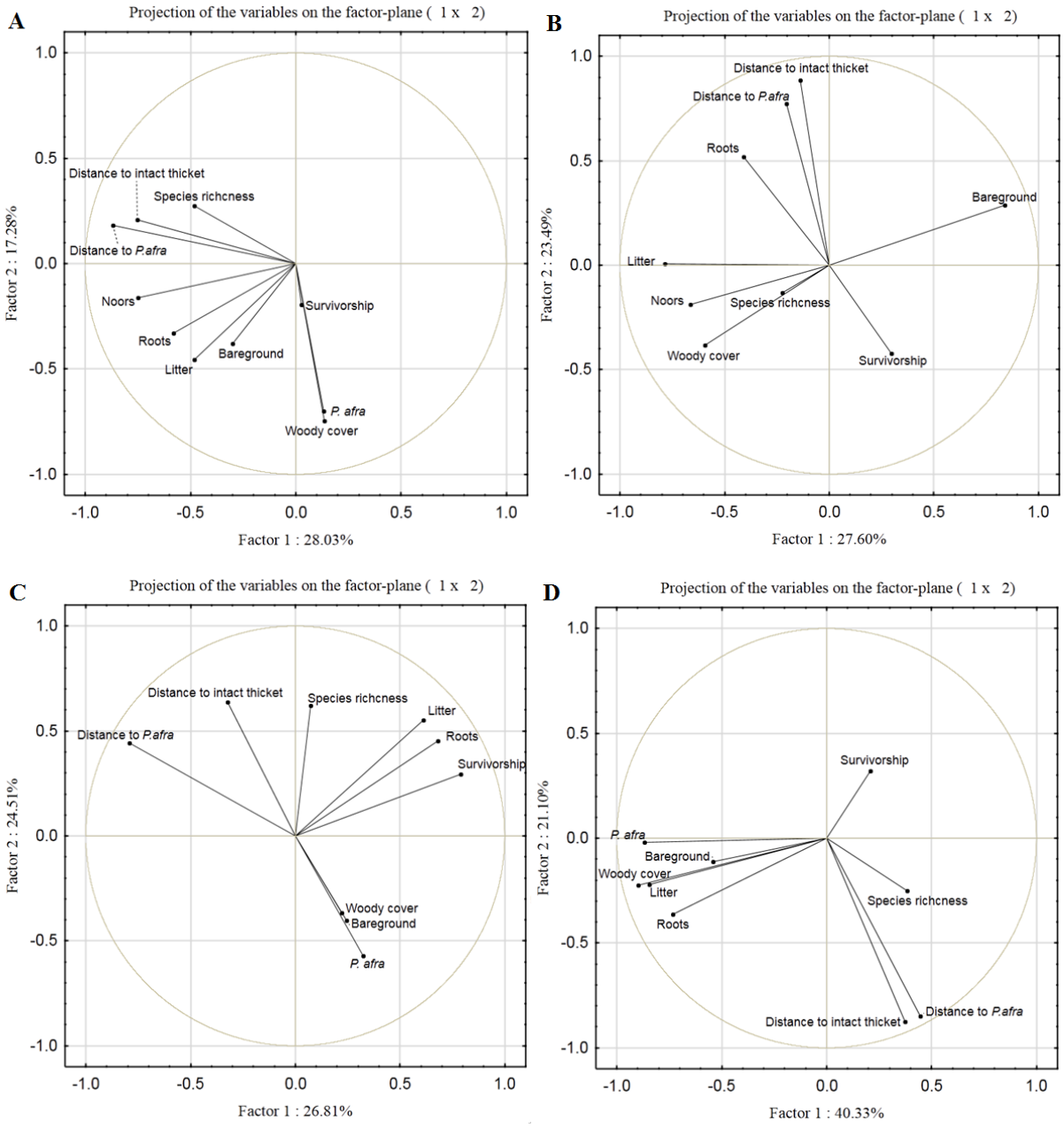

Figure 25: PCAs illustrating exploratory relationships between abiotic variables and survivorship of planted *P. afra* (a) across all sites, in (b) Darlington, (c) Kabouga, and (d) and Addo Main Camp.

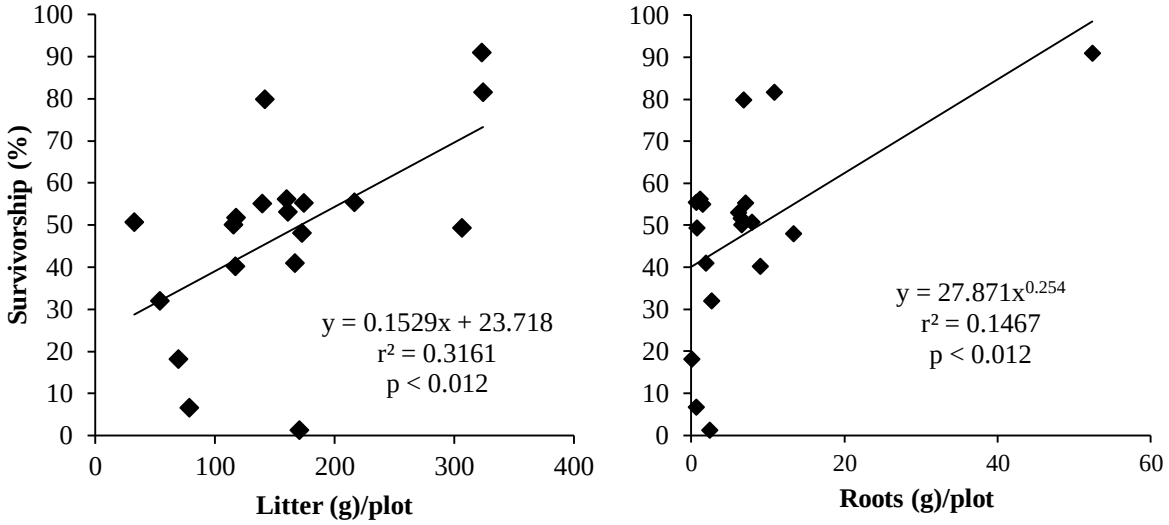

Figure 26: The relationship between litter mass (g) and root mass (g), and survivorship of planted *P. afra* in Kabouga.

4.5 Relationships between belowground abiotic variables and aboveground biotic variables.

To explore potential above ground indicators of suitable biophysical environments in which to plant *P. afra*, the relationships between the soil variables and the biological (or plant communities) were investigated. Distance based linear modeling (DistLM) was used to explain the patterns in the plant communities based on the below ground soil variables as well as the aboveground abiotic variables explored in the previous section. A model was developed to illustrate the variables which best describe the plant communities across all sites, as well as for each site independently. The variables which are significantly correlated to plant communities were then further investigated to establish if they can act as indicators of suitable biophysical environment for planted *P. afra* survivorship.

The environmental variables which best describe the plant communities across all sites are geology, woody cover, boron, and lithology (Figure 27). These variables have significant correlations with the plant communities both independently and when combined. The best-fit model sequentially adds each variable, explaining 31.1 % of the total variation in the plant community structure across all sites ($r^2 = 0.31$; $p = 0.001$). As one would expect, geology separates the three sites rather than distinguishing between plant communities. Woody cover segregates plant communities 1 and 2 in Darlington. Lithology and boron appear to have relationships with

plant community 5 which is exclusive to Kabouga. As the communities are distinctly separated and grouped by site, it is necessary to explore relationships between the plant communities and environmental variables within each site.

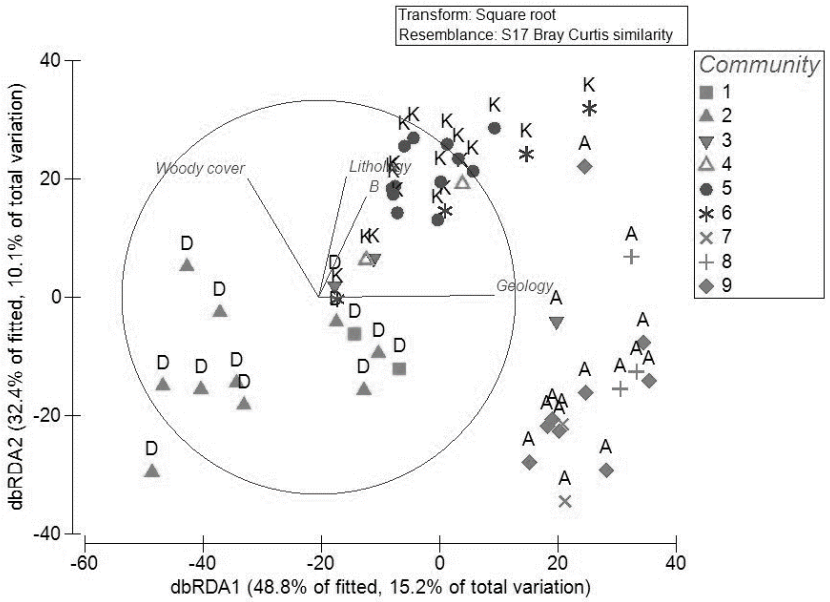

Figure 27: Distance based linear modelling (DistLM) illustrating environmental variables which best describe the plant communities across all sites.

Potassium (K) and pH best describe the plant communities at Addo Main Camp (Figure 28). The model containing these variables explains 22.7 % of the total variation in the plant community structure ($r^2 = 0.23$; $p = 0.007$). Plant community 9 seems to be clustered along a potassium gradient, while the pH gradient seems to have an influence on the distribution of plant community 8.

In Darlington, plant communities are best described by boron ($p = 0.007$) gradients, bareground ($p = 0.001$) extent, and lithological composition ($p = 0.019$). The model containing these variables explains 36.0 % of the total variation in the plant community structure. Plant community 2 is characterized by high bareground, confounding the level of degradation within this community, while variations in lithology and boron content seem to differentiate between the other plant communities found in Darlington (Figure 29).

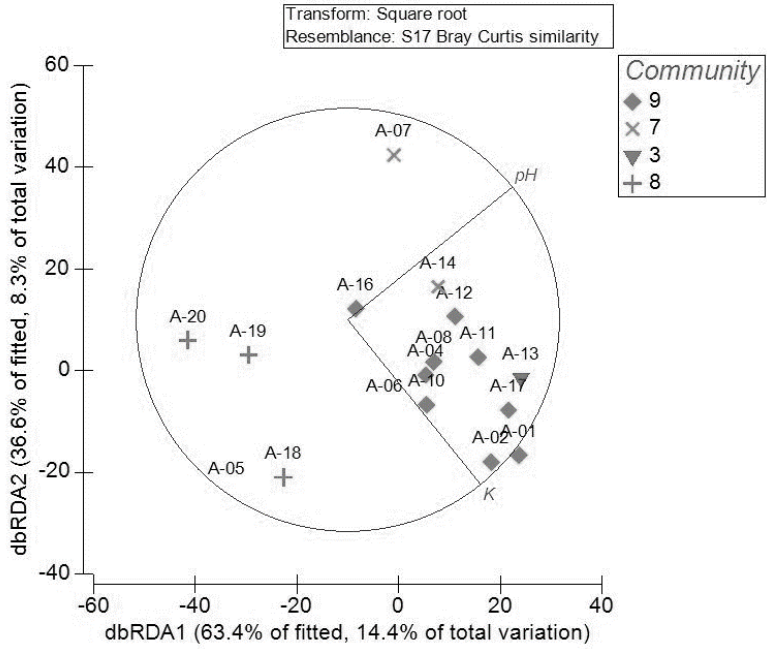

Figure 28: Distance based linear modelling (DistLM) illustrating environmental variables which best describe the plant communities at Addo Main Camp (pH and K).

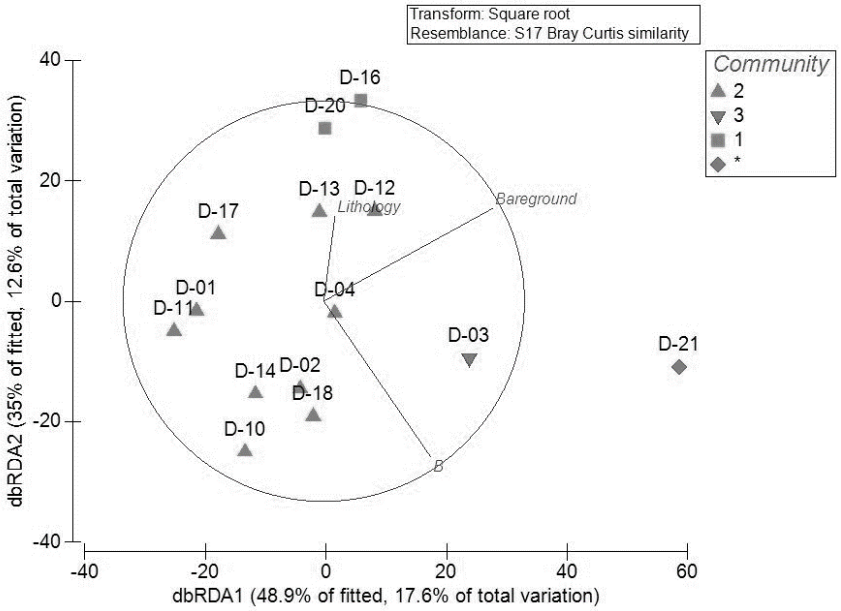

Figure 29: Distance based linear modelling (DistLM) illustrating environmental variables which best describe the plant communities at Darlington (bareground, lithology and boron).

The environmental variables which best describe the plant communities in Kabouga are manganese ($p = 0.005$), medium sand ($p = 0.016$), water-holding capacity ($p = 0.027$), and woody cover ($p = 0.001$). Survivorship of planted *P. afra* cuttings also has a significant correlation with

plant communities at Kabouga (p = 0.011). A model including these variables (including survivorship) explains 42.2 % of the variation in species compositions at Kabouga (Figure 30).

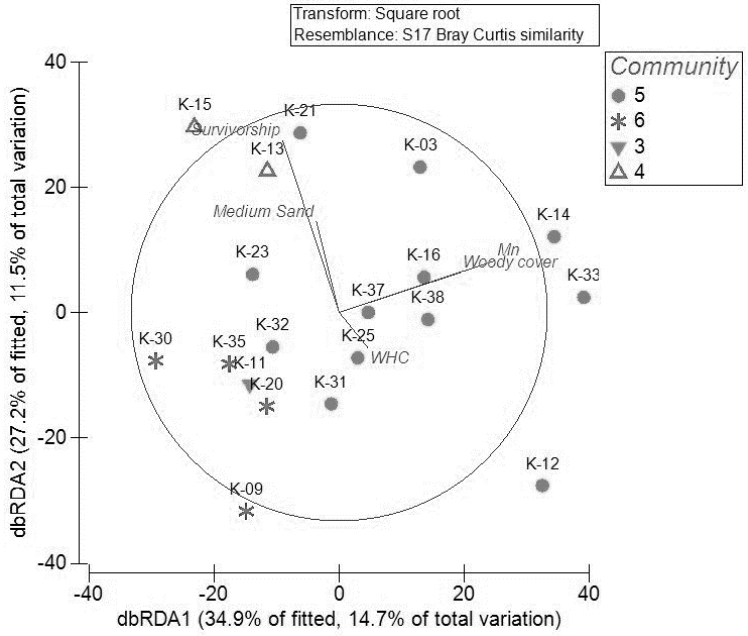

Figure 30: Distance based linear modelling (DistLM) illustrating environmental variables which best describe the plant communities at Kabouga (Water-holding capacity WHC, woody cover, medium sand and manganese).

The best-fit model to describe the patterns in the plant species compositions isolates woody cover ($r^2 = 0.15$; p = 0.001) which separates the communities found in Kabouga along a gradient (Figure 31). Community 6 is characterized by a low woody canopy, while community 5 is defined by higher canopy cover. Community 4, which had the highest survivorship of all communities (80.7 ± 1.3 %), has a moderate canopy cover and is found as an intermediary along the canopy cover gradient.

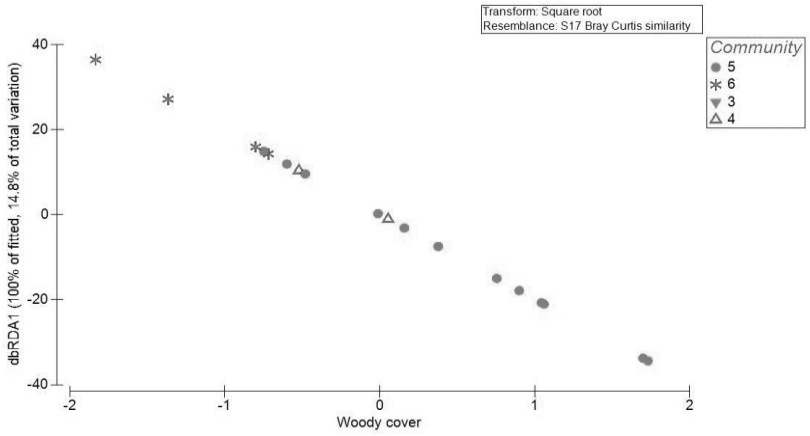

Figure 31: Distance based linear modelling (DistLM) illustrating plant communities separated by woody vegetation gradient at Kabouga.

4.6 The effects of herbivory on the survivorship of planted *P. afra*.

The impacts of herbivores on the survivorship of planted *P. afra* cuttings was analysed independently from the soil and plant composition variables. Herbivores are highly mobile and occur in different compositions and abundances in the different sections of the GAENP. Therefore, they do not form a permanent part of the vertical soil-root-plant biophysical interface which was investigated in previous sections. Furthermore, additional *P. afra* mortality counts were conducted outside the fenced area at Addo to make comparisons along a mega-herbivore utilization gradient. The vegetation type outside the fenced area is Sundays Spekboom Thicket, the same type as the majority of sites in Addo Main Camp. The area contained no mega-herbivores or introduced bulk grazing mammals. Naturally occurring kudu and duiker were recorded in the area. No soil or additional biodiversity data was collected for the sites outside the fenced areas.

Figure 32 illustrates exploratory relationships between dung counts of mammal species (A) across all sites, in (B) Darlington, (C) Kabouga, and (D) and Addo Main Camp. Possible correlations between dung counts of elephants, buffalo, baboons, bushbuck and planted *P. afra* cuttings were identified.

Dung counts of elephants (*L. africana*) illustrate a significant ($r^2 = 0.45$; $p < 0.003$) negative relationship with planted *P. afra* survivorship (Figure 33) in Addo Main Camp. Further investigation into the relationship between elephants and planted *P. afra* cuttings was conducted by comparing the survivorship of five plots excluded from elephants in the Kleinvlakte section of Addo Main Camp, as well as five plots immediately adjacent to Kleinvlakte within Main Camp (Figure 34). Survivorship of planted *P. afra* was significantly greater ($p < 0.0003$) in areas excluded from elephants.

Dung counts of baboons (*P. ursinus*) in Kabouga illustrate a significant ($r^2 = 0.27$; $p < 0.02$) negative relationship with planted *P. afra* survivorship (Figure 35). During fieldwork, a troop of baboons were observed removing an area of newly planted *P. afra* cuttings.

Baboon ($r^2 = 0.05$; $p < 0.377$) and buffalo ($r^2 = 0.08$; $p < 0.271$) dung counts did not illustrate a significant relationship with planted *P. afra* survivorship in Addo. There were not enough dung counts of bushbuck (*T. scriptus*) (n = 4) to test significance in Addo. No species had a significant relationship with *P. afra* survivorship in Darlington.

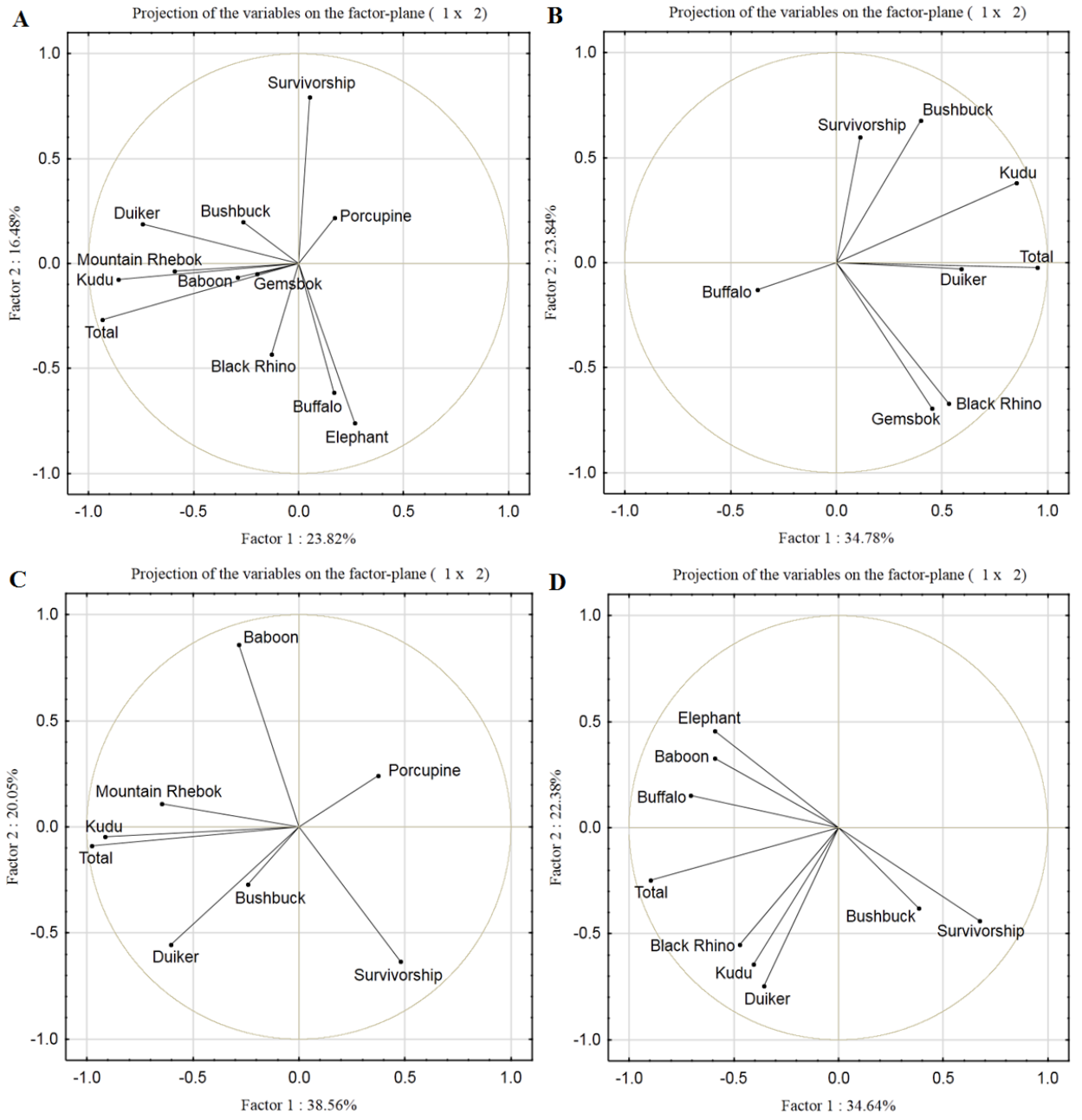

Figure 32: PCA illustrating exploratory relationships between total dung counts of mammal species (a) across all sites, in (b) Darlington, (c) Kabouga, and (d) and Addo Main Camp.

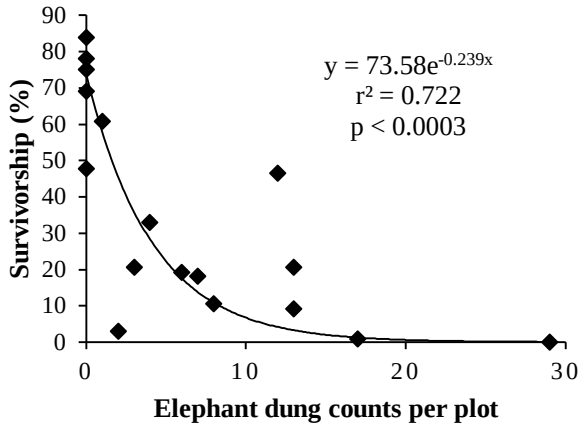

Figure 33: The relationship between elephant dung density and *P. afra* survivorship at Addo Main Camp (n = 17).

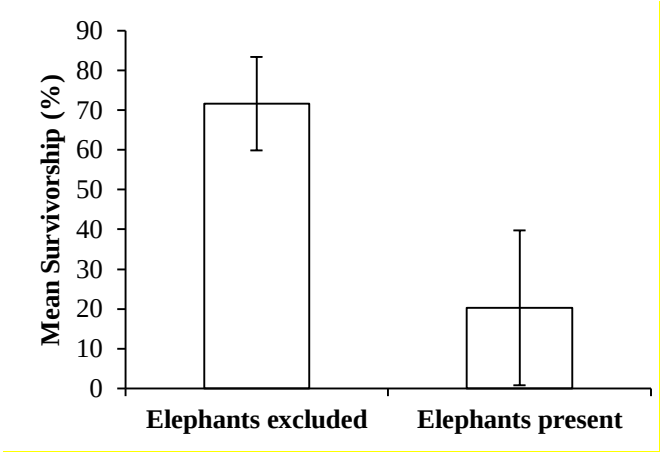

Figure 34: The mean (± SD) *P. afra* survivorship in plots exposed to *L. africana* and plots which exclude the species in Addo Main Camp.

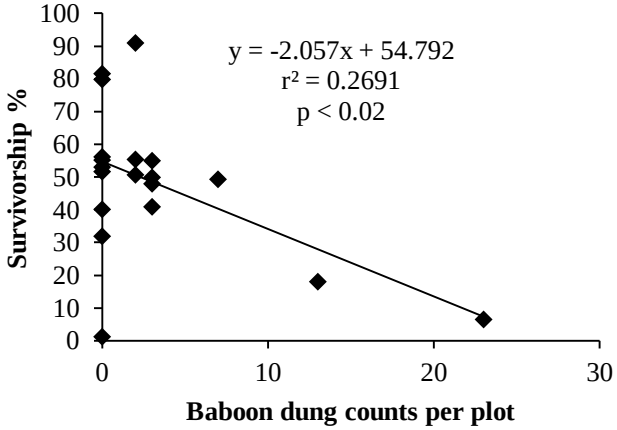

Figure 35: The relationship between baboon dung counts per plot and *P. afra* survivorship at Kabouga (n = 19).

5. DISCUSSION

5.1 Previous research of *P. afra* survivorship trends

Mills & Robson (2017) assessed planted *P. afra* survivorship at Darlington and the GFRNR in June 2015, almost a year after the data for this thesis was obtained. Mills & Robson (2017) found a mean survivorship of 28 ± 23 % between their two study sites, compared to the mean survivorship of 42 ± 23 % collected across the three sites for this study. The survivorship data for both surveys showed large variation, ranging from 0 to 91 % (Mills & Robson, 2017) and 0 to 93 % (this study), respectively.

For the Darlington section of the GAENP, Lagerwall (2010) found a mean survivorship of planted *P. afra* of 26.3 %, compared to the mean survivorship determined by Working for Woodlands of 32.9 %. Five years later, Mills & Robson (2017) found a mean survivorship of 31 % in Darlington, compared to the 42 % recorded during this survey. Contrary to Powell (2009) who found a drop in survivorship from 43 % in 2006 to 35 % in 2008 in the Baviaanskloof, findings suggest that the time since planting does not significantly influence the survivorship of planted *P. afra* cuttings in the study areas. The decrease of 11 % in mean survivorship between this study and Mills & Robson (2017) could be a result of the spatial variability of the sample effort, or alternatively an event or series of events which occurred between the counts conducted in mid-2014 and mid-June 2015. This hypothesis could further explain the long-term trends in the mortality of planted *P. afra* survivorship, as climatic events such as low rainfall, heavy frost, or short-term extremes in temperatures potentially result in mortalities in periodic events following planting. For instance, Duker *et al*. (2015) found that frost plays a vital role in determining the boundaries between thicket and Nama-Karoo vegetation, based on freezing tolerances of succulent species. This could be of particular relevance for both the Darlington and Kabouga sections which experience frost events. Swart *et al*. (1994) found that planting time or season or water regimes had no influence on mortality. However, Van der Vywer (2011) noted that the survival of planted cuttings coincides with rainfall events, finding 100 % survivorship rates within fenced off plots during productive rainfall patterns. Mills *et al*. (2015) describe planting season as one of the key factors determining the survivorship of planted *P. afra* cuttings.

The climatic data records obtained for this project were limited to monthly average minimum and maximum temperature and monthly rainfall measurements. To investigate the impact of climatic events on the survivorship of planted *P. afra*, short-term, fine-scale weather data would be required. Therefore, it is accepted that the lack of site specific climatic data is a limitation to the study as climatic events are likely to impact the observed survivorship trends, certainly in the short-term.

5.2 The reduced water retention ability of degraded thickets

Most plant communities in arid and semi-arid systems illustrate opportunistic responses to rainfall, with increases in growth of dominant species following significant rainfall events (Hoffman & Cowling, 1991). Each rainfall event produces water that either infiltrates the soil, is captured by the soil surface or canopy, or runs off the soil surface (Lechmere-Oertel, 2003). In degraded landscapes, the ability of soil to retain water is greatly reduced due to the loss of vegetation, soil crusting, and changes in soil properties (Lechmere-Oertel, 2003; Mills & Fey, 2004a; Mills *et al.*, 2009), which subsequently result in reduced infiltration and ability of soils to capture rainfall (van Luijk *et al*, 2013). The complete loss of the vegetation canopy in severely degraded areas can limit the ability of a landscape to capture water by up to 25 %, which can result in a primary production loss of up to 40 % (Ludwig *et al.*, 1999; van Luijk *et al* 2013).

All of the study sites for this project are considered to be severely degraded due to historical agricultural practices, apart from certain mountainous parts of the Kabouga section which remain in a transitional state, with some woody canopy species still remaining. The landscapes are generally characterized by the lack of woody and succulent canopy species and intact vegetation. The transformation of these landscapes has resulted in the soil surface with high bareground, low litter cover, and therefore exposed soils, displaying various levels of crusting and capping. In most cases the crucial litter layer and *A* soil horizon has been lost. Therefore, the soils within these landscapes will inevitably have reduced infiltration and ability to capture rainfall. The reduction in infiltration of water into the soil reduces the availability of water for plants (Mills & Fey, 2004a), as was found with the positive relationship between infiltration and the survivorship of planted *P. afra* cuttings.

Kabouga, which has the highest mean survivorship (48 ± 22 %) of planted *P. afra*, also has the highest average infiltration (23 ± 12.5 mm/m) and mean water holding capacity (22 ± 3.1 kPa %) of the three sites. This could be attributed to Kabouga having the highest mean woody vegetation cover (26 ± 10 %), as the loss of intactness of vegetation can be correlated with litter loss, which also reduces infiltration (Lechmere-Oertel, 2003), as crusting is correlated with litter cover loss. A significant positive relationship ($p = 0.01$) between litter mass and the survivorship of planted *P. afra* cuttings at Kabouga was found, further explaining the relationship between vegetation intactness and soil water retention. These findings suggest that the retention of canopy dominant species and thicket clumps ameliorate edaphic conditions which are more suitable for the planting of *P. afra* than landscapes with little to no intact vegetation.

Apart from the density of plants, the crusting of soils is influenced by factors such as clay mineralogy (Bühmann *et al.*, 1996 cited in Mills *et al.*, 2009), hydrophobicity (Hillel, 1998 cited in Mills *et al.*, 2009), silt content, sand content and the dispersibility of the clay fraction (Agassi *et al.*, 1981 cited in Mills *et al.*, 2009), which all influence the ability of water to infiltrate to plants roots A significant negative relationship between soil clay percentage and survivorship of planted *P. afra* in Kabouga was found, strengthening the case of Powell (2009) who suggests that degraded soils with high clay content and soil crusting could increase mortality of planted *P. afra* cuttings.

Medium sand percentage was also found to have a significant positive relationship with survivorship of planted *P. afra* cuttings in Kabouga. Although this finding suggests that the sand particle size may influence infiltration, which in turn influences survivorship, it could also potentially influence root competition as certain crusts can prevent root growth near the surface (Mills *et al.*, 2009). The finding that the root mass of all the residual plants has a positive significant relationship on survival of planted *P. afra* cuttings in Kabouga indicates that soil particle size may influence root growth and establishment. Alternatively, the presence of existing root structures maintains soil structure and porosity, providing permeable pathways for *P. afra* cuttings roots to establish. Norman (2016) found that the survivorship of planted *P. afra* cuttings is limited by root growth. The influence of roots and root structures on the survivorship of planted *P. afra* requires further investigation.

Aluminum (Al) tends to be correlated to clay content (Perkins *et al.*, 2013) and has also been suggested to be an accurate reflection of the ecological impacts of soil texture (Mills *et al.*, 2011). When the plots are grouped based on all soil chemical properties, the groups characterized by higher aluminium display a significantly higher survivorship of planted *P. afra*. Furthermore, aluminium was found to have a significant positive relationships with survivorship in Addo, further suggesting that lower levels of aluminium could have a negative impact on the survivorship of planted *P. afra* cuttings, supporting findings that *P. afra* is constrained at extreme levels of aluminium (Mills *et al.*, 2011). However, low levels of aluminium can increase plant growth, and higher levels of exchangeable soil aluminium can be a growth limiting factor for plants (Rout *et al.*, 2001). Further investigation into the optimal aluminium ranges for planted *P. afra* survivorship is required.

The reduction in infiltration, which is related to variables such as woody canopy and litter cover, soil crusting, clay and sand compositions, water-holding capacity, and root mass, clearly plays a significant role in the establishment and survival of planted *P. afra* cuttings in the GAENP. Powell (2009) found that micro-damming significantly increased the survivorship of planted *P. afra* cuttings, and Rossler (2010) found that the irrigation of unrooted *P. afra* cuttings prior to planting prevented the mortality of the cuttings. Rossler (2010) further found that clay soils require less regular irrigation to avoid water-logging. Therefore, site specific chemical or physical modification of soil, or alternative planting techniques, may be required in order to increase infiltrability and increase survivorship of planted *P. afra* cuttings.

5.3 The effect of micronutrients on planted *P. afra* survivorship

Although micronutrients are only required in small amounts, their balance and availability is vital for optimal plant performance (Perkins *et al.*, 2013). The micronutrient magnesium (Mg) which is an essential nutrient for plant growth and function, had a significant positive relationship with the survivorship of *P. afra* in Addo Main Camp, but it had a negative relationship with survivorship of planted *P. afra* cuttings in Kabouga, which is possibly linked to chemical processes we are yet to understand. Boron (B), which is also an essential micronutrient element, was found to be one of the variables which best described the differences between the plant communities across all three study sites. It was found that boron had a significant positive correlation with two plant

communities in Kabouga. These communities had the highest survivorship percentages out of all communities, with planted *P. afra* survivorship of 81 % and 50 % respectively. Kabouga also had the highest mean soil boron content of the three sites which could potentially relate to the site having the highest mean survivorship of planted *P. afra*. Furthermore, boron content also had a significant positive relationship with survivorship of planted *P. afra* in Addo Main Camp. It was also found that boron content explained significant variation between plant communities within Darlington. However, there were no relationships between these plant communities and the survivorship of planted *P. afra*. Boron plays a unique physiological role in plants. It is involved in the synthesis of plant cell walls which is required for normal plant growth and development to occur (Camacho-Cristobal *et al.*, 2008). Although it is not required in high amounts, if it is not supplied at the appropriate levels it can cause severe plant growth problems.

None of the other chemical soil properties investigated correlated with the survivorship of planted *P. afra* cuttings. Although certain chemical soil properties may act as indicators of planted *P. afra* survivorship, it is unlikely that *P. afra* is constrained by chemical properties as it is tolerant of such a wide range of soil conditions, with studies showing the successful growth of planted cuttings in degraded areas which have experienced severe losses of soil fertility (Mills & Cowling, 2006; Mills *et al.*, 2007; Sigwela *et al.*, 2009; Mills *et al.*, 2011).

5.4 Geology, aspect and slope

Although geology was a determinant of plant composition in the three study sites, the survivorship of *P. afra* did not have any relationships with either the geological or lithological groups they were planted on. This is not surprising and is consistent with the wide range of geologies which support *P. afra* dominated thickets (Vlok *et al.*, 2003). La Cock (1992) found seedling germination and sapling survival of thicket shrub species was higher on south facing slopes in Fish River Spekboom Thicket. Furthermore, Becker *et al.* (2015) suggest avoiding planting *P. afra* cuttings in bottomland habitats based on the low survivorship compared to sites on slopes. Becker *et al.* (2015) conclude that the absence of *P. afra* thickets is not under edaphic control, but is more likely explained by the frost-limitation hypothesis (Duker *et al.*, 2015). However, the results of this study found that neither slope nor aspect had any relationship with the survivorship of planted *P. afra*

cuttings, therefore supporting Mills & Robson (2017), who also found that geology, aspect, and slope have no relationship to the survivorship of planted *P. afra* cuttings. However, STRP protocols prevent planting in the valleys or bottomlands, and therefore not all points across slopes were tested in this study.

5.5 The plant communities in degraded thickets in the GAENP

Soils can have species-specific effects on plant growth, and plants can have species-specific effects on soil nutrient availability, soil microbial communities, and therefore the performance of plants (Perkins & Nowak, 2013; Perkins *et al.*, 2013). However, *P. afra* is tolerant of a wide range of soils and is found in abundance over a wide range of plant communities and even vegetation types, making it highly unlikely that individual plant species or compositions will influence the survivorship of planted *P. afra* cuttings. However, certain guilds and/or species could potentially act as indicators of suitable biophysical environments in which to plant *P. afra* cuttings which could be of great benefit to decision-makers and planners with regard to future planting efforts.

Based on species composition, nine plant communities were identified within the degraded landscapes of the study area. These communities are largely differentiated by site, driven by the variations in woody canopy cover, geology and lithology across the three different sections of the GAENP. In Kabouga, woody cover best describes the separation of communities along a gradient, with manganese, sand particle size, and water-holding capacity also differentiating plant communities. The community with the highest mean survivorship of planted *P. afra* (81 ± 1.3 %) was found in Kabouga, and characterized by the presence of canopy dominant species and high litter cover. The community is dominated by succulent shrub *D. subincanum*, dwarf shrubs *S. geniculata* and *G. pubescens*, the geophyte *B. narcissifolia*, the herb *L. pungens*, and the grass species *P. maximum*. A significant positive relationship between *P. maximum* and the survivorship of planted *P. afra* cuttings was found across all sites indicating that the species may be a potential indicator of good sites for planted *P. afra* survivorship.

In Addo Main Camp, the plant communities are correlated to variations in potassium (K) and pH. The community with the lowest survivorship of planted *P. afra* (14 %) was found in the Riversbend section of Addo Main Camp, and is dominated by the dwarf shrubs *H. rosum* var. *asculata* and *H.*

althaeoides, succulent shrub *D. hispidum*, herbs *C. bonariensis* and *S. campanulata*, and the grass species *C. dactylon*. This community was characterized by soils with low pH. The majority of the plots at Addo Main Camp fell within a plant community which had the highest mean survivorship of planted *P. afra* (45 %) in Addo Main Camp. This community was correlated with higher pH and potassium levels. The community is dominated by *C. incompletus*, *D. hispidum*, *G. pubescens*, and *A. semibaccata*. A significant positive relationship between *A. semibacata* percentage and the survivorship of planted *P. afra* cuttings was found across all sites. Although pH and potassium describe the variations in the plant communities at Addo Main Camp, they are not linked to the survivorship of planted *P. afra*.

The plant communities in Darlington are correlated with differing levels of boron and bareground. The community dominated by *E. coerulescens, P. incana, P. deustum, R. obovatum, M. aitonis,* and *F. hirsute* is characterized by low bareground and relatively high mean survivorship of planted *P. afra* (42 ± 12.4 %). The community dominated by *R. obovatum, R. humilis, P. incanca, F. filifolia,* and *E. ferox* is characterized by low levels of boron and differing lithology to the other communities found in Darlington. This community has a mean planted *P. afra* survivorship of 43 ± 16 %. The community dominated by *P. incana, L. capensis, A. suavolens,* and *E. scoparius* had a low mean survivorship (24 ± 20 %) and is characterized by higher bareground percentages. As previously discussed, the high bareground percentages relate to exposed soils which may promote crusting, reducing infiltration. Therefore, the microclimatic function of such plant compositions may be a factor which influences infiltration and hence influences the survivorship of planted *P. afra*.

The described plant communities are largely differentiated by site, with very few plots from different sites forming part of the same community. Therefore, it is not possible to confidently associate any communities or assemblages with trends in survivorship across the project area. Furthermore, both *A. semibacata* and *P. maximum* cover have low r^2 values as they are only abundant in Kabouga and Addo Main Camp, with *P. maximum* only occurring in low cover in four plots in Darlington. *A. semibacata* was not recorded in any plots in Darlington.

The trends in survivorship across the plant communities are largely due to the extent of degradation. Areas represented by more intact states, characterized by the retention of canopy dominant species, woody vegetation cover, low bareground and high cover of litter were found to have higher survivorship of planted *P. afra* cuttings than those in more severely degraded states. Although this does not aid in planning as degraded landscapes of all states require restoration, it does give insight into potential alternative approaches towards planting techniques. In areas with retained thicket patches or clumps, further research should investigate if the survivorship of planted *P. afra* would be increased by planting in close proximity to existing 'intact' thicket patches, with subsequent planting radiating away from the thicket clumps following successful establishment of initial plantings. This gradient could potentially be characterized by certain plant species and communities which may be tolerable of intermediate soil characteristics between degraded and moderately intact states, and may be significant in identifying suitable areas for restoration efforts. In addition, frost tolerant plant species could provide the necessary microclimate to protect planted *P. afra* cuttings on lower slopes during frost events. This too requires further investigation.

5.6 The impact of herbivory on planted *P. afra* survival

In the GAENP, elephants have influences on soil resources, litter production and landscape patchiness (Kerley & Landman, 2006), both negative and positive from a biodiversity perspective. It has been shown that elephants were responsible for increased run-off zones which led to resources such as water, litter, soil and nutrients being translocated (Kerley & Landman, 2006). Furthermore, elephants appear to significantly alter the size, nutrient content, and dynamics of the litter in thicket vegetation (Kerley & Landman, 2006), including the reduction in *P. afra* litter fall which is of vital importance to subtropical thicket functioning (Lechmere-Oertel, 2003; Lechmere-Oertel *et al.*, 2008).

Investigation into the relationship between elephants and planted *P. afra* cuttings at Addo Main Camp suggest that elephants also play a significant role in the survivorship of planted *P. afra*. Comparisons between plots excluded from elephants and those within Addo Main Camp found that the plots which are not exposed to elephant pressure had more than 50 % higher survivorship of planted *P. afra* than those within the park. Furthermore, dung counts found a significant negative

relationship between the presence of elephants in the planting area and the survivorship of planted *P. afra* in Addo Main Camp.

Penzhorn *et al.* (1974) compared plant species richness and biomass inside and outside an elephant enclosure in the GAENP. Total plant biomass was reduced by 55 % within the enclosure, including significant loss of *P. afra, S. afra, Azima tetracantha* and *E. undulata*. Species such as *C. sepiaria* increased by 50 % within the elephant enclosure, and *Viscum rotundifolium* and *Aloe africana* were not found in the enclosure at all. However, elephants can be selective for the plant species they feed on or damage. Cowling & Kerley (2002) found that species like *P. afra* experienced significantly more damage from elephants than other abundant thicket species such as *E. undulata, A. tetracantha* and *C. sepiaria*. In degraded areas with very little natural browse, the lure of newly planted *P. area* cuttings must be irresistible for elephants. Based on data collected at Addo Main Camp, Mills *et al.* (2015) describe elephant density as one of the key factors determining the survivorship of planted *P. afra* cuttings.

Beyond the scope of this study, we need to quantify what percentage of cuttings are actively removed or damaged by elephants in order to understand the full extent of the damage they cause to newly planted *P. afra* cuttings. This is of vital importance to assess whether the presence of elephants, in high densities, can reduce the economic feasibility of the *en masse* plantings of *P. afra* in attempts to restore degraded landscapes.

Dung counts in Kabouga indicated a significant negative relationship between the presence of baboons and planted *P. afra* cuttings. Furthermore, a troop of baboons were observed removing parts of a section of newly planted *P. afra* cuttings during data collection. This finding supports Powell (2009), who found that impacts from baboons following planting in unfenced plots can lead to extremely high mortality rates before roots develop and cuttings secure within the soil. As is the case with elephants, no extensive quantitative studies have explored the degree to which baboons impact the survivorship of planted *P. afra* cuttings. Due to their inquisitive nature, and based on the observations made during this study, it is more likely that baboons are likely to remove cuttings out of curiosity whilst foraging or moving through an area. Alternatively, the

newly planted cuttings in open areas provide easy pickings as fresh new roots for species such as baboons, duikers, porcupines and kudu.

Apart from removing the cuttings, Starkey (2015) found that herbivory negatively impacts the below ground root carbon storage capacity of *P. afra* cuttings. This has potentially detrimental consequences for future carbon farming efforts due to the loss of potential sequestered carbon. Additionally, Berriman (2010) found that herbivory negatively influences the survivorship, basal height and stem diameter of planted *P. afra* cuttings, amongst other subtropical thicket species. Berriman (2010) suggests that brush-packing areas exposed to herbivory is a suitable alternative to animal proof enclosures as a means to increase the survivorship of *P. afra* cuttings which are to risk of herbivory. The relationship between baboons, other browsing mammals, and newly planted *P. afra* cuttings requires further investigation. The defense of spinescent plant species against the herbivory of *P. afra* cuttings during early establishment should also be investigated.

6. CONCLUSION AND RECOMMENDATIONS

The survivorship of planted *P. afra* cuttings across degraded landscapes in the GAENP showed large variations between the plots, ranging from 0 to 91 % (n = 50). There was also variation between the three sites, ranging from 35 ± 29 % at Addo Main camp, to 42 ± 12 % in Darlington, and 48 ± 23 % at Kabouga. The loss of intact vegetation and degradation of the soils in these landscapes has resulted in soil crusting which has reduced the ability of water to be captured and retained by the soil. This reduction in the ability of water to infiltrate the soils in these landscapes was found to play a significant role in the establishment and survival of planted *P. afra* cuttings across the degraded lands of the GAENP. Furthermore, woody canopy cover, litter cover, clay and sand compositions, and root mass, which are either directly or indirectly associated to infiltration, were found to have positive relationships with the survival of planted *P. afra* cuttings in Kabouga.

The plant community with the highest survivorship of planted *P. afra* (81 ± 1 %) was characterized by the retention of some canopy dominant species and higher litter cover. However, this community only contained two plots (n = 2), and therefore this result should not be considered a finding of importance. The grass species *P. maximum*, which was found to be a dominant species in this plant assemblage, had a fairly weak (r^2 = 0.172) significant positive relationship with the survivorship of planted *P. afra* cuttings across all sites, demonstrating that the species may be a potential indicator of sites conducive to *P. afra* survivorship. This may be due to *P. maximum* being associated with more mesic or less degraded sites. However, this could be an indication of low browsing pressure and should not be considered a key indicator until further investigation has been carried out. The communities with the lowest survivorship of planted *P. afra* (14 – 24 %) were characterized by a total lack of canopy species, high bareground and low pH levels. The high bareground result in exposed soils which may promote crusting, reducing infiltration. Therefore, the microclimatic function of such plant compositions may be a factor which influences infiltrability and hence influences the survivorship of planted *P. afra*. In addition, the microclimatic function of certain frost tolerant plant species could provide protection to planted *P. afra* cuttings on lower slopes during frost events. The herb, *A. semibacata* showed a positive relationship with the survivorship of planted *P. afra* cuttings and may be an indicator of good conditions for planted *P. afra* survivorship. The trends in survivorship across the plant

communities are largely due to the extent of degradation, with findings suggesting that the retention of canopy dominant species and thicket clumps provide intermediate edaphic conditions which are more suitable for the planting of *P. afra* than landscapes with little to no intact vegetation.

Boron (B) was one of the variables which best described the differences between the plant communities across all three study sites, and it had a positive correlation with two plant communities in Kabouga. These communities had the highest survivorship percentages out of all communities, with planted *P. afra* survivorship of 81 % (n = 2) and 50 % (n = 12), respectively. Boron also had a significant positive relationship with planted *P. afra* in Addo Main Camp. However, the overriding impact of elephants in Addo Main Camp but may be significantly influencing this finding. None of the other chemical or soil properties investigated had correlations with the survivorship of planted *P. afra* cuttings.

Elephants had a significant negative impact on the survivorship of planted *P. afra* cuttings, with survivorship being 50 % greater in plots excluded from elephants in Addo Main Camp. Dung counts, indicating the presence of the species within the non-excluded plots, also had a significant negative relationship with planted *P. afra* survival. Dung counts in Kabouga found a significant negative relationship between the presence of baboons and planted *P. afra* survivorship. The findings of this study suggest herbivory, particularly elephants, are the greatest drivers of planted *P. afra* cuttings mortalities in the GAENP.

Recommendations

The findings of this study suggest that the ability of water to infiltrate the soils in many of the degraded landscapes in the GAENP may play a role in the establishment and survival of planted *P. afra* cuttings. Based on these findings, infiltration, and other variables associated with infiltration, should be used as tools to ground-truth and estimate likely survivorship percentages, aiding in decision-making. Further investigation into this finding as well as alternative planting techniques should be conducted. The method of planting *P. afra* cuttings in depressions or 'micro-basins' in Camdeboo National Park has been a successful alternative to the methods used in the GAENP (Taplin, B. 2016, personal communication, cited in Mills & Robson, 2017), as well as in

the Baviaanskloof (Powell, 2009). This method has proven to harvest rainfall and increase growth rates of cuttings (Mills & Robson, 2017). As this method greatly reduces run-off, it will increase the infiltration of water into the soil and therefore increase the survivorship of planted *P. afra* cuttings. Trials focusing on planting posture, angle and planting depth will provide insight into appropriate site specific optimal rooting zones which may further improve infiltration. Scarification of cuttings has shown to increase root biomass (Norman, 2016), which will also improve water uptake into newly planted *P. afra* cuttings. This too requires further investigation. Additionally, water infiltration may improve if degraded landscapes are only planted after tillage. The loosening of surface crusts could potentially not only increase infiltration but also improve cuttings root establishment. This requires investigation.

Areas represented by more intact states, characterized by the retention of canopy dominant species, woody vegetation cover, low bareground and high cover of litter had higher survivorship of planted *P. afra* cuttings than those in more severely degraded states. In areas with retained thicket patches or clumps, further research should investigate if the survivorship of planted *P. afra* would be increased by planting in close proximity to existing 'intact' thicket patches, with subsequent planting radiating away from the thicket clumps following successful establishment of initial plantings. This gradient could potentially be characterized by certain plant species and communities which may tolerate intermediate soil characteristics between degraded and moderately intact states, and may be significant in identifying suitable areas for restoration efforts. The microclimatic function of such plant compositions may be a factor which influences infiltration and hence influences the survivorship of planted *P. afra*. In addition, the microclimatic function of certain frost tolerant plant species could provide protection to planted *P. afra* cuttings on lower slopes during frost events.

Further research should investigate the extent to which elephants impact the survivorship of planted *P. afra* cuttings, to quantify what percentage of cuttings are actively removed and fed on by elephants to understand the full extent of the damage they cause to newly planted *P. afra* cuttings. This is of vital importance to assess whether the presence of elephants, in high densities, can reduce the economic feasibility of the *en masse* plantings of *P. afra* in attempts to restore degraded landscapes. Studies should explore the degree to which baboons and other herbivores

such as duikers, porcupines and kudu, impact the survivorship of planted *P. afra* cuttings. This can be done for elephants and other herbivores using exclusion fences across varying landscapes and species compositions The use of thorn bush cuttings for brush-packing, as well as the co-planting of spinescent plant species with *P. afra* cuttings, in attempts to discourage herbivory during early *P. afra* establishment, should also be further investigated.

As the findings of this study could be heavily influenced by the impact of elephants on the survivorship of *P. afra*, and therefore trends and correlations with other variables which were explored across the three sites may have been masked by the effect of elephants in Addo Main Camp, further investigation into other variables which were investigated should be conducted. In particular, further investigation into chemical soil properties under controlled conditions should be conducted. Survivorship of planted *P. afra* cuttings should be investigated using different soil types using potting or transplant experiments under controlled climatic conditions. This could overcome many of the shortcomings and limitations of this study, including rainfall variance and frost tolerance, as variables could be investigated individually.

Stakeholders and decision-makers involved in the STRP should incorporate pre-planting feasibility studies to determine the likelihood of survivorship of *en masse* planting of *P. afra* cuttings under varying environmental conditions. Future research should aim to explore the possibility of developing matrices which plot likely survivorship percentages with parameters of measurable variables, such as infiltration or browsing densities. This will allow management decisions to be made based on informed knowledge.

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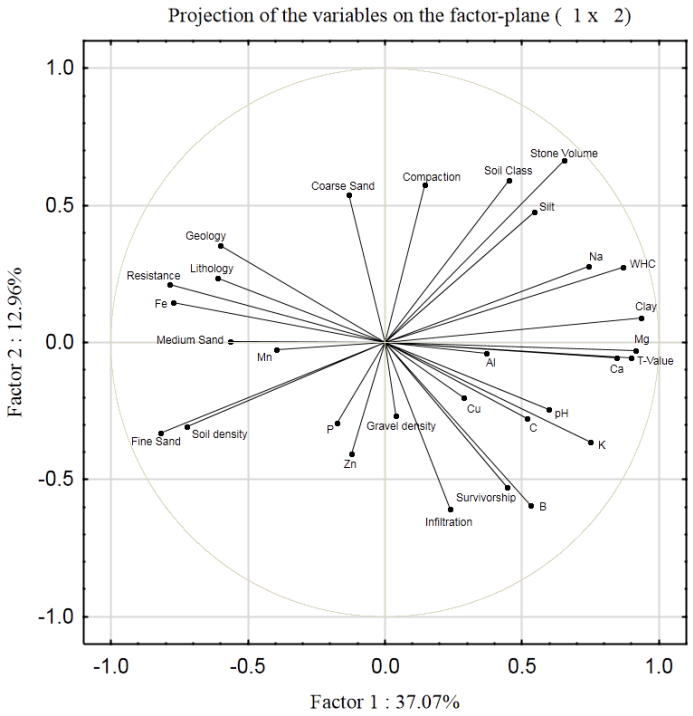
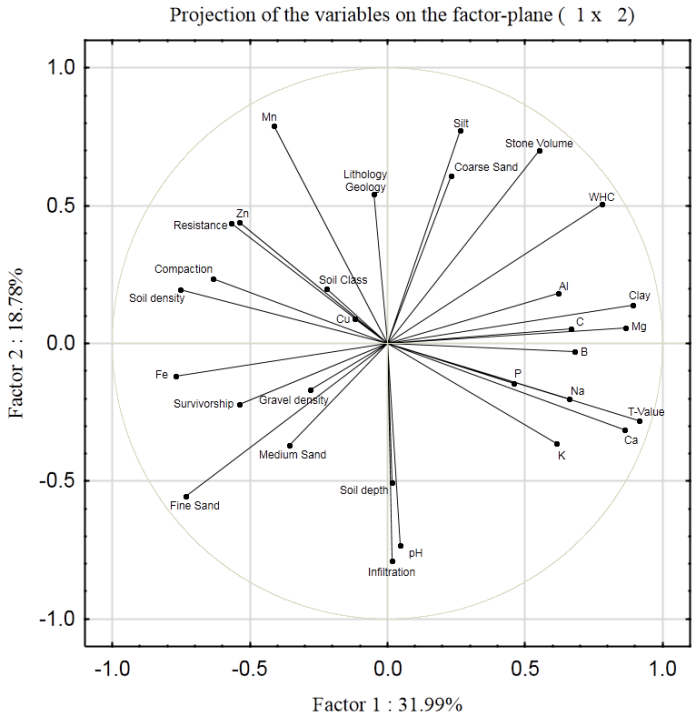
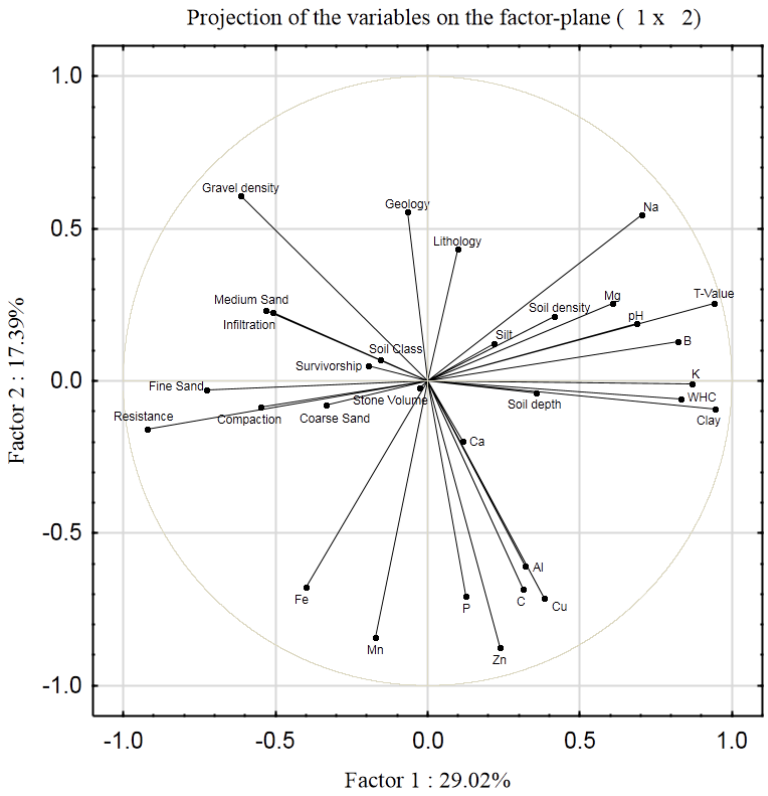
APPENDIX A



Principal Component Analysis (PCA) of soil properties at Addo (n =17).



Principal Component Analysis (PCA) of soil properties at Kabouga (n = 19).



Principal Component Analysis (PCA) of soil properties at Darlington (n= 14).

APPENDIX B: PLANT SPECIES LIST

A = Addo, K = Kabouga, D = Darlington

Genus	***Species***	**Guild**	**Site**
Abutilon	*sonneratianum*	Herb	A, K,D
Aizoon	*rigidum*	Succulent herb	D
Albuca	*bakeri (c.f)*	Geophyte	D
Albuca	*sp. 2*	Geophyte	K
Albuca	*sp. 1*	Geophyte	A
Ammocharis	*coranica*	Geophyte	A
Anacampseros	*arachnoides*	Succulent herb	D
Anagallis	*arvensis*	Herb	A
Arctotheca	*calendula*	Herb	A
Arctotheca	*prostrata*	Herb	A
Arctotis	*arctotoides*	Herb	A, K
Arctotis	*sp. 1*	Herb	K
Aristida	*congesta*	Graminoid	D
Asparagus	*aethiopicus*	Climber	A, K, D
Asparagus	*africanus*	Woody shrub	K
Asparagus	*capensis*	Woody shrub	K, D
Asparagus	*crassicladus*	Dwarf shrub	K, D
Asparagus	*retrofractus*	Woody shrub	D
Asparagus	*striatus*	Dwarf shrub	A, K, D
Asparagus	*suavolens*	Woody shrub	A, K, D
Asparagus	*sp. 1*	Dwarf shrub	K
Aspargus	*mucronatus*	Woody shrub	A
Atriplex	*lindleyi* subsp. *Inflata*	Herb	D
Atriplex	*semibaccata*	Herb	A, K
Azima	*tetracantha*	Woody shrub	A, K
Barleria	*irritans*	Dwarf shrub	A, D
Bergeranthus	*vespertinus*	Succulent shrub	K
Blepharis	*capensis*	Dwarf shrub	A, K, D
Boscia	*oleoides*	Woody tree	D
Bothriochloa	*insculpta*	Graminoid	D
Bromus	*catharticus*	Graminoid	A
Bulbine	*anyssinica*	Geophyte	A
Bulbine	*frutescens*	Geophyte	A
Bulbine	*narcissifolia*	Geophyte	A, K
Capparis	*sepiaria var. citrifolia*	woody shrub	K
Carissa	*haematocarpa*	woody shrub	K
Cenchrus	*ciliaris*	Graminoid	D
Chascanum	*cuneifolium*	Dwarf shrub	D

Chenopodiaceae	*sp. 1*	Herb	K
Chenopodium	*album*	Herb	A
Chenopodium	*mucronatum*	Herb	A, D
Cinerarea	*platycarpa*	Herb	A, K
Cirsium	*vulgare*	Herb	A
Cissampelos	*capensis*	Climber	A, D
Commelina	*africana*	Herb	A
Commelina	*benghalensis*	Herb	A
Conyza	*bonariensis*	Herb	A, K, D
Conyza	*obscura*	Herb	A
Crassula	*corallina*	Succulent herb	D
Crassula	*dependens*	Succulent shrub	A
Crassula	*expansa*	Succulent herb	A, K
Crassula	*mesembryanthemoides*	Succulent shrub	A, K
Crassula	*muscosa*	Succulent herb	A, K. D
Crassulla	*subaphylla*	Succulent shrub	A
Cuspidia	*cernua*	Herb	A, D
Cyanella	*lutea*	Geophyte	A, D
Cynanchum	*capense*	Climber	A
Cynodon	*dactylon*	Graminoid	A, K, D
Cynodon	*incompletus*	Graminoid	A
Cyperus	*rubicundus*	Herb	A, K, D
Cyperus	*usitatus*	Herb	K
Delosperma	*echinatum*	Succulent shrub	K
Delosperma	*fructescens*	Succulent shrub	K
Delosperma	*sp. 1*	Succulent shrub	K
Delosperma	*subincanum*	Succulent shrub	K
Digitaria	*argryograpta*	Graminoid	D
Digitaria	*eriantha*	Graminoid	A, K, D
Diospyros	*austro-africana*	Woody shrub	D
Dolichos	*falciformis*	Herb	K
Drimia	*anomala*	Geophyte	A
Drimia	*elata*	Geophyte	K
Drimia	*haworthioides*	Geophyte	K
Drosanthemum	*hispidum*	Succulent shrub	A, K
Drosanthemum	*lique*	Succulent shrub	A, D
Duvalia	*caespitosa*	Succulent shrub	D
Eberlanzia	*ferox*	Succulent shrub	D
Ehrharta	*calycina*	Graminoid	D
Emex	*australis*	Herb	A
Empodium	*pilicatum*	Geophyte	K
Empodium	*sp. 1*	Geophyte	K
Enneapogon	*scaber*	Graminoid	D

Enneapogon	*scoparius*	Graminoid	K, D
Eragrostis	*capensis*	Graminoid	A
Eragrostis	*curvula*	Graminoid	A, K, D
Eragrostis	*obtusa*	Graminoid	A, K, D
Eriospermum	*brevipes*	Geophyte	D
Eriospermum	*porphyrium (c.f)*	Geophyte	K
Euclea	*undulata*	Woody tree	K
Euphorbia	*catervifolia*	Succulent shrub	D
Euphorbia	*coerulescens*	Succulent shrub	D
Euphorbia	*mauritanica*	Succulent shrub	A
Euphorbia	*rhombifolia*	Succulent shrub	A
Exomus	*microphylla*	Dwarf shrub	A, K
Felicia	*aethiopicus (c.f)*	Dwarf shrub	K
Felicia	*dubia*	Dwarf shrub	A
Felicia	*fascicularis*	Dwarf shrub	A
Felicia	*filifolia*	Dwarf shrub	A, K, D
Felicia	*hirsuta*	Dwarf shrub	D
Felicia	*muricata*	Dwarf shrub	A, K
Felicia	*sp. 1*	Dwarf shrub	K
Fingeruthia	*africana*	Graminoid	D
Galenia	*papulosa*	Succulent herb	K
Galenia	*pubescens*	Dwarf shrub	A, K
Galenia	*secunda*	Dwarf shrub	A, K, D
Garuleum	*bipinnatum*	Dwarf shrub	D
Gazania	*linearis*	Herb	A
Grewia	*robusta*	Woody shrub	A, K, D
Gymnosporia	*polyacantha*	Woody shrub	A
Gymnosporia	*szyszylowiczii*	Woody shrub	D
Hebenstreitia	*dura*	Dwarf shrub	A
Helichrysum	*hirsuta*	Dwarf shrub	A
Helichrysum	*pentzioides (c.f)*	Dwarf shrub	D
Helichrysum	*rosum var. arcuatum*	Dwarf shrub	A, K
Helichrysum	*rosum var. asculata*	Dwarf shrub	A
Helichrysum	*rosum var. rosum*	Dwarf shrub	K, D
Helichrysum	*zeyheri*	Dwarf shrub	D
Hermannia	*althaeoides*	Dwarf shrub	A, K, D
Hermannia	*coccocarpa*	Herb	D
Hermannia	*cuneifolia*	Dwarf shrub	A, D
Hermannia	*desertorum*	Dwarf shrub	D
Hermannia	*filifolia*	Dwarf shrub	D
Hermannia	*fruticosa*	Dwarf shrub	A
Hermannia	*pulverata*	Dwarf shrub	K
Hermannia	*vestita*	Dwarf shrub	D

Hibiscus	*aridus*	Dwarf shrub	K
Hypertelis	*trachysperma*	Dwarf shrub	A
Hypoestes	*aristata*	Woody shrub	A, K
Indigofera	*disticha*	Herb	K, D
Indigofera	*procumbens*	Herb	A
Indigofera	*pungens*	Dwarf shrub	D
Isoglossa	*origanoides*	Herb	K
Jamesbrittenia	*aspalathoides*	Dwarf shrub	D
Jamesbrittenia	*atropurpurea*	Dwarf shrub	D
Jamesbrittennia	*foliolosa*	Dwarf shrub	A
Jamesbrittennia	*microphylla*	Dwarf shrub	A
Jatropha	*capensis*	Succulent shrub	K, D
Justicia	*orchioides*	Dwarf shrub	K, D
Kalanchoe	*rotundifolia*	Succulent shrub	K
Kedrostis	*africana*	Climber	K
Lachenalia	*campanulata*	Geophyte	K
Lactuca	*capensis*	Herb	A
Lasiopogon	*glomeratus*	Herb	D
Ledebouria	*ensifolia*	Geophyte	D
Ledebouria	*ovatifolia*	Geophyte	D
Ledebouria	*sp. 1*	Geophyte	A
Ledebouria	*sp. 2*	Geophyte	K
Leidesia	*obtusa*	Herb	A
Lepidium	*africanum*	Herb	A, D
Lepidium	*ecklonii*	Herb	K
Lessertia	*pauciflora*	Herb	A, D
Leucas	*capensis*	Dwarf shrub	A, K
Limeum	*aethiopicum*	Dwarf shrub	D
Lotononis	*laxa*	Herb	A, D
Lotononis	*pungens*	Herb	A, K
Lycium	*cinereum*	Dwarf shrub	A, D
Lycium	*ferocissimum*	Woody shrub	A, K, D
Lycium	*horridum*	Woody shrub	K, D
Lycium	*oxycarpum*	Woody tree	A, K
Malephora	*crocea*	Succulent shrub	D
Malephora	*sp. 1*	Succulent shrub	D
Malva	*parviflora*	Herb	K
Mariscus	*capensis*	Herb	K
Medicago	*aschersoniana*	Herb	A
Melenis	*repens*	Graminoid	A
Melolobium	*exudans*	Dwarf shrub	A
Mesembryanthemum	*aitonis*	Succulent shrub	A, D
Mesembryanthemum	*guecherianum*	Succulent shrub	D

Mesembryanthemum	*junceum*	Succulent shrub	D
Mestoklema	*copiosum*	Succulent shrub	A, K
Mestoklema	*elatum*	Succulent shrub	A, D
Mestoklema	*tuberosum*	Succulent shrub	A, D
Mohria	*caffrorum*	Herb	K
Moraea	*algoensis*	Geophyte	A
Myrsiphyllum	*asparagoides*	Climber	K
Nemesia	*capensis*	Herb	A, D
Oenothera	*rosea*	Herb	A
Oligocarpus	*calendulaceus*	Herb	A, K, D
Opuntia	*aurantica*	Succulent shrub	K, D
Opuntia	*ficus-indica*	Succulent shrub	K
Ornithogalum	*sp. 1*	Geophyte	D
Oxalis	*commutate*	Herb	D
Oxalis	*imbricate*	Herb	K
Oxalis	*sp. 1*	Herb	A
Oxalis	*stellata*	Herb	K, D
Oxalis	*stenorryncha*	Herb	A, K
Panicum	*coloratum*	Graminoid	A
Panicum	*deustum*	Graminoid	A, D
Panicum	*maximum*	Graminoid	A, K, D
Pappea	*capensis*	Woody tree	K
Pelargonium	*alchemilloides*	Dwarf shrub	A
Pentzia	*globifera*	Shrub	A
Pentzia	*incana*	Shrub	A, K, D
Pentzia	*lanata (c.f)*	Shrub	A
Pharnaceum	*salsoloides*	Herb	K
Phymaspermum	*aciculare*	Dwarf shrub	D
Plantago	*lanceolata*	Herb	A
Plumbago	*auriculata*	Shrub	A
Poaceae	*sp. 1*	Graminoid	A
Poaceae	*sp. 2*	Graminoid	A
Pollichia	*campestris (c.f)*	Herb	K, D
Polygala	*asbestina*	Dwarf shrub	A, K
Polygala	*leptophylla*	Dwarf shrub	D
Polygonum	*aviculare*	Herb	A
Portulaca	*oleracea*	Herb	D
Portulacaria	*afra*	Succulent shrub	K
Pseudognapholium	*undulatum*	Herb	A
Psilocaulon	*granulicaule*	Succulent shrub	A, K
Putterlickia	*pyracantha*	Woody shrub	K
Rhigozum	*obovatum*	Woody shrub	K, D
Rosenia	*humilis*	Dwarf shrub	D

Rumex	*sagittatus (c.f)*	Climber	D
Ruschia	*sp. 1*	Succulent shrub	A
Salsola	*aphylla*	Shrub	D
Sansevieria	*hyacinthoides*	Geophyte	A, K
Schotia	*afra*	Woody tree	K
Scirpus	*globiceps*	Herb	A
Searsia	*longispina*	Woody tree	K
Searsia	*pallens*	Woody tree	A, D
Searsia	*refracta*	Woody tree	D
Selago	*albida*	Dwarf shrub	A
Selago	*geniculata*	Dwarf shrub	A, K, D
Selago	*saxatilis*	Dwarf shrub	D
Selago	*sp. 1*	Dwarf shrub	A
Senecio	*inaequidens*	Herb	A
Senecio	*radicans*	Succulent herb	A, D
Setaria	*sp. 1*	Graminoid	A
Setaria	*sphacelata*	Graminoid	A
Solanum	*linnaenum*	Shrub	A
Solanum	*tormentosum*	Shrub	A
Sonchus	*oleraceus*	Herb	A
Sporobolus	*africanus*	Graminoid	A
Sporobolus	*nitens*	Graminoid	K, D
Stachys	*aethiopica*	Herb	K, D
Sutera	*campanulata*	Herb	A, K
Sutera	*halmifolia*	Herb	K
Sutera	*polyantha*	Herb	A
Tephrosia	*glomeratus*	Herb	A
Teucrium	*africanum*	Herb	A, D
Themeda	*triandra*	Graminoid	D
Thesium	*hystrix*	Dwarf shrub	D
Thesium	*lineatum*	Dwarf shrub	D
Trachyandra	*affinis*	Geophyte	A
Trachyandra	*sp. 1*	Geophyte	A
Tragus	*berteronianus*	Graminoid	K, D
Trichodiadema	*bulbosum*	Succulent shrub	A
Trichodiadema	*setuliferum*	Succulent shrub	D
Trichogyne	*verticillata*	Herb	A, K, D
Tripteris	*sinuata*	Dwarf shrub	D
Troglophyton	*capillaceum*	Herb	D
Unidentified	*Poaceae sp. 1*	Graminoid	K
Unidentified	*Poaceae sp. 2*	Graminoid	K
Unidentified	*sp. 2*	Herb	K
Vachellia	*karroo*	Woody tree	A, K, D

Viscum	*obscurum*	Woody shrub	D
Viscum	*rotundifolium*	Woody shrub	D
Wahlenbergia	*banksiana*	Herb	A, K
Zygophyllum	*retrofractum*	Succulent shrub	D