IMPACTS OF FORAGING BEHAVIOR BY CAPE PORCUPINES AND THEIR EFFECTS ON NUTRIENT CYCLING IN MESIC SAVANNAS

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Abstract

Through feeding and associated activities, herbivores play a major role in determining the structure of savannas. The Cape porcupine (*Hystrix africaeaustralis*) is a semi-fossorial, large (ca. 12 kg) herbivorous rodent with a generalist foraging strategy that feeds on plant parts occurring above- and below ground. Subterranean foraging by porcupine may influence biotic and abiotic processes in that area. The extent of soil and vegetation perturbation may be pervasive on the landscape so that these animals may be considered as ecosystem engineers. The digging activities of ecosystem engineers are significant as they influence soil properties (e.g. nutrient cycling) including germination of trapped seeds and establishment of seedlings. These changes may occur at small and large scale on a landscape. The utilisation of woody vegetation and ecosystem engineering by such animals, particularly by shy and nocturnal species, is understudied in African savannas. The study was aimed at: (1) quantifying the extent of herbivory by the porcupines on target trees during the wet and dry season in three mesic savanna sites, and (2) evaluating the effects of Cape porcupines' digging on nutrient cycling (total carbon and total nitrogen) and quantify establishment of vegetation on the mounds. Sampling was undertaken at three mesic savanna sites in South Africa: (i) Roodeplaat Farm in Gauteng Province; (ii) Goss Game Farm; and (iii) Bisley Valley Nature Reserve, both in KwaZulu-Natal Province. I used 30 m × 30 m plots to quantify porcupine foraging holes and bark damage on adult trees at Roodeplaat and Goss while 10 m × 10 m plots were used at Bisley where porcupines foraged on seedlings and saplings of woody plants. I also collected porcupine dung samples over the dry and wet season for micromorphological examination of porcupine diet. I collected soil samples from the mound soil of foraging holes and from adjacent locations within 0.5 m of the hole for analysis of amounts of total carbon and total nitrogen. Measurements of foraging holes comprised of two perpendicular diameters on the soil surface and the maximum depth. Porcupines utilised different tree species of various sizes at the three sites while targeting specific parts of these trees. At Roodeplaat, porcupines targeted *Vachellia robusta* on which they consumed the trunk part immediately below ground, whereas at Bisley, roots and the lower trunk of *V. nilotica* seedlings and saplings were utilised, also through digging holes while the bark of the lower trunk (up to 0.7 m) of *Spirostachys africana* trees was stripped off at Goss. I found that 70% of young *V. nilotica* trees in or adjacent to holes in Bisley were scarred or destroyed as a result of porcupine feeding on them, while 16% of *S. africana* trees were wounded at Goss. Only 7% of *V. robusta* trees were damaged at Roodeplaat. In Bisley, I found that grasses and forbs established faster on the mound than on the surrounds, i.e. seedlings germinated first on the mound than the adjacent not disturbed soil. I also found that foraging holes provide shelter to other animals especially those from the arthropod group e.g. spiders. Amounts of total carbon and total nitrogen were similar between the mounds and undug soil. These findings are discussed in terms of nutrient cycling through digging, breaking down of plant parts and herbivore-induced mortality of main tree species. I argue that tree thinning from ringbarking by porcupine through their foraging activities ameliorates woody plant encroachment in mesic savannas.

STUDENT DECLARATION

Utilisation of woody plants by the Cape porcupine in mesic savannas

I, **Unathi M. Kraai**, student number: **219095954** declare that:

i. The research reported in this dissertation, except where otherwise indicated, is the result of my own endeavours at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg.

ii. This dissertation has not been submitted for any degree or examination at any other university.

iii. This dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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DECLARATION BY SUPERVISORS

We hereby declare that we acted as Supervisors of this MSc student:

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Regular consultation took place between the student and ourselves throughout the investigation. We advised the student to the best of our ability and approved the final document for submission to the College of Agriculture, Engineering and Science Higher Degrees Office for examination by the [redacted] University appointed examiners.

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Chapter 1: General introduction and literature review

Background

Savannas are the second largest terrestrial biome covering over 30% of the earths surface, with Africa having the largest area of savannas estimated to cover about 65% of the continent (Snyman, 2003; Sankaran et al., 2008). In South Africa, savannas (including grasslands) make up a large portion (70%) of the surface of the country, which makes them the largest ecosystem used by animals and humans (Snyman, 2003; Cho and Ramoelo, 2019). The savanna biome is characterised by woody plants (i.e. trees and shrubs) and herbaceous plants (largely grasses but also many non-grass plants commonly referred to as forbs). The savannas are of biodiversity conservation importance because of the fauna and flora they support (Gillson, 2015; Bond, 2016; McCleery et al., 2018). South Africa is rich in flora and fauna exhibiting some of the highest species densities in the world, and some of these are found in the savanna which supports different plant and animal-life forms (Berjak et al., 2011; McCleery et al., 2018). The climate of savannas has two distinct seasons made up of a wet (or summer) and dry (or winter) (Mucina and Rutherford, 2006). The structure and functioning of savannas are mainly determined by resource availability (moisture and soil nutrients) (Mucina and Rutherford, 2006), while disturbance drivers such as fire and herbivory are secondary determinants which shape savannas (Scogings, 2014). Resources determine the vegetation of the savanna biome, while drivers reduce or minimise the vegetation cover (Cumming et al., 1997). Unlike fire, herbivores are selective in the plants they feed on and this affects the plant community of a region (Bonnington et al., 2009). However, both fire and herbivory may compete for the same herbaceous resources and as such are able to shape the structure of the savanna. Lack of fires and loss of megaherbivores particularly browsers have been linked to increased woody plants in savannas, a phenomenon called bush or woody plant encroachment (Moleele et al., 2002; Buitenwerf et al., 2012; Ward et al., 2014). Because of the resources and services savannas provide to humans and animals, they are under enormous pressure due to agricultural activities (crop production) as well as herbaceous plants for grazing and wood for firewood (O'Connor, 2014; Ramesh and Downs, 2014; McCleery et al., 2018). Over-utilisation of pastures for grazing leading to degraded vegetation as well as erosion are visible symptoms of disturbed savannas (Smit et al., 1999; Bonnington et al., 2009; O'Connor et al., 2014).

Bush encroachment is considered as one of the main problems facing savanna rangelands in southern Africa (Ward et al., 2014). This problem is reportedly about 100 years old in southern African rangelands. Beside Africa, bush encroachment is also a problem in Australia and North America (van der Westhuizen et al., 1999; O'Connor et al., 2014). Bush encroachment is the increase of woody vegetation at the cost of herbaceous vegetation. The occurrence of this phenomena is reported in all savannas including arid and semi-arid savannas (Blaum et al., 2007; O'Connor et al., 2014). The impact of vegetation change in savannas from herbaceous to woody cover may intensify with time due to changes in atmospheric conditions, mismanagement of fire, overgrazing and removal of browsers (Bond et al., 2000; Blaum et al., 2007, Bonnington et al., 2009; Strydom et al., 2019). These changes apply in Africa and present challenges to ecosystem functioning and health.

Large herbivores have strategies to deal with seasonal changes, which result in varying distribution of herbaceous and woody plants (Parker and Bernard, 2005; Fischhoff et al., 2007). Like all living organisms' herbivores have certain nutritional requirements and dietary preferences. For instance, grazers such as the African buffalo *Syncerus caffer* prefer to feed on nutritious grasses (Fischhoff et al., 2007). Mixed feeders, because of their dietary strategy, feed on both graze and browse material. The intake of grasses and browsing plants may be influenced by season. For example, impala *Aepyceros melampus* feed on nutritious grasses in the wet season and switch to browse in the dry season, when the grasses lose nutrition (Waldram et al., 2008). Browsers like giraffes *Giraffa camelopardis* on the other hand feed exclusively on woody plants (Parker and Bernard, 2005). Amongst the herbivores that inhabit savannas, are semi-fossorial mammals which are nocturnal and very little has been documented about these animals (Bragg et al., 2005). Semi-fossorial mammals are facultative burrowers, foraging underground as well as above ground, and are widely distributed in terrestrial ecosystems. Semi-fossorial animals occur in varying ecosystems (de Graaf, 1981; de Villiers and van Aarde, 1994; Hagenah et al., 2009). The Cape porcupine (*Hystrix africaeaustralis*) is an example of a semi-fossorial herbivore which is found in southern Africa (de Graff,1981). Digging activities of the species make it an important pest in agriculture, but like other burrowing rodents, it may have important landscape level impacts in natural ecosystems (e.g. Alkon, 1999; de Villiers and van Aarde, 1994; Hagenah et al., 2009).

Determinants of savanna structure

Savannas are distinct from other biomes through the coexistence of trees and grasses (Sankaran et al., 2004). The structure of savannas if affected and influenced by a variety of factors such as fire, herbivory, precipitation, and soil nutrients (Sankaran et al., 2008). The amount of rainfall received in a particular savanna may influence soil moisture and accumulation of organic matter, which may ultimately influence soil texture and growth of plants (Mucina and Rutherford, 2006). The variation in spatial and temporal rainfall in savannas lead to changes in the composition, diversity and productivity of vegetation (Mucina and Rutherford, 2006). Fires have been used over the years in savannas as they also play a role in decreasing woody plant establishment (Smit and Rethman, 1999). As a result, the application of frequent fires on savannas decreases woody plants, which favours grasses (Smit and Rethman, 1999). Fire is also used to increase the nutritional status of vegetation for herbivores (Little et al., 2015). Low herbivore pressure in grassland and savannas may result in increased grass biomass, which in turns fuels fires (Wigley et al., 2010). If intense, fires may result in high mortality of trees thus favouring the grasses. Low grazing pressure by herbivores may therefore facilitate hot fires. Larger herbivores such the African elephant *Loxodonta africana* may be effective at killing trees in savannas through uprooting (Morrison et al., 2016). This may compromise woody plants, particularly those preferred as food by elephants, as well as the general community structure of trees (Cumming et al., 1997; Mapaure and Campbell, 2002). The occurrence of herbivores in an ecosystem may have both negative and positive effects. For example, herbivores play a role in nutrient cycling and seed dispersal, which may facilitate the growth of encroaching woody plants (Wilby et al., 2001; Snyman, 2003).

Effects of herbivory on woody plants

Browsing can lead to death of trees or eliminate competitive plant species, while encouraging the less competitive species to establish (Belsky, 1994). Herbivore effects on trees depends on the magnitude and frequency of damage, the plant’s growing stage and resource relationships at the time of herbivory, as well as the plant tissues damaged or removed (Wilby et al., 2001; Parker and Bernard, 2005). Herbivore-induced damage to the plant negatively affects growth and reproduction of those parts which may, however, be offset by compensatory growth, but damage to the main stem may be fatal to the tree (Belsky, 1994). Many woody species in the semi-arid savannas can recover after browsing and resprout (Scogings, 2014). The ability of trees to recover from damage by herbivores may be influenced by the tree's ability to mobilise stored nutrient reserves to resprout from surviving buds (Berjak et al., 2011). Vegetation survival after herbivory depends on the intensity and the rate of herbivory especially for that particular species (Scogings, 2014). Herbivory mediates the balance between trees and grasses in savannas so that grazing reduces grass vigour and biomass which provides competitive release to establishing trees (Higgins et al., 2000). However, in wetter sites, fires and browsers decrease tree recruitment (Roques et al., 2001). Browsers can alter tree establishment through feeding on the young plants thereby slowing growth, or leading to death of the plant (Higgins et al., 2000). In more mesic areas sustained grazing pressure by livestock can reduce the grass layer leading to lower fuel loads and hence lower fire intensity (O'Connor et al., 2014); potentially enhancing the recruitment of woody saplings (Higgins et al., 2000; O'Connor et al., 2014). Browsing pressure by free ranging indigenous antelope acts directly on the woody component of the vegetation, limiting growth and potentially shaping savanna structure (Scogings, 2014).

Woody plant encroachment

Woody plant encroachment in the savannas and grasslands of southern Africa has been of major interest for rangeland management and ecological research since the early 1900s (Moleele et al., 2001; Wigley et al., 2010; Ward et al., 2014). The species of trees or shrubs responsible vary with area, but is dominated by *Vachellia* species (Shaw et al., 2002; O'Connor et al., 2014). The increase in woody plant cover is a global phenomenon that is attributed to certain factors (Wigley et al., 2010; Eldridge et al., 2011). These include changes in rainfall patterns (Roques et al., 2001), altered fire regimes (Roques et al., 2001), decreasing numbers of indigenous browsers (O'Connor et al., 2014), changes to grazer: browser ratios (Sankaran et al., 2008; Wigley et al., 2010), soil nutrients and soil structure and reduced fuel wood collection due to urbanisation (Russell and Ward, 2014). In the last 50 years, there has been growing emphasis on the roles of global scale drivers (e.g. climate change, greater amounts of CO_2 in the atmosphere and nitrogen deposition) in the increasing density of woody plants in savannas and grasslands (Wigley et al., 2010; Buitenwerf et al., 2012; Devine et al., 2017, Dlamini et al., 2019). However, there are also reports of diminishing woody plant cover or loss of large trees in some parts of Africa which is driven by elephant herbivory and greater use of fire (Yeaton, 1988).

Future potential consequences of woody plant encroachment and the expansion of woodland into grasslands may have many ecological and social unfavorable consequences. It has been shown to compromise ecosystem service delivery in rangelands and directly impact human livelihoods – largely through the impacts of canopy cover on the herbaceous layer resulting in less grazing pastures for livestock (Moleele et al., 2001; Ward et al., 2014).

Impacts of semi-fossorial foraging animals on terrestrial ecosystems

Some organisms can control the availability of resources for other organisms through altering the biotic or abiotic environment. Large mammalian herbivores may affect the habitat through selective feeding on a specific plant species and plant parts, and by so doing disturb the plants and the soil on which the plants are rooted (Bragg et al., 2005; Louw et al., 2017). With their foraging activities, large semi-fossorial herbivores can structure plant communities or entire ecosystems (Bragg et al., 2005; Clark et al., 2016). Bioturbations cause spatial and temporal heterogeneity in the structure and dynamics of biological communities, i.e. the holes they dig in search of food later become filled with litter, and seeds may also fall into the pits whose temperature and moisture conditions may promote plant species regeneration (Alkon, 1999; Mori et al., 2017). Cape porcupines are generalist feeders with a preference for geophytes but also occasionally feed on roots or just above ground parts of some trees. For example, the Cape porcupine has been reported to feed on *Burkea africana*, *Vachellia* spp. and *Dombeya rotundifolia* trees (Yeaton, 1988; de Villiers and de van Aarde, 1994).

Through senescence, living organisms and their materials eventually become detritus and, if not blown away by wind or washed away by run-off water, end up in the soil (Seastedt, 1984). Decomposition breaks down plant and animal litter and releases organic and inorganic elements. For example, the carbon released from plant materials can be sequestered in the soil (Clark et al., 2016; Dlamini et al., 2019). Decomposition and associated nutrient cycling are important in maintaining productivity in natural ecosystems (Eldridge et al., 2011). Many animal groups ranging from arthropods to vertebrates play crucial roles in nutrient cycling at global scales. For example, the digging and burrowing activities of many species of mammals have been identified as facilitating biogeochemical cycling at landscape scales (Alkon, 1999; Eldridge et al., 2011). In the digs and burrows, soil organisms further break down organic materials and enhance decomposition rates which ultimately influence nutrient cycling (Clark et al., 2016). Although the role of digging or burrowing animals in breaking down organic matter has rarely been quantified, digging mammals alter soil conditions in multiple ways (Eldridge et al., 2011). Herbivore activities such as consumption of plants and digging of soil may influence abiotic processes leading to the formation of patches which heterogenises the landscape in various ways (de Villiers and van Aarde, 1994; Louw et al., 2017). Such habitat patches may differ substantially in terms of soil structure, aeration, fertility and water-holding capacity (de Villiers and van Aarde, 1994; Grossman et al., 2019).

Taxonomy and ecology of the Cape porcupine

Old World porcupines belong in the Order Rodentia and are the largest rodents (Mohamed, 2011). The family Hystricidea if is further divided into two genera: *Atherurus* and *Hystrix*. There are eight living species in the genus *Hystrix* namely: *H. africaeaustralis, H. brachyura, H. crassispinis, H. cristata, H. indica, H. javanica, H. pumila,* and *H. sumatrae.* Two of these species are found in Africa the crested porcupine (*H. cristata)* and the Cape porcupine (*H. africaeaustralis)*. The Cape porcupine occurs mostly in the southern parts of Africa, but both species are found in East Africa (Barthelmess, 2006). Cape porcupines are terrestrial herbivorous rodents (diet includes bark, bulbs, fruits, leaves, roots, shoots, and tubers) and can have a body mass of up to 24 kg (Bragg, 2003, Barthelmess, 2006). Cape porcupines stay in burrows or caves. Porcupine either dig their own burrows or occupy extensive burrows dug by aardvarks *(Orycteropus afer)* (de Graaf, 1981). Sexual maturity is reached during the second year of life for females and about 18 months for males (van Aarde, 1986). Porcupines are considered agricultural pests and are hunted for their meat.

Rationale

Herbivory is important in structuring plant communities (Wilby et al., 2001). While the influences of large mammals that are active during the day, such as the elephant (*Loxodonta africana*), in structuring vegetation, are evident in the ecosystems in which they occur (e.g. Mapaure and Campbell 2002; Pringle et al., 2014; Ramesh and Down, 2014), the role of smaller and nocturnal mammals such as the Cape porcupine (*Hystrix africaeaustralis*), are less apparent. Yet, the digging activities of porcupines, coupled with their feeding on roots of trees, may lead to tree felling and subsequent tree death in ways akin to elephant activity, albeit at much smaller scales. Also, porcupines are seed predators (see Beaune et al., 2012; Mori et al., 2017). The effects of porcupines on soil and vegetation may be substantial (Alkon, 1999). Likewise, the Cape porcupine ring-barks several tree species including *Cordyla africana, Spirostachys africana,* and *Strychnos pungens,* among others (de Graaf 1981; de Villiers and van Aarde, 1994), which may lead to mortality of the trees. For example, at Roodeplaat Farm in Gauteng Province of South Africa, porcupines dig out and feed on roots of *Vachellia* spp. leading to mortality of trees. Several species of *Vachellia* and *Senegalia* are important woody plant encroachers in savannas (de Villiers et al., 1994). Herbivore-mediated mortality of trees may influence the demography of the species and may affect the diversity of plants in impacted ecosystems. However, digging by these animals may create sites where organic matter, water, and seeds accumulate, which consequently increase seed germination and plant recruitment (Bragg et al., 2005; Clark et al., 2016; Louw et al., 2017).

Seasonal changes in forage availability have been attributed for the seasonal migration of many species of large ungulate herbivores in many terrestrial ecosystems (Holdo et al., 2008). Unlike ungulate herbivores who migrate between seasons, large rodents like the Cape porcupines do not migrate with seasons and as such, must utilise available food source in cases of scarce resources. Porcupines are known to utilise underground plant parts as their staple food, but also utilise woody plant material and as such are pests in agriculture and commercial forestry (Yeaton, 1988; de Villiers et al., 1994).

Through digging for roots, bulbs and feeding off the bark of selected tree species, the foraging activities of porcupines may lead to mortality of trees (de Graaf, 1981; Alkon, 1999), which is desirable in bush encroached ecosystems, particularly if the impacted trees are encroachers. However, the same digging and burrowing activities have been associated with the establishment of safe sites for germination of seeds because the soils at dug out sites tend to be richer in amounts of seeds, soil organic matter and nitrogen than non-disturbed sites (de Villiers and van Aarde, 1994; Bragg et al., 2005; Louw et al., 2017). The magnitudes of these contrasting effects of the Cape porcupine in plant dynamics in mesic savannas is largely unknown. The nocturnal habit of the Cape porcupine makes it a difficult study species. Therefore, this study sought to determine the effects of porcupine foraging activities on woody plants and soils at impacted sites.

Aim of the study

The aim of the study was to determine the effects of the Cape porcupine foraging behavior on woody species and soil nutrient status at Roodeplaat Experimental Farm (Gauteng), Goss Game Farm and Bisley Valley Nature Reserve (KwaZulu-Natal).

Objectives

1. To determine the extent of herbivory by Cape porcupines on the affected tree species and quantify how much of the woody material contributes to the porcupines' diet during the dry and wet season.
2. To assess the effects of the Cape porcupine's digging activities on soil disturbance, soil nutrients and mortality of targeted tree species.

Structure of the dissertation

This thesis is written in a paper format, except Chapter 1 (General introduction and literature review) and Chapter 4 (General conclusions). The experimental chapters are each composed of an introduction, methods, results and a discussion. Each experimental chapter is a manuscript in preparation for publication to a journal.

Chapter 1 covers the general introduction and literature review on savannas, modification of savannas through bush encroachment, and herbivory as a determinant which shapes the savannas. It also describes the significance of the study, including the aim and specific objectives.

Chapter 2 reports on the targeted tree species which are utilised by Cape porcupine in three savanna habitats, how much of these make up the diet of the porcupine during the dry and wet season. It addressed objective one.

Chapter 3 addresses objective two of the study and reports on how diggings made by porcupines modify the landscape.

Chapter 4 entails the major findings, general conclusion and recommendations of the study.

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Chapter 2: Utilisation of woody plants by the Cape porcupine in mesic savannas may ameliorate effects of bush encroachment

Abstract

Herbivory plays a fundamental role in determining the structure of savannas. The impacts of small herbivores on trees in savannas remain poorly understood because most research attention focuses on large herbivores such as elephants whose destructive effects on trees can be pervasive at landscape scales. Cape porcupines are generalist herbivores foraging on herbaceous as well as woody plants but their feeding activities on woody plants can lead to tree mortality. The study was aimed at investigating the utilisation of woody plants by the Cape porcupine in three mesic savanna sites in South Africa. I quantified porcupine woody plant diet for the dry and wet season at Roodeplaat Farm in Gauteng Province and at Goss Game Farm and Bisley Valley Nature Reserve in KwaZulu-Natal Province. Large quadrats (30 m × 30 m) were laid at Roodeplaat and Goss while smaller quadrats (10 m × 10 m) were laid at Bisley. I measured stem diameter and the length and width of bark scars made by porcupines on stems of woody plants. I collected ten dung samples from each study site in the wet and dry seasons for quantification of woody material in porcupine diet. Porcupine foraging behaviour impacted different tree species at each site: *Vachellia robusta* at Roodeplaat, *Spirostachys africana* at Goss and *Vachellia nilotica* at Bisley. Each of these trees was dominant at each site. More scarring and tree mortality was recorded at Bisley with almost 70% tree sapling mortality occurring on trees which porcupine fed on. The size of bark scars was greater at Goss ($P < 0.01$) than at Roodeplaat and Bisley, which were similar. Damage on the bark of *S. africana* trees differed significantly by size class ($P = 0.007$) and was greater for size class 1.6-7 cm than 8-14 cm and 15-21. For all the study sites dung samples revealed that woody material contributed over 80% of the porcupine diet during the dry season, which declined to 35% during the wet season for Roodeplaat and was still high for Bisley at 79%. Porcupine foraging activities substantially contributed to tree mortality at each site. I posit that porcupine induced mortality on dominant tree species at each site may contribute to structural heterogeneity in woody plant vegetation in mesic savannas.

Key words: Bark damage, Cape porcupines, diet, herbivory, scarring and woody plants.

Introduction

The extent of herbivory varies greatly depending on the type of ecosystem (Maron and Crone, 2006; Marquart et al., 2019). Large herbivores have considerable impacts on the landscape, such that herbivory is considered a major determinant of the savanna structure (Frost et al., 1986; Sankaran et al., 2005). Without herbivory most African savannas could develop into closed woodlands, but the influence of herbivores on vegetation is evident for extensively studied species such as the African elephant (*Loxodonta africana*) (e.g. O'Connor et al., 2007), but are poorly understood for less charismatic and cryptic species such as the Cape porcupine (*Hystrix africaeaustralis*). As such, the utilisation of woody vegetation by such animals, particularly the cryptic species, is understudied in African savannas.

Seasonality is associated with changes in vegetation. The dry season is characterised by decreased availability of and quality of grasses and deciduous trees whereas evergreen trees tend to be more available (Aide, 1992; Duru and Ducrocq, 2000). The decrease in forage quality and quantity results in food scarcity for herbivores, more so for grazers. To deal with the changes in forage availability, some animals such as elephants, migrate (Fryxell and Sinclair, 1988). Others feed on less nutritional foods to meet their dietary requirements (Sklenar, 2011). mixed feeders simply shift to incorporate a greater portion of woody plants in their diet during the dry season (Codron et al., 2007).

Cape porcupines are generalist herbivores that occur throughout southern Africa (van Aarde, 1987). Porcupines feed on natural vegetation and cultivated plants (Bragg et al., 2005; Hafeez et al., 2011), and are considered serious pests both in agriculture and commercial forestry (Khan et al., 2000; Mushtaq et al., 2010). A porcupine's diet is mainly made up of tubers, corms, roots, and tree bark, and the foraging activities of porcupines may lead to death of the trees whose roots are dug out or whose trunks are ring-barked (Bruno and Riccardi, 1995; Mohamed, 2011). Because tubers and rhizomes are less available during the dry season, porcupines utilise other food sources such as the bark as well as roots of certain tree species (Hafeez et al., 2011). Damage of the tree bark makes the trees susceptible to fire as well as diseases which may come about due to attack by insects (e.g. ants) and pathogenic microbes (i.e. bacterial and fungal attack) (Vospernik, 2006; Wigley et al., 2019). Apart from herbivory, trees may have scars from accidental damage and natural processes. These scars may result in the removal of bark from the tree, which exposes a section of the stem (Shannon et al., 2013;

Korell et al., 2017). The removal of the bark and cambium does not impact on the movement of water and nutrients in plants (Holtta et al., 2006). Ringbarking does not result in sudden death of trees most trees possess enough carbohydrate reserves to continue growth but may die over time, as the reserves become depleted (Holtta et al., 2006). The lack of carbohydrate in plants may negatively influence water and nutrient uptake, which then results in the death of the tree (Cleary and Holmes, 2011).

Porcupines are nocturnal, territorial and solitary foragers, although they can occasionally be found foraging in groups of two to three animals (Coppola et al., 2019). Their nocturnal and shy nature hinders direct studies on their feeding behaviour, but evidence of their feeding can be seen in the wild as some trees have bite marks on the trunk which is a clear indication of the animal feeding on those. The foraging behaviour of porcupines is also indicated by their digging through the soil for subterranean plant parts. Through their feeding and foraging activities, porcupines have trophic and landscape level effects on the ecosystem through digging and feeding (Sharma and Prasad, 1992; Mori et al., 2017, 2018). Extensive excavation of holes and burrows is known as ecosystem or soil engineering (Jones et al., 1994). Such animals modify the landscape through digging and make resources readily available to other organisms (Alkon, 1999; Haussmann et al., 2018; Grossman et al., 2019). It is thus important to understand how soil engineers such as porcupines utilise the landscape and what characteristics of the landscape influences their abundance, distribution and foraging behaviour (Ogurtsov, 2017). Resource availability may influence the utilisation of the landscape by porcupine (Alkon, 1999). Unfortunately, the engineering aspects of porcupines such as digging are seen as a problem particularly in farming systems. Porcupines are thus viewed as pests in these systems, as they interfere with crop production and harvest (Alkon and Saltz, 1985). The effects of porcupine foraging behaviour in agriculture shows that they may have potential to deal with problem plants even if it is at a smaller scale than larger herbivores. A higher density of porcupines may have greater and negative effects on plants.

In this study, the utilisation of woody plants as porcupine food during the wet and dry seasons, and the foraging activities of porcupines were monitored at three geographically distant sites in South Africa. The study was aimed at quantifying the extent of herbivory by the porcupines on target trees during the wet and dry season in savannas. I hypothesised that Cape porcupines adjust their diet according to the season due to the availability of preferred plants. I used dung samples to determine and quantify plant materials the porcupines consumed during the wet and dry season. I also quantified the extent of bark damage by porcupines on target trees at each site and related bark damage to woody plant constituents in the dung for each study site.

Methods and materials

Study sites

The study was conducted at three different locations: the Roodeplaat Experimental Farm (25°60′26″S, 28°33′40″E) of the Agricultural Research Council (ARC) located in northern Gauteng, Goss Game Farm (27°56′22″S, 31°75′02″E) near Pongola in northern KwaZulu-Natal and at Bisley Valley Nature Reserve (29°65′82″S, 30°38′50″E) in Pietermaritzburg, also located in KwaZulu-Natal, South Africa (Figure 1). Although the sites were far apart and of different sizes the common aspect amongst them was bush encroachment.

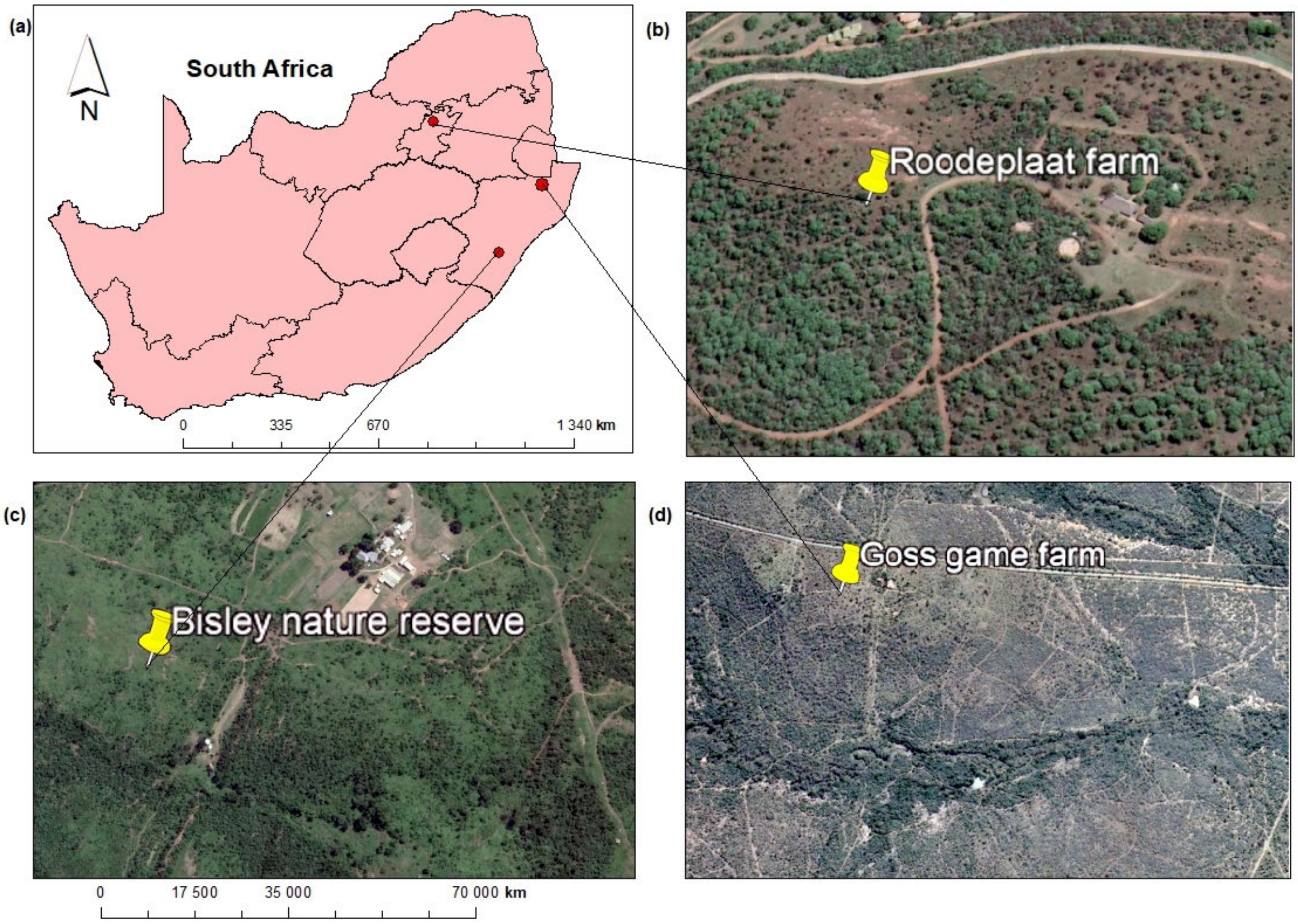


Figure 1: (a) Map of South Africa showing the three study sites. The vegetation at each site is exemplified by Google images for (b) Roodeplaat in Gauteng Province, (c) Goss in KwaZulu-Natal (KZN) Province and (d) Bisley, as in KZN.

The three sites are in mesic savannas with minor differences in mean annual precipitation (Roodeplaat: 646 mm; Bisley: 694 mm; Goss: 543 mm) which largely occurs during the summer months (November-April). The vegetation at Roodeplaat is described as Marikana Thornveld, which consists of open *Vachellia karroo* woodland occurring in valleys, undulating plains and lowland hills (Mucina and Rutherford, 2006). The mean maximum temperature in summer can reach 29°C and mean minimum temperatures in winter can drop to 2°C with frost occurring during winter months (Mkhize et al., 2018). The common tree species that occur in Roodeplaat Farm include *V. nilotica, V. tortilis*, *V. robusta* subsp. *heteracantha* and *Ziziphus mucronata* (see Appendix for authorities of species). *Grewia flava, Searsia pyroides* var.

pyroides, Diospyros lycioides subsp. *guerkei* are among some of the tall shrubs occurring in Roodeplaat Farm. The grasses include *Melinis nerviglumis, Elionurus muticus, Heteropogon contortus* and *Fingerhutia africana*. Some herb species found there are *Hermannia depressa, Ledebouria revoluta* and *Ipomoea obscura*. The vegetation type at Goss Game Farm is classified as Northern Zululand Sourveld, which occurs in most parts of northern KwaZulu-Natal. The vegetation is characterised by wooded grasslands and dense bushveld thickets, with tall shrubs of *Gardenia volkensii* and *Gnidia caffra* (Mucina and Rutherford, 2006). Goss Game Farm lies in a hot, semi-arid to mesic region, with mean temperatures reaching a maximum of 38.5°C in summer and a mean minimum of 7°C in winter (Mucina and Rutherford, 2006). Common trees in the area include *Spirostachys africana, Sclerocarya birrea, Z. mucronata, V. robusta, V. tortilis, V. nilotica, V. caffra,* and *V. karroo*. The common grasses found in Goss Game Farm are *Eragrostis curvula* and *Themeda trianda*.

The vegetation at Bisley Valley Nature Reserve (Bisley) forms part of the grassland biome and is categorised as a transition zone between KwaZulu-Natal Hinterland Thornveld and Ngongoni Veld and is thus susceptible to invasion by woody plants (Ward et al., 2017). Bisley experiences hot summers with a mean maximum of 26.4°C in February and mild winters with a mean minimum of 8.8°C in July. The common trees that occur in this area are *V. nilotica* and *V. sieberiana* while the common grasses include *E. curvula* and *Panicum maximum* (Ward et al., 2017). *Rhus pentheri* and *Justicia flava* are shrubs which occur in this area, while *Aloe pruinose* is an endemic herb. The main growing season for all sites is summer, and the dry season starts in May and peaks in July. All three sites are normally dry in winter with lower availabilities of forage, and most of the available food for large mammalian herbivores (> 4 kg, *sensu* Bragg et al., 2005) is derived from shrubs and trees (Mucina and Rutherford, 2006).

Field sampling

Sampling was undertaken during the dry season between July and October 2019. Revisits were made to the sites during the wet season (January-March 2020). Quadrats were randomly laid out according to the size of the site. At Roodeplaat, porcupine diggings were mainly for below ground parts of the trunk of *Vachellia robusta*. Using thirty 30 m x 30 m quadrats, stem diameters of all *V. robusta* trees were measured at a height of 0.5 m, which is consistent with the height to which porcupine bark damage occurred. I also measured the length and width of scars on the bark and roots made by the porcupines. At Goss, porcupine tree damage was mainly on the stems of *Spirostachys africana*, so tree diameter was measured at 0.5 m above ground, again using 30 m x 30 m quadrats. At Bisley, porcupines dug to reach a portion of the main root of *V. nilotica* seedlings and saplings. The diameter of the dug-out tree stem was also measured in smaller quadrats of 10 m x 10 m. In some instances, portions of the tree stem cut out from the roots were found near the foraging hole. The diameter of these stems was also recorded. The stem diameters were further divided into size classes (i.e. small, 1.6-7 cm; medium, 8-14 cm; and large, 15-21 cm) for *S. africana*. *V. robusta* diameter size classes were 0.1-4 cm for small trees, 4.5-8.5 cm for medium and 9-14 cm for large trees. Finally, *V. nilotica* comprised of only two size classes, that is, 0.5-3.5 cm for the small category and 4-7.5 cm for the medium sized trees. Faecal samples were collected at each site along animal tracks for the dry (August-October) and wet seasons (January-March) to identify components of the diet derived from woody plants.

Debarking by porcupines was identified by marks on the bark of trees. Signs of debarking were categorised as new and old. New bark damage was estimated to have occurred approximately a few weeks to a few months (less than 3 months) prior to sampling. Old bark damage was more than 3 months old and was distinguished from the new because of the change in colour of the scar to brown for all the trees. The length and width of scars on trees damaged by porcupine were measured for each tree. I also took note of whether tree seedlings or saplings were completely dug out and destroyed, or they were damaged but remained alive. Due to different sizes of targeted trees, I used larger quadrats (30 m × 30 m) at Roodeplaat and Goss (where mature trees were damaged) than at Bisley where smaller quadrats (10 m × 10 m) were used because the porcupines only utilised seedlings and saplings at this site. The number of quadrats was also influenced by the area of porcupine activities, which was much larger at Roodeplaat (5-8 ha; 30 quadrats) than Goss (< 5 ha, 20 quadrats) and at Bisley (approx. 3 ha; 10 quadrats).

Faecal analysis

Porcupine droppings are easily identifiable as they form a stack of elongate pellets. Faecal samples were collected along the quadrats and opportunistically from all three sites and oven-dried (60°C, 48 h) for storage before analysing the samples for diet composition. For analyses, ten samples were analysed for each site per season. The dung samples were first weighed and then cut into smaller pieces and a representative portion of the whole dung sample was then analysed. The sample was washed in 70% ethanol to separate the different components and then air- dried, sieved through a 1-mm sieve and weighed again. The different diet components were then grouped according to their categories, e.g., woody material, herbaceous material and seeds, and then examined under a dissecting microscope.

Data analysis

All statistical analysis was carried out in IBM SPSS statistics for windows v. 27. Categorical data of constituents of porcupine dung was expressed as a percentage of total weight of a dung sample. Bark damage on the main stems of trees was expressed using the mean and standard error of the means for all the sites. For each study site and species, the highest extent of bark damage on the tree trunks was determined to calculate the area of bark available to the porcupine. Thus, I determined that the bark of *V. robusta* and *V. nilotica* was available to a height of 0.2 m, and that of *S. africana* to 0.5 m. I then calculated the total area of the porcupine scars on each tree and expressed this bark damage as a proportion of the total bark available for each tree. I compared proportional bark damage per tree among three stem diameter size classes of trees (small, medium and large) for *S. africana* using a Kruskal-Wallis test because the assumptions of analysis of variance (ANOVA) were not met and no transformation allowed the assumptions of a parametric test to be satisfied. For *V. robusta,* I used one-way ANOVA. For *V. nilotica*, I used a t-test because there were only small and medium size categories of damaged trees. Sample sizes of *V. karroo* and *D. rotundifolia* trees were too small for use in the size class analysis. I also determined bark damage on trees across sites using one-way ANOVA.

Results

Some 7% trees of *V. robusta*, 16% *S. africana* and 40% of *V. nilotica* were bark damaged at Roodeplaat, Goss and Bisley, respectively. These trees constitute most of the bark damage shown in Figure 2. The sizes of the bark scars were much greater at Goss ($P < 0.01$) than at Roodeplaat and Bisley, which were similar (i.e. $P > 0.05$). At Goss, bark damage of *S. africana* trees differed significantly by size class (Kruskal-Wallis $\chi^2 = 9.854$, $P = 0.007$). There was significantly lower bark damage on small than medium and large trees (Table 1).

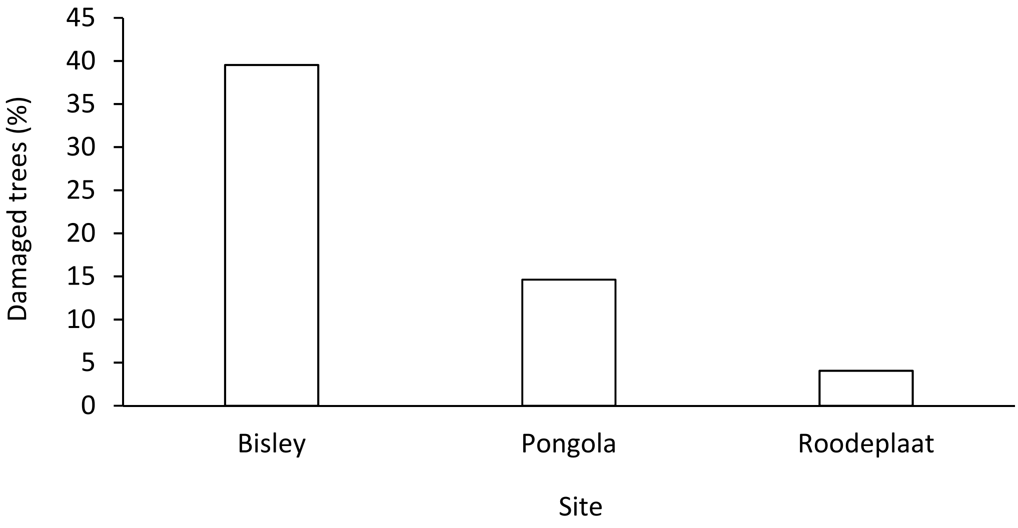


Figure 2. Number of bark-damaged trees (%) by porcupines at Bisley, Goss and Roodeplaat.

Porcupine damage on trees was mild at Roodeplaat where *V. robusta* was the most targeted tree species, whereas at Goss, *Spirostachys africana* was the utilised tree, while *V. nilotica* seedlings and saplings were highly utilised at Bisley (Figure 2). Tree mortality was high at Bisley as most of the main stem was completely cut off, with over 70% of the trees fed on of *V. nilotica* seedlings or saplings dying because of porcupine foraging activities (Figure 3). Tree mortality for the other two study sites was not evident as the damaged trees were mature and still standing.

Table 1. Mean (±SE) size of scars on trees caused by porcupines. In each row different lower-case letters denote significant differences among size classes ($P < 0.05$).

	Diameter size class (cm^2)		
Species	Small	Medium	Large
Spirostachys africana	105.1 ± 29.5 a	340.0 ± 23.9 b	304.5 ± 76.5 b
Vachellia nilotica	72.2 ± 38.8 a	18.5 ± 9.5 a	-
Vachellia robusta	42.3 ± 6.6 a	80.0 ± 20.0 a	45.0 ± 25.3 a

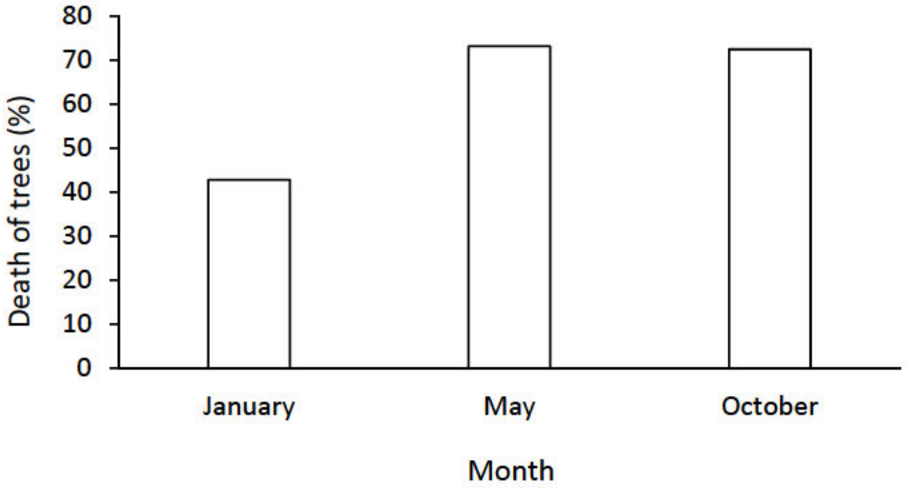


Figure 3. Percentage tree mortality at Bisley at different times of the year.

Seedling mortality of *V. nilotica* trees was noticeable at Bisley, with numbers increasing mostly during the dry season (Figure 3). The percentage of dead trees because of porcupine feeding on them was greater in May and October (70%) than during the wet season in January (45%).

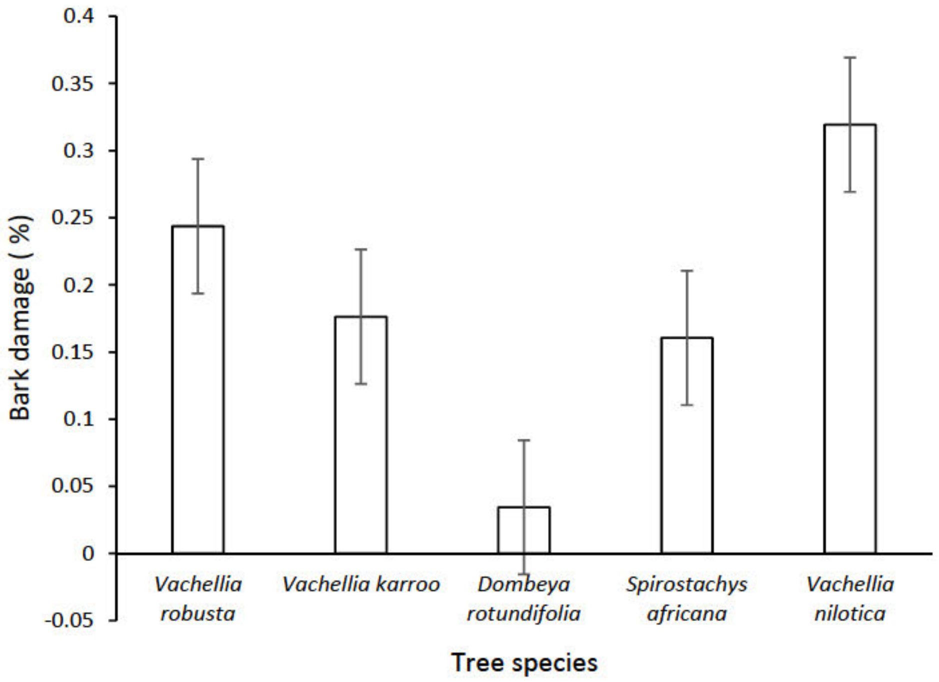
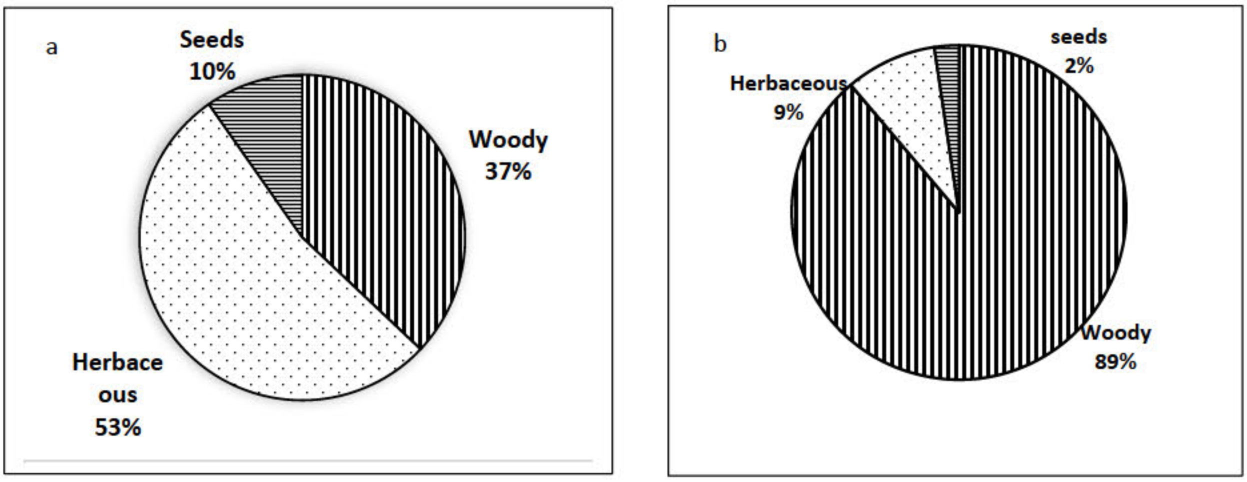


Figure 4. Mean (±SE) percentage of bark damaged by the porcupine on trees at Bisley, Goss and Roodeplaat.

Figure 4 indicates the amount of woody material which was scrapped off the bark for different tree species. *Vachellia robusta* was the most preferred tree species at Roodeplaat, with *V. karroo* and *D. rotundifolia* occasionally targeted. At Goss porcupines were mainly interested in the bark of *S. africana*. Bark damage on *V. nilotica* was intense as it was observed for both the wet and dry season (Figure 5). The size of scars on trees across sites was significantly different ($F = 7.428$, $P < 0.0001$) (Table 2). Tree damage by porcupines was greater at Goss than at Roodeplaat and Bisley. Mature trees were porcupine damaged at Roodeplaat and Goss +while seedlings and saplings were damaged at Bisley.

Table 2. Mean (±SE) size of scar on trees at each site. Different letters indicate significant differences among sites ($P < 0.05$).

Site	Size of scar (cm^2)
Roodeplaat	95.1 ± 68.5 a
Goss	192.7 ± 38.3 b
Bisley	63.5 ± 69.9 a



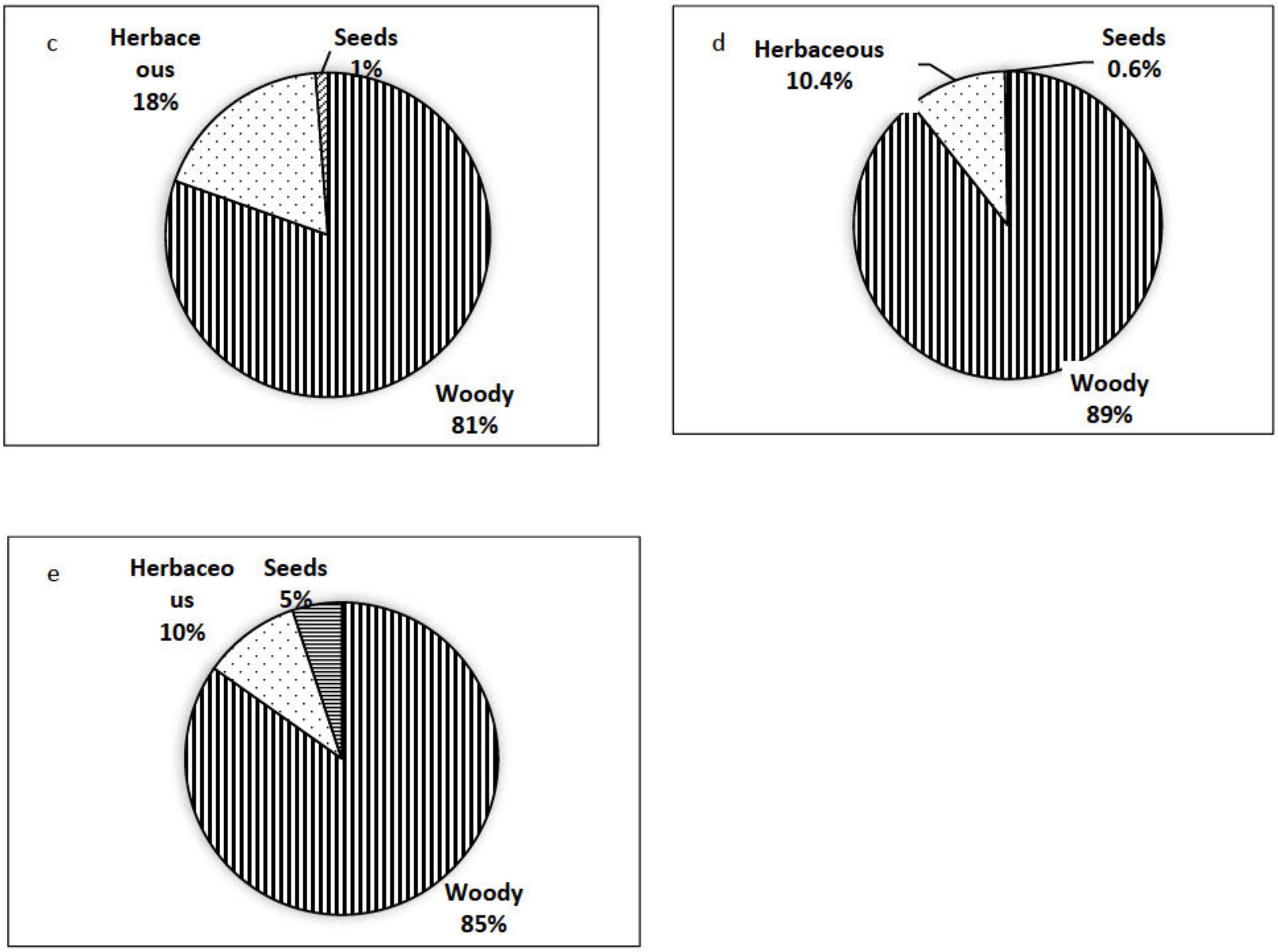


Figure 5. Food constituents of a porcupine diet at Roodeplaat, Goss and Bisley. (a) Wet season diet at Roodeplaat, (b) dry season at Roodeplaat, (c) wet season diet at Bisley, (d) dry season diet at Bisley and (e) dry season diet at Goss.

For all three sites, the diet was mainly made up of woody material which constituted > 80% of the dry weight of the dung samples (Fig. 4). Herbaceous material and bulbs contributed a similar amount for all the sites while seeds contributed minimally to the porcupine diet.

Discussion

I found that spatial and temporal variation in food availability may result in changes in food preference from one habitat to another during different times of the year. For example, Yeaton (1988) found that porcupines showed a preference for *Burkea africana* trees over *Vachellia* spp. in Nylsvley Nature Reserve in Limpopo, South Africa. In the Bokkeveld Plateau in the Northern Cape Province of South Africa, porcupines consumed geophytes which were more abundant, with over hundred species (Bragg et al., 2005. Like *Vachellia* species, there has been documented information on other herbivores feeding on *S. africana* even though the tree produces poison in the form of latex (Lennox and Bamford, 2015). Despite its poisonous nature, *S. africana* is also eaten by African elephants (see Shannon et al., 2013).

In seasonal environments such as of this study, wild fruits and bulbs are mainly available in the wet season and may thus constitute part of the diet of porcupines in the wet season (Bragg et al, 2005; Mori et al. 2017). I found that porcupines utilised different food resources between seasons, which is related to seasonality of availability as reported in other studies (e.g., Alkon, 1999; Bragg et al., 2005; Mori et al., 2017). Different trees were targeted and utilised by porcupines in the different areas. Although *V. karroo* and *V. robusta* occurred at all three sites, the trees were only utilised at Roodeplaat. Porcupines seem to forage on trees of a certain age for a particular tree species (Yeaton, 1988). At Roodeplaat porcupines scarred trees between 0.5-14 cm in diameter, while at Goss they targeted trees with a stem diameter of up to 21 cm, and at Bisley only seedlings with a diameter less than 0.5 cm were targeted although mature trees of that species were available. At Bisley, stem damage on the targeted trees differed in that seedlings and saplings were largely dug out completely or partially, leading to mortality of most damaged plants. At Roodeplaat, because porcupines targeted mature plants, tree death would be a slow process, but most of the scars were located below ground. Damage on *S. africana* was mainly on the bark and porcupines ringbarked the trees thereby decreasing chances of recovery. The porcupine preference for feeding on the bark of certain trees over others has been reported in other studies (Yeaton, 1988; Hafeez et al., 2011). The current study found that there was more utilisation of woody material during the dry season at all the sites, however, it was also evident that woody material is one of the major constituents of a porcupine’s diet even during the wet season (see Figure 3). Although these findings are consistent with the suggestion that the Cape porcupine is a generalist herbivore, I noted that the utilisation of woody plants is limited to only a few species at each site. Similarly, the North American porcupine (*Erethizon dorsatum*) feeds on the phloem of *Pinus ponderosa,* an evergreen coniferous tree during the dry winter season and as such can be said to be a selective feeder (Snyder and Linhart, 1997). The Cape porcupine can also be regarded as a selective feeder, at least on woody plants. The findings suggest that porcupines switch from grazing to browsing when food resources become scarce in the dry season.

Tree damage by porcupine was through debarking of the lower parts of the trees (Figure 6), up to 60 cm height and in some cases, resulting in complete debarking. Ringbarking may sometimes lead to the death of a tree. However, in most cases scars on the tree may not kill it but negatively influence growth (Vospernik, 2006; Wigley et al., 2019). Large scars may compromise the lifespan of a tree. Some trees may recover from the damage manifesting through scars by adding new layers of growth to cover the damaged area (Cleary and Holmes, 2011). Other scars however permanent (Nichols et al., 2016). Scarred trees may likely be attacked by insects and fire, in some instances, the latter may result in death of the tree.

Generally, elephants are viewed as the main herbivores in the control of tree densities in savannas (Shannon et al., 2013). Elephant feeding behaviour is different from other large browsers because they can knock down large trees (Wigley et al., 2019; Thornely et al., 2020). The death of trees as a result of elephant herbivory creates open spaces in savannas and thus creates microhabitats that can be used by other smaller animals (Kerley et al. 2008). Ringbarking of a seedling, leading to the removal of the entire seedling by porcupines can have the same effects on the tree densities. In Pakistan, a recorded damage of 60% on *Pinus roxburghii* and 42% on *Robinia pseudoacacia* in different areas of the Tarbela Watershed Management Project was caused by porcupines (Khan et al., 2000). In addition, Khan et al. (2000) reported that seedlings of *Bombax ceiba, Dalbergia sissoo,* and *Eucalyptus* spp. were up-rooted by the Indian crested porcupine after transplantation.

Figure 6. *Spirostachys africana* tree bark damaged by porcupines at Goss Game Farm.

Although the combination of savanna determinants like fire and herbivory appeared sufficient to prevent tree growth, woody plant encroachment is a major problem in many savannas (Ward 2005; O'Connor et al., 2014). The three study sites are in mesic savannas which are undergoing woody plant encroachment (O'Connor et al., 2014). In the current study, one of the study sites (Bisley) has megaherbivores (giraffes), but unlike elephants their foraging behaviour has minimum effects on vegetation density as they feed mainly on the leaves and twigs of tree branches. The foraging behaviour of elephants has been documented for reducing tree density and possible effects on ameliorating woody plant encroachment. The Cape porcupine seem to play similar roles but relative to their body size and numbers, their effects will be smaller. Tree mortality brought about by porcupines foraging behaviour as observed on young individuals of *V. nilotica* at Bisley decreases structural homogeneity of the woody plant layer which ultimately ameliorates woody plant encroachment. Unlike elephant-induced damage on woody plants, which may lead to resprouting of damaged trees (Thornely et al., 2020), porcupine activities as observed at Bisley and Roodeplaat consists of digging and cutting out the trees below ground so that chances of resprouting are minimal. Ringbarked *S.*

africana trees are unlikely to flower and produce seeds as carbohydrate reserves are used for recovery (Holta et al., 2006). This has implications on population dynamics of the species and vegetation structure.

Conclusion

This study demonstrated the importance of cryptic herbivores in structuring savannas. Herbivores directly influence the densities and distribution of plants through their foraging activities. For the Cape porcupine, the targeted tree species are woody encroachers in the study sites (e.g. *V. nilotica* at Bisley). *Spirostachys africana* is known to form mono-specific stands while *V. robusta* dominated the low hills at Roodeplaat. Porcupines in these study sites can be said to be biological control agents in the sense that their impact on these tree species reduces the dominance of the species so that there is taxonomic and structural heterogeneity in the woody plant layer. Future studies could be conducted to investigate the reproductive performance of ringbarked trees and selection of tree size classes as well as species.

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Chapter 3: Effects of Cape porcupine foraging activities in savanna ecosystems

Abstract

The physical and chemical impact of semi-fossorial herbivores (adapted to digging and living underground), such as Cape porcupines can be significant, with contributions on direct and indirect landscape formation. In terrestrial ecosystems, the activities of semi-fossorial animals are important influencers of the landscape, their influence may be noticeable at a spatial scale likely in the dry season. This study was aimed at investigating the effects of foraging activities of porcupine on the landscape. I observed foraging holes of porcupine in three geographical distant mesic savanna sites (i.e. Roodeplaat Farm, Goss Game Farm and Bisley Valley Nature Reserve) of South Africa. Thirty foraging holes were marked with metal pegs at Bisley. I observed these holes over a period of 10 months with visits happening every two months for vegetation cover as well as animal life. Soil samples were collected from the three sites from the mound (disturbed soil) and from the control (undug soil), total carbon (TC) and total nitrogen (TN) were measured from the soil samples using the LECO method. The depth of holes differed with age ($P = 0.004$), as new holes in Bisley were significantly deeper than new and old holes from Roodeplaat. The depth and width of foraging holes decreased with age. Newer holes were deeper in Bisley, while old holes were wider ($P < 0.05$ in both cases) in Roodeplaat. Total carbon and TN concentrations were significantly different in Bisley compared to Roodeplaat and Goss ($P < 0.0001$). Bisley had the lowest TC and TN concentrations compared to Roodeplaat and Goss. Holes dug by porcupine facilitated shelter for arthropods such as spiders and termites and germination of herbaceous plants. The holes dug by porcupines also trapped plant litter, which could in turn result in increased nutrient cycling. This study showed that porcupines do not only facilitate growth of vegetation on disturbed soils and in the holes but also create shelter for invertebrate species. This may in turn contribute to the diversity of both plants and invertebrates.

Key words: Burrowing, digging, foraging holes, savanna, soil, vegetation.

Introduction

Burrowing mammals in terrestrial ecosystems fulfil a necessary role in making resources such as shelter and food available to other animals (Skinner and Taylor, 2010; Haussman et al., 2018). For example, aardvark (*Oryceteropus afer*) and Cape porcupines (*Hystrix africaeaustralis*) dig burrows large enough to be used as shelter and nesting sites by other animals (Melton, 1976; Whittington-Jones et al., 2011; Alexander, 2018). Although porcupines are nocturnal, their activities can be observed through their generalist foraging behaviour of consuming plant parts occurring above and below ground (Alkon, 1999; Akram et al., 2017). When foraging or constructing burrows either for food or shelter, porcupines disturb the plant community in that area and cause soil disturbance (Andersen, 1987; Haussman et al., 2018). For these animals, the extent of soil and vegetation disturbance may be prevalent on the landscape, a characteristic of ecosystem engineers (Jones et al., 1994). Digging enables the animals to access buried foods such as bulbs and roots that may be unavailable to non-fossorial species (Fattorini and Pokheral, 2012). The diggings provide temporal and spatial heterogeneity in the landscape by mixing of topsoil with the subsoil (Root-Bernstein and Ebensperger, 2013; Muvengwi et al., 2018). Little has been studied about the foraging behaviour on foraging pits of porcupines and the extent of their soil disturbances in African savannas.

Digging by animals may result in soil erosion on the mound while it creates soil pockets on the actual pits (Travers et al., 2012). Foraging pits are depressions in the soil that may reduce water run-off, and hence, increase water infiltration rates (Grossman et al., 2019). Such soil perturbations may influence population dynamics of certain plant species or the whole community (Alkon and Olsvig-Whittaker, 1989; Gutterman, 2003). Digging activities may result in soil formation through the mounds, and may affect the rate of fungal associations, and seedling recruitment (Alkon and Saltz, 1988; Eldridge et al., 2012). Soil excavation by digging animals may influence nutrient cycling through the burying of organic matter and potentially increase the rate of litter decomposition (Eldridge et al., 2012, 2015).

Ecosystem engineers also occur in semi-arid environments (Jones et al. 1994). The excavated pits in these dry areas have higher moisture levels than the surrounding and this may favour litter decomposition, which ultimately affects nutrient cycling (Coûteaux et al., 1995; Zaitlin and Hayashi, 2011). These effects on soil moisture levels, litter decomposition and nutrient cycling may affect the plant community in terms of composition and diversity particularly around or within the foraging holes dug (Alkon and Olsvig-Whittaker, 1989). The foraging holes of digging animals may also influence the recruitment of seedlings. For example, buried seeds are unavailable to some seed predators and this results in more seeds available for germination, while the foraging holes may contribute to plant growth (Whitford and Kay, 1999; Louw et al., 2017). Digging or uprooting of plants by animals such as rodents directly influences plant species composition and species richness (Hagenah and Bennett, 2012). This digging behaviour may result in loss of untargeted plants especially those close to the targeted bulbs, roots, or tubers.

Soils are fundamental as they support diverse ecosystems. It is important to determine soil nutrient dynamics (soil organic carbon (SOC) and total nitrogen (TN) in order to understand an ecosystem in terms of structure and functioning (Craine et al., 2008; Muvera et al., 2018). Total carbon and total nitrogen are used as key indicators to estimate soil quality (Albaladejo et al., 2013). For example, TN contributes to primary production and varies spatially and temporally in different terrestrial ecosystems (Xue and An, 2018). A decreased or limited availability of TN limits plant growth, as a result of poor TN in soils (Craine et al., 2008). Nitrogen is thus a key requirement for plant growth (Matiwane et al., 2019), and may contribute positively to the structure of vegetation in ecosystems. In savannas, TN interacts with vegetation composition where woody legumes, potentially fix nitrogen by root symbionts (to a form which plants can use) and as such forms a significant part of the plant communities (Clark et al., 2016; Matiwane et al., 2019). Soil organic carbon is an equally important component of soil structure. Carbon can be cycled through the interaction between vegetation and soil (Clark et al., 2016; Xue and An, 2018). Plants and microorganisms use photosynthesis to convert atmospheric CO_2 into organic material. The SOC pool stores are estimated to be 344 million tons of C, up to 3 m depth in the soil, this large reservoir of SOC undergoes continuous recycling in different terrestrial ecosystems (Albaladeio et al., 2013; Mureva et al., 2018). Two primary gases of carbon include carbon dioxide and methane. Semi-fossorial herbivores can influence the N and C content of the soil through soil excavation. Excavating soils results in litter on the surface of the soil being buried underground (Coûteaux et al., 1995; Clark et al., 2016). This may in turn influence nutrient cycling.

Although diggings of porcupines have been shown to facilitate seed germination (Alkon, 1999), there is little information on the variation of the foraging holes on the landscape and the effect of season on these holes. There is also little known about the role of porcupines on seed germination and plant composition. In this study, the characteristics of these foraging holes as well as their temporal variation were investigated to determine their extent and persistence on the landscape. A better understanding of these aspects of foraging diggings of porcupines is important to determine the potential environmental impact of these animals, and the role of this species in savanna ecosystems. The study was aimed at evaluating the digging effects of Cape porcupines on nutrient cycling and to quantify vegetation in and around the disturbed soil as well as measure soil turnover over a 9-month period. I predicted that there would be a greater number of freshly dug holes during the peak of the dry season as compared to the wet season. I also predicted that soil disturbance results in greater germination of seedlings on mounds than on the surrounding undisturbed soil around the holes and mounds.

Methods and materials

Study sites

The study was conducted at three sites, namely; Roodeplaat Farm (25°60′S, 28°33′E) in Gauteng Province, Goss Game Farm (27°56′S, 31°75′E) in the Magudu area of northern KwaZulu-Natal Province and Bisley Valley Nature Reserve (29°65′S, 30°38′E) south of Pietermaritzburg, also in KwaZulu-Natal.

Roodeplaat has the Marikana Thornveld vegetation, which consists of trees such as *Vachellia karroo, V. tortilis* and *V. nilotica* and the common grasses are *Heteropogon contortus, Elionurus muticus, Melinis nerviglumis,* and *Fingerhutia africana* (Mucina and Rutherford, 2006). The mean maximum temperature in summer can reach 29°C and minimum temperatures in winter can decrease to 2°C with frost occurring during winter (May-August). The mean annual rainfall is 646 mm. Soils at Roodeplaat are derived from melanic clays which have a loam sandy texture that is brought about by the sediment rocks. The vegetation type at Goss Game Farm is Northern Zululand Sourveld, comprising of wooded grasslands and dense bushveld thickets, and the common trees found in this area are *Spirostachys africana* and *Sclerocarya birrea* while common grasses include *H. contortus* and *Fingerhutia africana* (Mucina and Rutherford, 2006). Goss game farm has temperatures reaching a maximum of 38.5°C in summer and a minimum of 7°C in winter, with a mean annual rainfall of 543 mm (Mucina and Rutherford, 2006). Mispah soil are found at Goss, with coarse sand particles with a red clay texture.

Bisley Valley Nature Reserve's vegetation forms part of the grassland biome. The reserve falls between KwaZulu-Natal Hinterland Thornveld and Ngongoni Veld and may be invaded by woody plants (Ward et al., 2017). The mean maximum temperature of this area can reach 26.4°C in February and a mean minimum of 8.8°C in July. The average annual rainfall is 694 mm. The most common trees that occur in this area are *V. nilotica* and *V. sieberiana* while the common grasses include *Eragrostis curvula* and *Panicum maximum* (Ward et al., 2017). The site contains red and yellow apedal soils with coarse sands, while having fine gravel fragments derived from the Pietermaritzburg formation.

Study species

The Cape porcupine is a large (~12.5 kg), nocturnal rodent, which occurs in a broad range of natural, urbanised as well as agricultural ecosystems and is a generalist herbivore (van Aarde, 1987). Porcupines are monogamous in nature and are found living as a family with two adults and their offspring. They are hunted for their bushmeat and in some cases because they are considered pests in agriculture may be persecuted by landowners. Porcupines inhabit burrows and caves, and often dig their own burrows but may use burrows dug by aardvarks (Skinner and Taylor, 2010). Due to their wide tolerance of different ecosystems, these rodents are found in different regions and their foraging activities often indicate their presence in that area (van Aarde, 1987).

Study protocol

Biortubation by porcupines is a process which requires follow up visits and because the study sites are hundreds of kilometres apart that meant that only one study site could be observed for this aspect of the study. Data were collected for all the sites but follow up visits were only done at Bisley. Though the sampling times differed with each site, I collected data for the sites before the season changed. Sampling took place in July-August at Roodeplaat, September at Goss and November at Bisley 2019 (the first rains only came in mid-November at Bisley after sampling for the dry season was already completed). Data collection in Bisley continued to February, March, May, June, August and in October 2020. I also collected wet season data in January at Roodeplaat 2020. I collected data on the soil engineering aspect of porcupine in Roodeplaat and Bisley in the wet and dry seasons. These data included collection of soils and examination of foraging holes dug by porcupines.

I examined changes in the soil and litter properties of porcupine foraging holes compared to adjacent (approximately 50 cm) undug ground at Bisley, thirty newly excavated foraging holes were individually marked with metal pegs in November 2019. Twenty of these foraging holes were situated mid-slope of an area approximately 1.5 ha and the other ten were situated at another mid-slope location of ca. 0.50 ha. The locations were ca. 1 km apart. I monitored these foraging holes for 10 months (November 2019-August 2020) visiting the site every two months as they aged. The mounds and foraging holes were categorised as new and old, based on the following observations and criteria: new mounds and holes were formed in the current season, with the disturbed area still having a mound (loose soil settling) but with no vegetation on the mound and little to no disturbance to the mound. Old mounds and holes were formed 3 months before sampling with the mound disappearing and the pit almost filled with litter/soil (Eldridge and Mensinga, 2007; Jones et al., 2008). In each hole, I measured two perpendicular lengths to determine surface area on the ground surface and the maximum depth during the first visit. In subsequent visits, I measured new holes and the marked old holes taking the same measurements as the ones I did before, and field trip visits were made to the reserve every second month. Holes were considered filled when there was no evidence of a prior digging but only a mark with the number I had assigned the foraging hole.

Quadrats (10 m × 10 m) were made and within those, a sub-quadrat (0.5 m × 0.5 m) was used to mark the area surrounding each foraging hole and a similar area immediately adjacent to undug ground was chosen randomly as its paired control. Each quadrat-pair was more than 50 m away from other foraging holes to ensure minimal interference between holes. For each quadrat-pair I recorded the type (woody, forb or grass) and quantity of plants inside the hole, on the mound and near (within 0.5 m) the hole, which was used as a control. I also recorded evidence of animal life inside the hole, such as arthropods (insects, insect larvae, spiders, spider webs, etc.). I observed the vegetation on the mound, around and inside the hole during the wet season when growth was taking place. Indistinguishable plants were recorded as unidentified.

Soil sampling and analysis

Soil samples were collected from each study site for measurement of TC and TN. Three scoops were collected from each soil sample location on mounds and adjacent undisturbed soil to a depth of 50 mm. The soil from the three scoops was bulked to form a composite sample for that quadrat. Soil samples were air dried and passed through a 1-mm sieve before analysis. Total carbon and TN were analysed by an automated Dumas dry combustion method using a LECO TruSpec CN (LECO Corporation, Michigan, USA).

Data analysis

I used percentages to present descriptive data on foraging holes in Roodeplaat and Bisley. I then used IBM SPSS Statistics v. 27 (SPSS Inc., Chicago, IL, USA) to assess the diggings made by porcupines. Once the assumptions of normality were met, I performed a two-way ANOVA with study sites (Roodeplaat, Bisley) and age of foraging holes (old, new) as the independent variables to determine size of the foraging holes i.e. depth and surface area lengths as the dependent variables. I then used a post hoc test (Tukey) of between-subjects effects to show differences among means when significant differences were indicated by the ANOVA test. I also used a two-way ANOVA to determine TC and TN concentrations (dependent variables) in mounds (independent variable) and sites (independent variable). The concentration of TN was transformed because it did not meet the assumptions of normality. I then used a post hoc test of between-subjects effects to show differences among means when significant differences were indicated by the ANOVA test. I used a frequency table to present data on vegetation and animal life on the mound, inside the hole and within 0.5 m away from the hole.

Results

The number of foraging holes dug by porcupines varied with season and site. I measured a total of 120 foraging holes at Bisley and 77 at Roodeplaat. Of those, 61 were old foraging holes at Roodeplaat, while Bisley had 34 old holes (Figure 1). Sixteen new holes were measured at Roodeplaat while Bisley had 86 new foraging holes. Bisley tended to have newer holes than Roodeplaat.

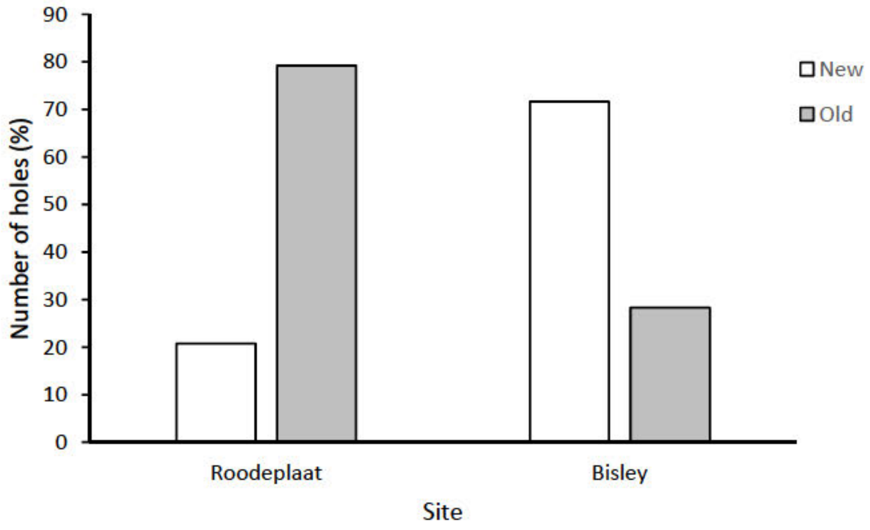

Figure 1. Number (%) of new and old porcupine foraging holes in Roodeplaat Farm and Bisley Valley Nature Reserve.

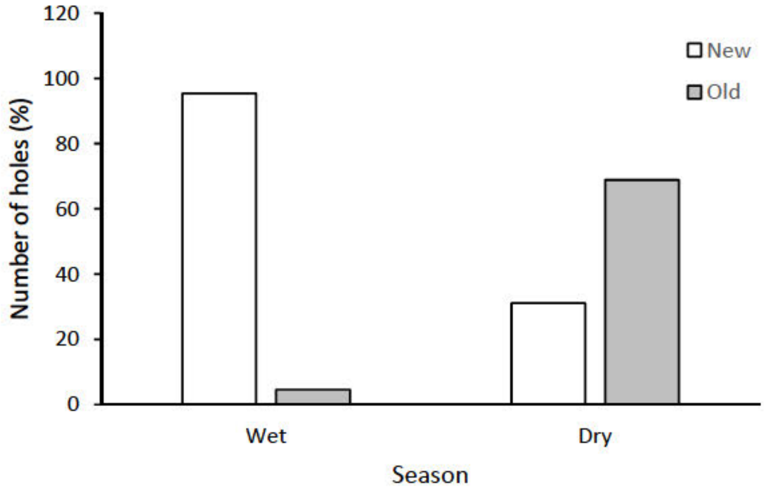

Figure 2. Number (%) of new and old porcupine foraging holes during the wet and dry seasons in Bisley Valley Nature Reserve.

Shallow foraging holes were excavated during the wet season, not next to any tree. As the dry season (April 2020) began new foraging holes were dug by porcupine next to *V. nilotica* trees

(Figure 2). These holes aged with the dry season. Thus, a greater number of old holes was observed in the dry season.

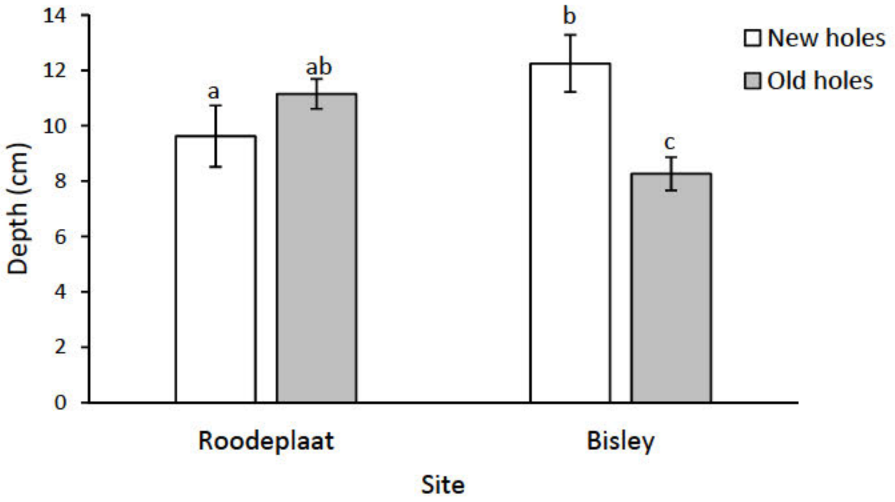

Figure 3. Mean (±SE) depth of new and old porcupine foraging holes in Roodeplaat Farm and Bisley Valley Nature Reserve. Different lower-case letters were used to denote significances ($P < 0.05$).

The depth of new and old holes was significantly different in Bisley and Roodeplaat ($F = 8.598$; $P = 0.004$). New holes at Roodeplaat were shallower (9.6 ± 1.1 cm) compared to Bisley (12.3 ± 0.5 cm) (Figure 3). Similarly, new holes were deeper (12.3 ± 0.5 cm) compared to old holes (8.3 ± 0.6 cm) in Bisley.

Table 1. Surface area of foraging holes dug by porcupines in Roodeplaat Farm and Bisley Valley Nature Reserve. Different letters denote significance ($P < 0.05$).

	Surface area (cm^2)	
Site	New	Old
Roodeplaat	261.4 ± 19.3 a	1223.1 ± 127.5 b
Bisley	627.0 ± 39.0 c	854.7 ± 53.9 d

The size of foraging holes excavated by porcupines was different by age and site (*F* = 5.980; *P* = 0.015). Size of old foraging holes was wider in Roodeplaat than new and old holes from Bisley (Table 1). In contrast, new holes were wider in Bisley than Roodeplaat.

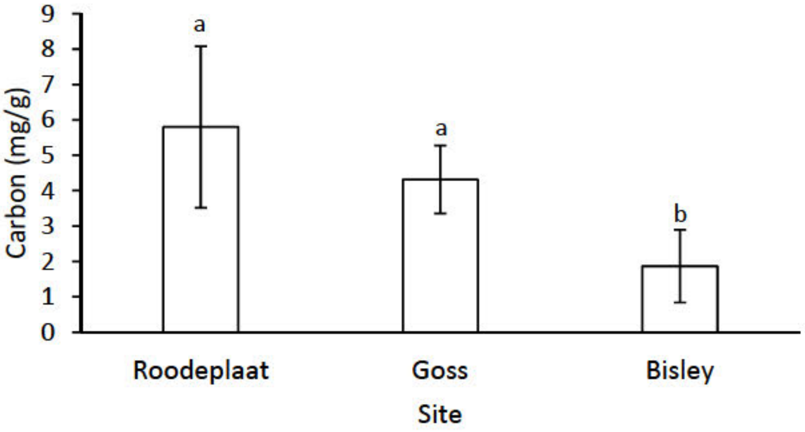

Figure 4: Total carbon (mean ± SE) concentration across three savanna habitats, South Africa. Different lower-case letters were used to denote significance at $P < 0.05$.

Total carbon concentration was not significantly different in the mound in the study sites (*F* = 0.104; *P* = 0.902). However, TC concentration was significantly different in Bisley compared to Roodeplaat and Goss (*F* = 15.216; $P < 0.0001$). TC was higher in Roodeplaat (5.8 ± 2.3 mg/g) and Goss (4.3 ± 1.0 mg/g) than Bisley (1.9 ± 1 mg/g).

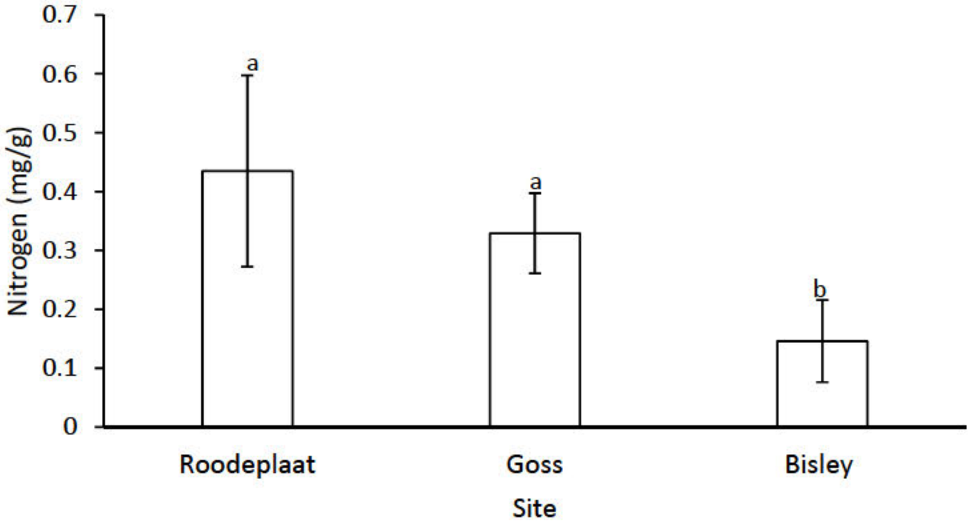

Figure 5. Concentrations of total nitrogen at Roodeplaat Farm, Goss Game Farm and Bisley Valley Nature Reserve. Different lower-case letters denote significance.

Similar to TC, TN concentration was not significantly different in the mound in the study sites (*F* = 0.073; *P* = 0.930) (Figure 5). However, TN was significantly higher in Roodeplaat and Goss than Bisley (*F* = 19.710; *P* < 0.0001). Roodeplaat (0.4 ± 0.2 mg/g) and Goss (0.3 ± 0.1 mg/g) had higher TN concentrations, while Bisley had a low concentration of 0.1 ± 0.1 mg/g.

Table 2. Total number of biological materials found inside new (n = 86) and old (n = 34) holes, on the mound and within 0.5 m of a porcupine foraging hole.

Material	Hole		Mound	Within 0.5 m
	New	Old		
Spider web	2	14	0	0
Termites/ants	3	0	0	0
Dung	1	1	0	-
Litter	0	9	0	-
Forbs	0	110	175	500
Grasses	0	20	153	139
Unidentified seedlings	0	76	197	359

New holes had little to no plant or animal life (Table 2). I only found termite or ants in new holes. In contrast, old holes showed signs of new plant growth, mainly forbs and grasses as well as animal life (spider webs). I also found plant debris on old holes. Except for signs of animal life, mounds also showed evidence of sprouting vegetation. Growth of new vegetation happened to a greater (twice as much) extent on mounds than on old holes (Table 2).

Discussion

Foraging holes

The extent, and persistence of the foraging holes of the Cape porcupines indicated that these animals have ecosystem engineering capabilities (Jones et al. 1994). This is also supported by Bragg et al. (2005). The density of holes, area disturbed, and soil excavated during this study were comparable diggings which were made by old world porcupine species in two other studies, the Cape porcupine in South Africa (Bragg, 2003) and the Indian crested porcupine (*Hystrix indica*) in Israel (Alkon and Olsvig-Whittaker 1989; Alkon 1999). Foraging holes by Indian crested porcupines were reported to last for over 20 years due to the area being in a desert ecosystem (Alkon, 1999). The holes recorded in my study aged within a year of being dug. This was likely be facilitated by animal movements and the rain, particularly on foraging holes found on gentle slopes. The holes may thus disappear after continuous heavy rains. Despite the short lifespan of foraging holes, these holes may however have a long-term impact on soil and plants through secondary succession as result of the seeds and litter which may be buried in the soil (Gutterman, 2003; Jones et al., 2008; Travers et al., 2012). The growth which took place in the hole and on the mound indicated that seeds which might have been buried came alive when the soil was excavated by porcupines. This was indicative of their engineering capabilities in the savanna ecosystem. The scale of the engineering effects caused by porcupines in the Northern Cape of South Africa was great, covering an area of 510.391 m^2 per hectare with most digging done due to the diversity in geophytes in that area, which form the main component of the diet of porcupines (Bragg et al., 2005). In my study, diggings varied with each study site and the extent of digging differed, with Bisley having more diggings for both seasons compared to Roodeplaat. Most (72%) of the diggings that took place in Bisley during the dry season were on or near *V. nilotica* trees. In contrast, diggings during the wet season targeted bulbs of *Hypoxia* spp. Regular diggings for geophytes by porcupines in the Northern Cape not only created patches but showed that porcupine are selective in their diet as the area had about 350 species of geophytes and only 27 species were consumed (Bragg, 2003). In Roodeplaat, porcupine diggings were mainly observed on or near *V. robusta* trees in the dry season and fewer diggings were observed during the wet season and these were shallow in open spaces suggesting that bulbs were targeted. The age of the targeted species *(V. robusta* and *V. nilotica*) influenced the size of the foraging holes dug by porcupines. As a result, porcupines often dug just below the trunk base of *V. robusta* trees and occasionally on *V. karroo* and *Dombeya rotundifolia* in Roodeplaat. In Bisley, porcupines dug for the below ground portion of the trunk and roots of seedlings of *V. nilotica* up to 12 cm.

Total soil carbon and nitrogen

As semi-fossorial mammals, porcupines alter soil structure through burrowing and deposition of soil on the surface thus creating mounds. Like most biotubators, porcupines may increase SOM and N. However, C and N concentrations in soil may decrease because of redistribution of soil from below to above ground, this may cause soils with different nutrient contents to mix and alter the concentration of soil nutrients (Xue and An, 2018). In the current study, there was no significant difference in amounts of TN and TC in soil collected from the mound and that collected from undug soil, this could be because the mounds were fairly recent with not much decomposition having taken place (a year or less old). In a similar study which was done on plateau pika (*Ochotona curzoniae*) in China, it was found that TN and SOC increased in disturbed areas over 2 years compared to undisturbed areas (Yu et al., 2017). Similarly, Yurkewycz et al. (2014) found that new diggings made by pocket gopher (*Thomomys talpoides*) mounds decrease soil nutrients, but over time increased due to plant burial which facilitates rapid decomposition. The fine soil particles which are dug out by porcupine create a mound which is gradually eroded or disturbed by other animals such as ungulates, leaving uncovered gravel, which potentially lead to soil organic carbon loss (Clark et al., 2016; Briones, 2018) as carbon is not stored on gravel.

Vegetation and animal life in or near the foraging holes

The findings on this study revealed that the foraging holes of porcupines provide shelter for other invertebrates (e.g. spiders). Older holes were used by spiders as well as millipedes (see Table 2). This potentially indicated that porcupines create shelter for other animals such as invertebrates. Spiders using these holes may also use them to hunt. This is another attribute of an ecosystem engineer. For example, aardvark foraging holes were found to be used by reptiles and birds in South Africa (Whittington-Jones et al., 2011). I found that newly excavated foraging holes, may also disturb ant and termite nests. This was likely indicated by the presence of ants and termites on new holes (Genise, 2017). I also found that plants on the mound germinated faster than those on the undug adjacent soil. In addition to facilitating invertebrates, porcupines also facilitated the germination of seeds likely buried in the soil through excavation. This may result in increased species composition. Louw et al. (2017) found that soils excavated by aardvarks resulted increased plant species composition closer to the holes in disturbed soils compared to the undisturbed soils in South Africa. Most of the plants germinating inside holes and on the mounds were herbaceous. This may benefit grazers in Bisley, which is encroached by woody plants, thereby contributing positively to the savanna ecosystem (Mucina and Rutherford, 2006). The process of redistributing soil nutrients may likely have effects on plant community composition (Hale et al., 2020). Over time foraging holes (old holes) contained greater amounts of litter compared to adjacent undug surfaces, indicating that foraging holes may provide microhabitats for litter decomposition. Trapped litter may not easily be blown away from the holes by wind; instead, wind could facilitate deposition of litter into these holes. Excavation of soil by foraging porcupines may thus speed up litter decomposition by mixing organic matter with soil, which increases microbial activity (Eldridge and Mensinga, 2007; Briones, 2018). This may in turn result in increased soil quality.

Conclusion

The study showed that Cape porcupine are soil engineers through digging for food. Diggings by porcupines resulted in increased disturbance to the soil surface in the dry season, which may coincide with their increased intake of woody plants. The foraging holes became shallower as they aged due to soil deposition. The digging activities also resulted in germination of herbaceous plants in the wet season. At a larger scale, this could potentially contribute to the restoration of the grassland in Bisley. The effects of porcupine digging on soil may not be immediate. As a result, such studies require time to investigate vegetation on the disturbed as well as undisturbed soil over a longer period after the disturbance.

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Chapter 4: General discussion and recommendations

General discussion

The aim of the study was to investigate foraging activities of the Cape porcupine in mesic savannas. I identified tree species which make up the main diet of porcupines in three geographically distant savanna sites (Chapter 2). I also quantified the porcupine effects on the landscape through their digging and foraging activities (Chapter 3). The study indicated that porcupine-induced bark damage is not seasonal; however, during the wet season the diet has more food constituents than the dry season.

I found that the tree species selected by porcupines differed with site and that targeted tree sizes also differed. This was readily apparent because trees with different stem diameters were utilised. The results also suggested that foraging holes dug by porcupines may have positive outcomes for other organisms as these holes are used constitute habitat for other animals (Chapter 3).

Findings of this study revealed that food availability influences the foraging patterns of porcupines. For example, I found that porcupine foraging during winter can be considered selective although this may represent availability more than choice, at least in terms of woody plants. This selectivity may be rather consistent within an area but can vary in different areas. For example, in Roodeplaat, *Vachellia nilotica* trees were not impacted by porcupines although in Bisley it was the preferred woody species while *V. robusta* occurs at all sites but is only utilised at Roodeplat.

Porcupines feeding on woody plants have been documented in many studies (e.g. Yeaton, 1988; Sharma and Prasad, 1992; Augustine and McNaughton, 2004). Tree damage estimates at the three study sites suggested that different trees are differently prone to porcupine damage. *Vachellia nilotica* faced the highest damage (70%) at Bisley Nature Reserved followed by *S. africana* at Goss (16%) and *V. robusta at* Roodeplaat (7%). The results suggest these study sites may have different densities of porcupines or that porcupines had more than one foraging site. The general observation suggests that porcupines are interested in the trunk of the tree in order to access the inner parts, i.e. cortex, xylem and phloem. Many of the trees in Bisley are saplings and at this stage, porcupine foraging leads to death of the plants. Such tree mortality coupled with germination and establishment of herbaceous plants on disturbed soils may contribute positively to decreasing the effects of bush encroachment (e.g. increased grass biomass and species richness of herbaceous plants). This study shows that through ringbarking and gnawing of stems and roots, porcupines can reduce woody plant cover.

As ecosystem engineers, porcupines fulfil an important role of facilitating resource availability for other species. In this study, the results of the vegetation on the dug soil suggest that, mounds act as sites where germination occurs quicker than at the adjacent undug soil. Greater amounts of litter were observed in old foraging holes than in the adjacent undug soil, indicating that holes act as sinks for litter and seeds. Soil dug out by porcupines when foraging may speed up litter decomposition by mixing detritus with soil, which may ultimately enhance microbial activity (Louw et al., 2018; Palmer et al., 2020).

Although porcupines are considered agricultural pests, it may be of importance to view the animal in terms of its role in shaping the ecology of an area. For example, it might be important to test whether the porcupine method of feeding and food preferences alter or affect the structure of the plant community in which it is found. Also important is a determination of the long-term implications for a plant community when herbivores such as porcupines increase in number.

Recommendations

I. Future studies can be carried out to relate porcupine densities to foraging activities (i.e. amount of bark damage and density of foraging holes) per site.

II. The level of bark damage may also determine the way in which tree species recover. A future study can be undertaken to determine how plants recover after porcupine bark damage. In particular, it would be relevant to investigate whether damaged plants reprout.

III. Processes such as decomposition requires longer time periods, and this study did not address that aspect. Future studies can measure rates of decomposition in foraging holes and outside the holes based on the premise that litter pockets in foraging holes facilitate nutrient cycling.

IV. Foraging holes constructed by porcupines act as dispersal sinks for seeds and fruits. A follow up investigation can be done to determine whether plant species rates of regeneration may be influenced by porcupine foraging activities.

V. Life span of foraging holes could be influenced by several factors such as slope animal trampling especially large herbivores and exposure, for example the life span of foraging holes on gentle slopes may be influenced by run-off from heavy rainfalls. An experiment can be carried out to observe the persistence of foraging holes.

VI. A study can be done on the different targeted tree species to test if they emit a specific volatile compound which attracts porcupine.

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Appendix. Authorities for plant species

Species name	Family
Diospyros lycioides subsp. guerkie (Kuntze) De Winter	Ebenaceae
Dombeya rotundifolia (Hochst) Planch	Malvaceae
Elionurus muticus (Spreng.) Kuntze	Poaceae
Eragrostis curvula (Schrad.) Ness.	Poaceae
Fingerhutia africana Nees	Poaceae
Gardenia volkensii K. Schum.	Rubiaceae
Gnidia caffra (Meisn.) Gilg.	Thymelaeaceae
Grewia flava De Candolle	Malvaceae
Hermannia depressa N.E.Br.	Malvaceae
Heteropogon contortus (L.) P. Beauv	Poaceae
Ipomoea obscura (L.) Ker Gawl.	Convolvulaceae
Ledebouria revoluta (L.F.) Jessop.	Hyacinthaceae
Melinis nerviglumis (Franch.) Zizka.	Poaceae
Panicum maximum (Jacq.)	Poaceae
Sclerocarya birrea (A.Rich.) Hochst.	Anacardiaceae
Searsia pyroides (Burch.) Moffett	Anacardiaceae
Senegalia caffra (Thumb) P.J.H. Hunter & Mabb	Fabaceae
Spirostachys africana Sond.	Euphorbiaceae
Vachellia karroo (Hayne) Banfi and Galasso	Fabaceae
Vachellia nilotica (L.) P.J.H. Hurter & Mabb	Fabaceae
Vachellia robusta (Burch) Kyalangalilwa & Boatwright	Fabaceae
Vachellia sieberiana (DC.) Kyalangalilwa & Boatwright	Fabaceae
Vachellia tortilis (Forssk.) Galasso & Banfi	Fabaceae
Ziziphus mucronata (Willd)	Rhamnaceae