

**The causes and consequences of *Seriphium plumosum* L. encroachment in  
semi-arid grassland communities of Gauteng Province, South Africa**

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**Submitted in fulfilment of the academic requirements of**

**Doctor of Philosophy (Botany)**

School of Life Sciences

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## **PREFACE**

Hosia Turupa Pule in the School of Life Sciences, College of Agriculture, Engineering and Science of the University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa carried out the research results in this thesis under the supervision of Dr Michelle Tedder and Dr Julius Tjelele from the University of KwaZulu-Natal and Agricultural Research Council, respectively.

The thesis is submitted for the degree of Doctor of Philosophy (PhD) in Botany and has not been submitted in any form to another university and, except where the work of others is cited and acknowledged.

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## **DECLARATION 1: PLAGIARISM**

I, Hosia Turupa Pule, declare that:

- (i) The research results reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;
- (ii) This dissertation has not been submitted in full or in part for any degree or examination to any other university;
- (iii) This dissertation does not contain other persons' data, pictures, graphs or other information, unless acknowledged as being sourced from other persons;
- (iv) This dissertation does not contain text, graphics or tables copied and pasted from internet, unless specifically acknowledged, and the source being cited in the dissertation and in the references sections.

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Date: July 2021

## DECLARATION 2: PUBLICATIONS AND PRESENTATIONS

The four paper chapters and presentations were written and presented by Hosea Turupa Pule. Michelle Tedder and Julius Tjelele contributed comments to all the manuscripts and presentations. The paper chapters presented in this dissertation were prepared according to the requirements of particular journals, to which they were submitted or published.

### Publication/s

Formatted for submission to the African Journal of Range and Forage Science

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### **Presentation/s**

Hosea Turupa Pule presented the following papers and posters at local and international conferences.

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Pule, H.T., Tedder, M.J., Tjelele, T.J. 2019. The effect of *Seriphium plumosum* L. canopy cover, fire and soil depth on components of soil fertility in South African semi-arid grassland community. Proceedings of the 54<sup>th</sup> Congress of the Grassland Society of Southern Africa. Kimberley, Northern Cape Province, South Africa.

Pule, H.T., Tedder, M.J., Tjelele, T.J. Dawood, H. 2018. The effect of season and fire on *Seriphium plumosum* L. forage quality in South African semi-arid grassland communities. Proceedings of the 53<sup>rd</sup> Congress of the Grassland Society of southern Africa. ARC-Vegetable and Ornamental Plants Training Centre, Pretoria, Gauteng Province, South Africa.

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Pule, H.T., Tedder, M.J., Tjelele, T.J. 2016. Slope position and grassland community influence on *Seriphium plumosum* L. encroachment. Proceedings of the 51<sup>st</sup> Congress of the Grassland Society of Southern Africa. Wilderness, Western Cape Province, South Africa. Pule,

H.T., Tedder, M.J., Tjelele, T.J. 2016. *Seriphium plumosum* L. encroachment is influenced by landscape factors and variation in grassland communities. 10<sup>th</sup> International Rangeland Conference 2016. Saskatoon, Canada.

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Signed: Hosia Turupa Pule (Candidate)

Date: July 2021

## **DEDICATION**

I would like to dedicate this dissertation to my wife, Refilwe Bridget Tshepo Pule and my sons (Thuso, Thato and Tlotlo Pule) for their understanding and patience, especially during my studies.

To my parents (Alpheus and Gladys Pule), who guided and supported me, especially when both my work and studies were frustrating me.

To my brothers (George and Tebogo Pule) and sisters (Boitumelo and Lesego Pule), who always encouraged and believed in me, even when I had lost the will to continue with my studies.

## Abstract

*Seriphium plumosum* L encroachment in the semi-arid grassland communities of South Africa results from a complex interaction of environmental factors, which pose a major challenge to managing the rate and extent of its encroachment. Woody plant encroachment effects on ecosystem functioning are non-universal, with both positive and negative effects equally probable. Although the causes and consequences of woody plant encroachment are documented worldwide, this research on *S. plumosum* is lacking, thus hindering the development of control measures for its encroachment.

In chapter 2, the effect of abiotic (aspect, rockiness, sand and soil fertility (soil organic carbon, phosphorus, magnesium and pH) and biotic (*S. plumosum* density, basal cover and veld condition) factors on *S. plumosum* encroachment susceptibility in grassland communities was explored using logistic regression. A decrease in basal cover had 0.926 times likelihood estimate of increasing *S. plumosum* encroachment susceptibility. An increase in *S. plumosum* susceptibility was also observed with decrease in sand and magnesium concentrations. These results have showed that, overgrazed and/or burned areas with well-drained, nutrient poor soils in the semi-arid grassland communities of Gauteng Province are likely to become encroached by *S. plumosum*.

In chapter 3, we used two grassland communities, Carletonville Dolomite Grassland (CDG) and Rand Highveld Grassland (RHG), and abiotic factors (Soil Organic Carbon (SOC), Total nitrogen (TN), Phosphorus (P), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg) and pH) to investigate habitat preferences of *Seriphium plumosum* L. in the semi-arid grassland communities of Gauteng, South Africa. Bottom slope regions in RHG had significantly higher *S. plumosum* density ( $59.00 \pm 8.62$  plants/50 m<sup>2</sup>) than bottom slope regions in CDG ( $19.75 \pm 3.01$  plants/50 m<sup>2</sup>). Soil sodium content was similar in CDG slope positions and higher than in RHG. Furthermore,

*Seriphium plumosum* density was positively related to components of soil fertility; P ( $r^2 = 0.1270$ ;  $P = 0.0036$ ), K ( $r^2 = 0.0786$ ;  $P = 0.0237$ ), Na ( $r^2 = 0.0686$ ;  $P = 0.0350$ ), Ca ( $r^2 = 0.0681$ ;  $P = 0.0358$ ), and SOC content ( $r^2 = 0.0669$ ;  $P = 0.0374$ ). The results revealed that *S. plumosum* density in grassland communities increases with increasing soil sand content and decreasing soil fertility.

Chapter 4 was aimed at exploring the interactive effects of *S. plumosum* canopy cover, fire and soil depth on components of soil fertility; K, P, Mg, TN, Na, Ca, SOC and pH. All the components of soil fertility measured showed a significant decrease with increasing soil depth and post-fire treatment ( $P < 0.05$ ). The results have shown that *S. plumosum* encroachment contributes to accelerate rather than reverse rangeland degradation. Furthermore, fire alone is not sufficient to control *S. plumosum* encroachment in grassland, since it may reduce grass competitive ability, which in turn improves the conditions for *S. plumosum* seed germination and recruitment.

In Chapter 5, an experimental study was designed using a 3 x 4 factorial analysis of variance to investigate the effect of season (dry and wet), burning (burned and unburned), slope position (top and bottom), and their interaction on *Seriphium plumosum* L. crude protein (CP), neutral detergent fibre (NDF), total phenolics (TPs) and condensed tannins (CTs) concentrations. *Seriphium plumosum* CP concentrations from post-burned sites was higher than from unburned sites. Crude protein concentration was higher during the wet season in burned sites than in unburned sites, which were also higher than CP concentrations during dry season at unburned sites and burned sites. In contrast, *S. plumosum* NDF concentrations were similar during the dry season in burned and unburned sites, but higher than similar NDF during the wet seasons on both post burned and unburned areas. Generally, the study showed that *S. plumosum* encroachment control in the semi-arid grasslands requires understanding its drivers and effects on rangeland composition and

functioning. Furthermore, integrating ecological control measures might potentially contribute to the development of its sustainable management programmes.

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# CHAPTER 1: INTRODUCTION & LITERATURE REVIEW

## 1. INTRODUCTION

### 1.1. Rationale

Woody plant encroachment is an increase in density, cover and biomass of indigenous and invasive woody plant species (van Auken, 2009). The term woody plant encroachment is synonymous with other wide-ranging terminologies such as bush thickening (Wiegand et al. 2006), woody weed invasion (Kiswaga et al. 2020) and woody plant regrowth (Eldridge et al. 2003). Although it is widespread across a range of biomes and a rainfall gradient from arid (de Klerk 2004), to mesic areas (Montane ´ et al. 2011), it is particularly problematic in arid and semi-arid grasslands and savannas (Kulmatiski and Beard 2013). Woody plant encroachment occurs at different times in different countries, but at comparable rates in grassland and savanna ecosystems (Archer et al. 2017). The encroachment rate is particularly comparable in North America (Barger et al. 2011), South America (Anadón et al. 2014), Australia (Noble 1997), Africa (Bond et al. 1994; Venter et al. 2018), and southern Asia (Kumar et al. 2020). It involves many woody plant species that range from shrubs to trees in stature, from evergreen to deciduous, and broad-leaved to needle-leaved in leaf habit (Liu et al. 2013). The fact that it is reported in the arctic tundra, in temperate, subtropical, tropical, coastal and montane grasslands, in hot and cold desert grasslands, and in savannas and steppe (Tape and Racine, 2006, Knapp et al. 2008a, Naito and Cairns, 2011), shows the complexity of its drivers, both temporally and spatially.

In South Africa, approximately 10 to 20 million hectares of rangeland are affected by woody plant encroachment (Hoffman and Ashwell, 2001), and areas encroached and the rate of encroachment are likely to continue based on the past trends and future projections (Hughes, 2003; Van Auken, 2009). Woody plant encroachment poses a major concern for land users, especially

beef and sheep farmers because it reduces grazing capacity of rangelands through displacing grasses, as well as negatively affecting other ecosystem services like water retention and soil protection from erosion (Gillson and Hoffman, 2007). Although this phenomenon is well documented worldwide (Archer et al. 2017; Ward et al. 2014; Venter et al. 2018), research on its causes and consequences in rangeland communities is still not well understood. This is due to the fact that, woody plant encroachment is modified by local patterns that include disturbance (e.g. fire and grazing), topography, soil texture and fertility, either alone or in combinations (Archer et al. 2017). Furthermore, once woody plant encroachment has occurred, its effect on ecosystem processes is non-universal (Eldridge et al. 2011), with both positive and negative effects equally probable and dependent on land use objectives (Archer and Predick 2014). These complexities pertaining to the causes and consequences of woody plant encroachment on rangeland communities limit managing or controlling their rate and extent of encroachment (Archer et al. 2017). It is not only the extent, but also the rate of woody plant encroachment that is a concern. Consequently, understanding woody plant encroachment on rangelands worldwide necessitates the use of multi-factorial experiments to aid in the understanding of underlying factors and the development of management strategies.

## **1.2. Justification**

The arid and semi-arid rangelands of the world cover about 40% of the earth land surface, constituting the largest terrestrial area on the planet (Schimel, 2010) and providing home to approximately 2.3 billion people (World Resource Institute, 2002). Globally, these ecosystems are experiencing extensive environmental change that causes woody plants to encroach into grasslands and change open savannas to dense woodlands (Zafar et al. 2005; van Auken, 2009). Although extensively debated, the causes of woody plant encroachment at a local scale are

centered on disturbances such as a land-use history of intensive, continuous grazing (van Auken, 2009; Archer et al. 2017) and fire suppression (Bond et al. 2003). At a global scale, the causes of woody plant encroachment are centered on changing climate and increased atmospheric CO<sub>2</sub> (Ward, 2010; Wigley et al. 2010; Buitenwerf et al. 2012). Other researchers propose that the lack of browsing domestic and wild animals contributes to the advancement of woody plant encroachment (Sankaran et al. 2013; Archer et al. 2017). However, browsing animals also contribute to the spread of viable woody plant seeds in rangelands (Tjelele et al. 2014; 2015b). Ascribing a single factor as the cause of woody plant encroachment is impossible (Ward, 2005; Kraaij and Ward, 2006; van Auken 2009), particularly because plant species adaptation, land use history and changes in climate vary markedly among bioclimatic zones (Archer et al. 2017).

Generally, woody plant encroachment has both positive and negative effects on a range of ecosystem functions from a land management perspective (Eldridge et al. 2003; 2011). These effects depend on the encroaching woody plant species functional traits (Eldridge and Ding 2021) and the encroachment stage (Archer et al. 2017). To develop management strategies for encroaching woody plant species, there is a need to understand the causes and consequences of encroaching woody plant species and their interactions with climate, edaphic factors, land use history and fire (Bond, 2008; Lohmann et al. 2014).

In South Africa, *Seriphium plumosum* L., previously known as *Stoebe vulgaris* (Nkosi et al. 2018) is an indigenous, hardy, multi stemmed dwarf-shrub that grows to an average height and width of 60 cm (Schmidt et al. 2007). Although well distributed in grassland, it thrives in nutrient poor sandy soils, with an average annual rainfall of 620 – 750 mm (Snyman, 2009a). The density of *Seriphium plumosum* has increased within its geographic range in the South African semi-arid grassland biome (du Toit and Sekwadi, 2012), caused by among others, changes in environmental

conditions. Its encroachment in South African rangelands is estimated at approximately 150 202 ha (Avenant, 2015), predominantly in the arid and semi-arid grassland communities of the Eastern Cape, Free State, Mpumalanga, Northwest and Gauteng Provinces (Snyman, 2011). *Seriphium plumosum* is also naturalized in other southern African countries such as Angola, Namibia, Mozambique and Zimbabwe (Koekemoer, 2001), and in Madagascar and the USA (Schmidt et al. 2002). However, due to its sparse distribution in these countries, its impact on their grassland communities and ecosystem services is relatively insignificant. Nevertheless, an increase in the rate and extent of *S. plumosum* encroachment on rangeland communities will compromise the potential of these ecosystems to support a large population of grazers, with negative impacts on the pastoral economy.

In South Africa, conventional management of *S. plumosum* encroachment using mechanical and chemical measures is labour intensive and expensive, thus making these approaches unsustainable (Snyman 2011), especially to the resource poor or emerging livestock farmers. The combination of fire and browsing has not been explored in managing *S. plumosum* encroachment, despite their potential as management tools for encroaching woody plant species. Domestic and wild animals seldom browse *S. plumosum*, particularly during the early wet season (Avenant 2015). This may suggest that nutrients and plant secondary metabolites in *S. plumosum* foliage vary seasonally and geographically. However, the nutrient and secondary metabolite content and concentrations in *S. plumosum* forage material remain poorly understood. Variations in nutrients and plant secondary metabolites are well reported for many encroaching woody plant species in the semi-arid savanna, but less so for encroaching *S. plumosum* in South African semi-arid grassland communities. As such, this may limit the potential impact of *S. plumosum* on

rangeland and livestock sector. There is a need for more ecological research on *S. plumosum*, particularly in the semi-arid grassland communities of South Africa.

### **1.3. Literature review**

#### **1.3.1. Woody plant encroachment**

Savannas are communities or landscapes with a continuous herbaceous layer, usually dominated by grasses, herbs and forbs as well as trees and shrubs that constitute an important source of food for wild and domestic animals (Reynolds et al. 2007). Grasslands, shrublands and savannas, termed “rangelands,” constitute about 50% of the Earth’s land surface (Bailey and Ropes, 1998). Although rangelands are characterized by low, yet highly variable annual rainfall, (Robinson et al. 2019). These rangelands contain over 30% of the world’s human population and support the majority of the world’s livestock production (Safriel and Adeel, 2005; Reynolds et al. 2007). One of the most striking land-cover changes over the past 150 years in rangelands worldwide has been the proliferation of indigenous trees and shrubs at the expense of perennial grasses (Fensham et al. 2005; Wiegand et al. 2006; Archer, 2010), a phenomenon known as woody plant encroachment. This phenomenon is synonymous to other wide-ranging terminologies such as desertification (Archer et al. 2017), woody weed invasion (Ayres et al. 2001), bush encroachment (Ward, 2005) and shrub invasion (Throop et al. 2012).

Encroaching woody plant species vary in functional traits, from shrubs to trees in stature; from evergreen to deciduous, malacophyllous to sclerophyllous, and macrophyllous to microphyllous in leaf habit, structure and size;  $N_2$  fixing and from deep rooted to shallow rooted (Nelson et al. 2002). Because woody plant encroachment occurs across a wide range of climates from tropical to arctic and arid to humid, the drivers of woody plant encroachment likely vary

among climatic zones (Archer et al. 2017). These encroaching woody plant species increase in density, cover and biomass on rangelands because of changes in one or more abiotic and biotic factors (van Auken, 2009). The major concern for agriculturalists, conservationists and livestock farmers is not only the extent of woody plant encroachment, but also on the rate at which woody plant encroachment occurs (Kraaij and Ward, 2006). To manage woody plant encroachment, it is important to understand its ecology on rangeland communities.

### **1.3.2. Causes of woody plant encroachment**

The causes of woody plant encroachment in rangeland communities worldwide are intensively investigated (Bond and Midgley, 2000; Kraaij and Ward, 2006; Archer et al. 2017), but the extent of encroachment is still increasing at an alarming rate. This is because there are number of global and local scale factors that alone or in combination cause woody plant encroachment. Woody plant encroachment at a global scale is driven by climate change and increased atmospheric CO<sub>2</sub> concentrations (Stevens et al. 2006; Wigley et al. 2010). Locally, woody plant encroachment is caused by overgrazing, fire exclusion (Fuhlendorf et al. 2008), lack of browsers and the spread of viable woody plant seed by livestock (Tjelele et al. 2014; Tjelele et al. 2015a, b) among other factors. Although research into the cause of woody plant encroachment has received much attention, there is still uncertainty as to how these local and global factors either exclusively or in combination, contribute to cause woody plant encroachment worldwide.

#### **1.3.2.1. Global scale factors**

Global scale factors, such as increased CO<sub>2</sub> (Bond and Midgley, 2000) and climate change (Ward, 2010), are proposed as major global drivers of woody plant encroachment (Stevens et al. 2016).

Elevated atmospheric CO<sub>2</sub> is purported to reduce transpiration rates of grasses, causing deeper percolation of water into subsoils, thus creating conditions, which favour woody plant encroachment (Polley et al. 2003; Ward, 2010). Increased atmospheric CO<sub>2</sub> has driven the recent C<sub>3</sub> shrub and woody plant encroachment into grasslands throughout the semiarid regions of North and southwest America (Morgan et al. 2007). This notion is however, still a subject of considerable debate (e.g. Körner 2006; Ward, 2010; Bond and Midgley 2012). This is because, little to no effect of increased CO<sub>2</sub> levels on tree: grass ratios has been observed to date (Körner et al. 2005; Stock et al. 2005). The expected facilitation of woody plant encroachment by increased atmospheric CO<sub>2</sub> needs cautious application, especially in field experiments (Leakey and Lau, 2012). Wigley et al. (2010) and Buitenwerf et al. (2012) proposed long-term experiments investigating the effect of CO<sub>2</sub> on woody plant encroachment, during which other major factors such as fire and grazing are held constant. To date, it is still not clear how or to what extent elevated atmospheric CO<sub>2</sub> affects woody plant encroachment.

Woody plant densities have been increasing throughout a matrix of land use histories, ranging from areas heavily disturbed by fire and grazing to ungrazed and rarely burnt areas, suggesting climate rather than disturbance may be driving increasing woody plant encroachment in rangelands of South America (Silva et al. 2001) and probably elsewhere. Several studies have shown that elevated atmospheric CO<sub>2</sub> can increase the water-use efficiency of woody plant species, thereby increasing levels of soil moisture, and thus reducing their moisture stress (Centritto et al. 2002; Leakey et al. 2012). Plant available moisture is the function of the amount and timing of precipitation in combination with the effect of temperature on evaporative demand (Hatfield and Prueger 2015). Consequently, both temperature and moisture interact to influence the distribution of woody vegetation (Bond et al. 2003). In arid and semi-arid rangelands

worldwide, rainfall is the most important environmental parameter governing crucial life history processes in woody plants (Tews and Jeltsch 2004). Changes in rainfall patterns and volumes partly explain the increases in woody vegetation cover (Benhin, 2006), with an increase in mean annual rainfall reported to correlate with increasing woody plant encroachment (Venter et al. 2018). Although small experimental increases in precipitation intensity can push soil water deeper into the soil profile for exclusive use by woody plants, multiple interacting factors such as soil type and precipitation among others, hinders large-scale experimental tests on the effects of precipitation intensity on woody plant species growth (Wigley et al. 2010; Buitenwerf et al. 2012). In savanna systems, this will result in increasing aboveground woody plant growth and decreasing grass growth (Kulmatiski and Beard, 2013). At a gross scale, annual rainfall is a coarse index of seasonal plant available moisture and therefore determines rangeland dynamics (Shackleton, 1999). When annual precipitation increases above 250 mm, woody plants would increase in density with increasing rainfall because the grasses would not utilize all the rainwater (Ward and Ngairorue, 2000). Although there is research evidence on the role of rainfall (Tews and Jeltsch, 2004) and temperature (Criado et al. 2020) on woody plant species encroachment, more research is still required on how rainfall alone or combined with other factors contributes to an increase in woody plant encroachment.

The boundary between savannas and highland grasslands is caused by the greater frequency of freezing nights in grasslands or at least a greater frequency of low temperature during days below the minimum temperatures required for plant growth (Wakeling et al. 2012). Climate is one of the most important factors creating a savanna, thus a decline in temperatures may result in transition from grassland to savannas. Woody plant encroachment is related positively to global warming in the tundra (Criado et al. 2020), but less is known about the effect of global warming

in other areas. In contrast, studies have shown that freezing temperatures reduce tree survival and growth in savannas and deserts (Brando and Durigan, 2005; Holdo, 2006). There has been more research into the effect of moisture in combination with temperature on woody plant encroachment (Tews and Jeltsch 2004; Archer et al. 2017), than the effect of temperature alone (Brandt et al. 2017; Russell et al. 2019; Russell and Tedder 2020). Consequently, this lack of research on the effects of temperature limits understanding of how woody plants will response to temperature extremes.

#### **1.3.2.2. Local scale factors**

Domestic grazing herbivores (cattle and sheep), including some microbes and insects are the primary users of grasslands worldwide (Asner et al. 2004). The arrival of domestic herbivores with Anglo-European settlers in America, Australia, and Southern Africa, despite arriving at different times, resulted in the current woody plant encroachment in rangelands (Archer et al. 2017). These herbivores overgrazed grasses, reducing their above ground biomass and fine fuel load needed for grassland fires (van Auken, 2009). There is evidence that intense and frequent herbivory exerts a major influence on woody plant distribution and abundance across arid and semi-arid rangelands (Van Auken and Smeins, 2008), especially when coupled with reduced fire frequency. These factors create conditions that favour the establishment, survival and recruitment of woody plants over the grasses (Archer et al. 2017). They also contribute to conversion of grasslands into shrublands or woodlands (Knapp et al. 2008a; Knapp et al. 2008b). Generally, when these conditions occur, trees germinate *en masse* (Savadojo et al. 2007), thus enhancing the woody plant encroachment rate. These findings are consistent with the overgrazing hypothesis (Coetzee et al. 2008) and the two-layer soil moisture hypothesis (Ward et al. 2013). However,

other research proposes that high levels of herbivory, competition for moisture between trees and grasses, and the absence of fire are not the sole factors responsible for woody plant encroachment (Ward et al. 2014), but multiple interacting global and local factors (van Auken, 2009; Eldridge et al. 2011). Woody plant encroachment is also widespread in areas where grazing is infrequent and/or of light intensity (Ward, 2005; Ward et al. 2014; Tjelele et al. 2015a). Consequently, generalising grazing as a sole factor causing woody plant encroachment is unsupported and misleading.

Generally, fire is considered a major determinant of the ecology and distribution of African semi-arid rangelands (Higgins et al. 2000; Bond et al. 2005; Sankaran, 2019). It determines the vegetation community structure (Liedloff and Cook, 2007; Buitenwerf et al. 2012) by limiting woody plant seedling recruitment (Joubert et al. 2012), while maintaining woody plants species in the resprouting phase (Bond and Archibald, 2003; Hoffmann et al. 2009). In the early stages of shrub encroachment, when sufficient herbaceous biomass is present, fires might provide some reversibility to woody or shrubby plant encroachment process by negatively affecting their demography and by homogenizing soil resources across patches within weeks to months after burning (Sankey et al. 2012). Despite the importance of fire in savannas and grassland systems, the effect may differ depending on the frequency, intensity and time of burning. In mesic areas, fire is usually common and intense after good rain due to high grass biomass production (Skarpe, 1991). The frequency of fire is variable, but recurring fires are required to control or reduce the establishment, density and growth of woody plants in most rangeland communities (Simmons et al. 2007).

The recent widespread elimination of megafauna, such as elephants, in Africa and the overall reduction in the number of domestic browsers (Hester et al. 2006), contributed to cause

wide-scale woody plant encroachment in these regions (Stevens et al. 2014). Browser abundance exerts a major influence on woody plant distribution and abundance (van Auken and Smeins, 2008; Tjelele et al. 2014). Their activities may prevent shrubs and trees from establishing and exerting dominance by maintaining them at a stature vulnerable to fire (Archer et al. 2017). Many woody plant species support browsers, but some encroaching macrophyllous species, such as *Euclea* and *Searsia* (formerly *Rhus*) are unpalatable (van Auken, 2009; Gordijn et al. 2012; Sankaran et al. 2013). Consequently, this will result in browsers selecting palatable woody plant species and increasing the relative abundance of unpalatable ones (Wiseman et al. 2004; Goheen et al. 2007; Holdo, 2007), thus contributing to cause their encroachment in rangelands (Gordijn et al. 2012).

The potential of browsers as control agents for woody plant encroachment is broadly recognized (Estell et al. 2012), but more research is still needed on how the absence of browsing mammals contributes to causing woody plant encroachment (Midgley et al. 2010; Sankaran et al. 2013). Furthermore, investigation into how the absence of browsing herbivores alone or in combination with other local and global factors may contribute to cause woody plant encroachment is needed (Bond et al. 2003; Ward, 2005). In Africa, managing fire and herbivory at a local scale provides tools for mitigating woody plant encroachment (Venter et al. 2018). However, research into the effects of browsing herbivore exclusion alone or in combination with insufficient fire in causing woody plant encroachment still need more attention. This is because the effects of livestock on the rate of woody plant encroachment are variable due to the differences in the inherent characteristics of the study area or intensity, duration, or timing of grazing or browsing (Archer et al. 2017).

### **1.3.2.3. Edaphic and topographic factors**

Topographic position is one of the major determinants of soil depth and texture and therefore soil properties (Salako et al. 2006). Soil properties (i.e., texture, depth, and fertility) interact in complex ways to influence the patterns of woody plant abundance and distribution (Browning et al. 2008). Landscapes with varying slope positions differ in their ability to retain water and nutrients, due to their differences in soil depth and texture (Oztas et al. 2003), which are important determinants of woody plant distribution (Wu and Archer, 2005). For instance, aboveground biomass of woody plant species is often high on crests, decrease midslope, and then increased near stream channels (Colgan et al. 2012). Generally, coarse soils favour shrubs and fine-textured soils favours grasses (Holdo, 2013).

Runoff from upslope regions concentrates water and nutrients in downslope areas and augments incoming precipitation, enabling arroyos, washes, and intermittent drainages to support higher densities of woody plants than upslope portions of the landscape (Archer et al. 2017). Consequently, topography-mediated patterns of run-off/run-on can override or reinforce texture constraints on woody plant distribution, such that woodlands can develop on fine-textured soils that might otherwise, support grassland and open savanna (Wu and Archer, 2005). Evidence on the influence of soil properties and topography on woody plant stand structure and dynamics is limited and inconclusive. This is because local disturbance patterns can have continental consequences for woody plant encroachment and are of equal importance to edaphic and climatic variables in explaining the spatial variation in woody cover change (Venter et al. 2018). Furthermore, topo-edaphic properties can amplify or ameliorate climate-induced changes in woody plants and perennial grasses (Munson et al. 2016). It is therefore important to understand

woody plant encroachment in general terms if we are to anticipate and predict where and how their abundance might change under the current and future environmental conditions (Liu et al. 2013).

### **1.3.3. Consequences of woody plant encroachment**

Generally, woody plant encroachment is linked to land degradation and desertification processes (MEA, 2005), but this view is questioned (Eldridge et al. 2011; 2013). This is because woody plant encroachment results in both positive and negative effects on rangeland community functioning (Archer et al. 2001; van Auken, 2009; Eldridge et al. 2011). In addition, the effect of woody plant species on a range of ecosystem functions is species dependent and are modified by disturbances such as grazing (Roques et al. 2001) and fire. The effects of woody plant encroachment on rangeland communities are extensively studied, but the influence on a range of ecosystem functions is contradictory. This is probably because some aspects of ecosystem function improve while others deteriorate, and most exhibit variable responses (Eldridge et al. 2011). Furthermore, different land users view the effects of woody plant encroachment on rangelands differently.

#### **1.3.3.1. The negative effects of woody plant encroachment**

Woody plant encroachment is associated with land degradation (Huxman et al. 2005; Schlesinger et al. 2006; Knapp et al. 2008a). It causes major implications on biodiversity, productivity, decomposition, carbon storage, nitrogen and water dynamics (Jackson et al. 2000; Maestre et al. 2009). Woody plant encroachment is a phenomenon viewed in the context of its negative impact on pastoral production (Eldridge et al. 2011). As such, in the arid and semi-arid rangelands with very limited dryland farming (Morgan et al. 2007), woody plant encroachment reduces herbaceous

biomass production (House et al. 2003; Sharp and Whittaker, 2003) and the area available for grazing, by transforming grassland into savannas or woodlands (Eldridge et al. 2011). The effects of woody plant encroachment are complex, with reported decreases in annual net primary productivity in xeric sites, but dramatic increases at higher precipitation sites (Knapp et al. 2008a). In some areas, a small increase of approximately 10% in shrub cover can result in a marked reduction in pastoral production (Oba et al. 2000). *Prosopis glandulosa* shrub removal improves grass annual primary productivity by orders of magnitude during the years with above-average rainfall (Pierce et al. 2018). Grellier et al. (2013), reported an increase in the quality of grass biomass under tall *Vachellia* (formerly *Acacia*) trees species compared to open areas and under medium sized trees. These results confirm reports that the effects of woody plant encroachment on the herbaceous layer are variable, depend on woody plant species and age/ size (Treydte et al. 2009; Grellier et al. 2013) and are limited by rainfall or availability of water (Sankaran et al. 2005; Sankaran and Anderson 2009). An increase in woody plant encroachment will negatively affect the sustainability of pastoral, subsistence, and commercial livestock production (Anadón, et al. 2014). Consequently, woody plant encroachment affects negatively on the local human populations, especially in the rural areas, where people are dependent on livestock for their livelihood (Grellier et al. 2013).

There are studies reporting reductions in soil nutrients and plant diversity and increases in soil erosion following woody plant encroachment (Baez and Collins, 2008). In contrast, other studies have shown that woody plant species, particularly leguminous trees, can substantially enhance soil nutrient acquisition at a landscape scale, or increase the diversity of plant, animal, soil biota (Throop and Archer, 2008; Maestre et al. 2009) and resistance to soil erosion (Sanjuan et al. 2018). Wind and water transport nutrients, detritus and seeds which accumulate under shrub

canopies, leading to higher levels of infiltration (Bhark and Small, 2003), while the bare interspaces experience higher temperatures and evapotranspiration, retarded organic N incorporation, denitrification, ammonia volatilization, and increased erosion (Whitford, 2002). Woody plant encroachment is reported to decrease plant diversity and the value of land for grazers (Eldridge et al. 2011) by transforming grasslands to shrub or tree savannas and shrub and tree savannas to shrublands and woodlands (Archer et al. 2017). However, these effects of woody plant encroachment on a range of ecosystem functions are species specific and mediated by other disturbance factors.

Research studies have shown that woody plant encroachment impairs water resource availability in the semiarid and subhumid areas by reducing streamflow or ground water recharge as well as ground and surface water interaction, and carbon cycling by changing the atmosphere – ecosystem interaction (Huxman et al. 2005; Huang et al. 2006). Furthermore, annual water yield increased by approximately 200 mm when woody plant cover was reduced by up to 40 percent (Brown and Raines, 2002; Bumgarner and Thompson, 2012). Although woody plant encroachment is reported to have adverse effects on stream flow and ground water recharge (Archer and Predick, 2014), the evidence supporting this is limited (Wilcox et al. 2008). Consequently, an improved understanding of the effect of woody plant encroachment on soil water and hydrology on rangelands requires more research attention.

#### **1.3.3.2. The positive effects of woody plant encroachment**

Woody plant encroachment may significantly contribute to forage for wild and domestic browsers, household fuel-wood provision, and increased carbon sequestration, with consequences for global carbon budgets and climate change (Archer et al. 2017). In the arid and semiarid regions, trees and

shrubs affect the spatial distribution and cycling of nutrients by altering soil structure, microbial biomass, soil moisture, and microclimate by concentrating organic matter beneath their canopies (Liu et al. 2019). This results in the formation of “fertile islands” - a phenomenon widely described in cold desert scrub (e.g., Burke et al. 1989), hot desert scrub (Schlesinger et al. 1990, Kieft et al. 1998), temperate woodlands (Padien and Lajtha, 1992), and tropical rangeland communities (Scholes and Archer, 1997). Once a “fertile island” is formed, it may reinforce the persistence of shrubs (Whitford, 2002) and increase species richness by stabilizing soil and attenuating water stress (Thompson and Eldridge, 2005; Maestre et al. 2009; Pugnaire et al. 2011). The resource island formation is also accompanied by a decrease in resources in inter-shrub spaces, which might outweigh the positive effects of shrub dominance (Schlesinger et al. 1990). There is extensive literature reporting the facilitative effect of shrubs on the understory vegetation and on soil fertility in many different semi-arid ecosystems worldwide (Soliveres et al. 2011). As such, understanding of the developmental rates of “fertile islands” is of particular relevance in grassland and savanna systems, where woody plants have displaced grasses in recent history (Hibbard et al. 2001). This calls for more ecological research on woody plant encroachment to aid in developing and evaluating the trade-offs that must be considered when managing or controlling their encroachment into rangeland communities (Archer et al. 2017).

In South Africa, the semi-arid grassland biome supports extensive domestic and wildlife populations (Rutherford and Westfall, 1994). However, this biome is encroached by *Seriphium plumosum* L., previously known as *Stoebe vulgaris* (Avenant, 2015; Nkosi et al. 2018). *Seriphium plumosum* is a shrub, indigenous to South Africa, in the Astereaceae family that is well known by farmers as “slangbos” (i.e. snake bush) and/or “bankrupt bush/bankrot bos” (Snyman 2011). It is highly unpalatable to livestock and the chemical compounds responsible for this are not well

studied. Generally, tannins are among the most ubiquitous group of chemical defences produced by woody plants (Gross et al. 2008), and of this group, condensed tannins are the main chemical compounds that affect woody plant leaf defoliation by browsing ruminants (Chapman et al. 2010; Scogings et al. 2011). When tannins are over-ingested ( $> 55 \text{ g CT kg}^{-1} \text{ DM}$ ) by herbivores, they may bind with diverse proteins, thus making them inaccessible to herbivores (Moore et al. 2014). Condensed tannins reduce ruminant nutrient intake and live weight gain with negative consequences for productivity (Huang et al. 2018). In addition to condensed tannins, the fibre content of woody plants may also increase the toughness and digestibility of plant materials (Jung and Allen, 1995), thus negatively affecting microbial degradation of ingested feed (Waghorn and McNabb, 2003; Sun and Oba, 2014). For instance, mopane foliage is particularly ingested by herbivores at the end of the dry season when the re-foliation occurs (Skidmore et al. 2010), possibly because of chemical deterrents such as polyphenols have lower concentration during this stage (Styles and Skinner, 1997). A common feature of food resource distribution is that quality and quantity are often inversely correlated (Fryxell, 1991). However, research on *S. plumosum* forage quality remains little understood, yet its encroachment in the semiarid grasslands is viewed as a serious threat to sustainable animal production (Jordaan and Jordaan, 2007; Snyman, 2012). This is because its rapid spread displaces grasses by forming dense stands (Snyman, 2010) that can suppress grass productivity by 65 % (Snyman 2012). Consequently, its encroachment in grasslands reduces the grazing capacity and economic viability of livestock farming (Wepener et al. 2008; Snyman, 2012).

The first and most important step in understanding the shift from grass to woody plant dominance is by studying how woody plant seedlings establish in grass-dominated patches (Jurena and Archer, 2003). This is because the soil seed bank plays an important role in determining the




composition and dynamics of the vegetation through time (Gioria and Osborne, 2009). However, the extent to which fire may deplete existing soil seed reserves (Auld and Denham, 2006), especially of encroaching shrub species such as *S. plumosum* is not clear. Interaction of heat and smoke has been reported to break the seed dormancy for some species (Auld and Denham, 2006), thus stimulating their germination and subsequent recruitment (Keeley and Fotheringham, 2000). However, an understanding of the effect of fire in combination with other factors on *S. plumosum* seed germination is still lacking.

Fire is reported to kill *S. plumosum* seedlings, while stimulating its seed germination from the soil seed bank (Snyman, 2011), thus potentially contributing to controlling its encroachment. Simmons et al. (2007) proposed that, recurring fires are required to control or reduce the establishment, density and growth of woody plant encroachment in most grasslands. However, this research on *S. plumosum* encroachment in South African semi-arid grasslands is lacking, yet important in the development of ecological management measures in grassland communities.

Fire can affect plant foliar chemistry through changes in nutrient availability and light intensity, which can positively influence herbivore-feeding behaviour (Adams and Rieske, 2003). Generally, crude protein content of burned semi-arid rangeland is significantly higher, at least in the first season following a fire, than that of unburned areas (Snyman, 2015), particularly during spring (Waterman and Vermeire, 2011). Increased nutrient concentrations, can potentially improve animal performance, especially after burn (Tainton and Mentis, 1984). Other factors influencing plant foliar chemistry are season and growth stage (Emmerich, 1999). Although the chemistry of many encroaching woody plant species has received research attention, this research is lacking for *S. plumosum* chemistry, particularly as influenced by fire and season, thus limiting its management in rangeland communities. An integrated approach to managing woody plant

encroachment requires, amongst others, a better understanding of herbivore impact on the woody and herbaceous components of the system (Scogings, 1998). Consequently, a combination of fire and browsers, rather than one of these factors, is likely to yield positive results in controlling shrub cover (Hester et al. 2006). In light of the rate and the extent of *Seriphium plumosum* encroachment in the semi-arid rangeland communities of South Africa, and the controversy around the role of fire in determining its structure and composition, this research investigated the ecology of *S. plumosum*. The focus of this study was to understand the causes and consequences of its encroachment in South African semi-arid grassland communities (Table 1.1).

**Table 1. 1.** Theoretical framework showing how the different components of this thesis interact and the expectations that emerged from a critical evaluation of the literature

Scale	Local		Global	
Causes	Overgrazing, intense fires, edaphic factors and lack of browsing herbivores		Increased carbon dioxide, temperature and annual rainfall variability	
Consequences	Increased/decreased soil fertility, species composition, cover and ecosystem functioning			
Chapter	1	2	3	4
				
Chapter title	The effects of environmental factors on <i>Seriphium plumosum</i> L. encroachment susceptibility in the semi-arid grassland communities	The effects of abiotic factors in the semi-arid grassland communities on <i>Seriphium plumosum</i> L density and canopy size	The effect of <i>Seriphium plumosum</i> L. canopy cover, fire and soil depth on components of soil fertility in the semi-arid grassland community	The effect of season, fire and slope position on <i>Seriphium plumosum</i> L. forage quality in the semi-arid grassland communities
Control measures	Explore <i>S. plumosum</i> habitat preference (i.e. soils, slope positions and grassland communities) and factors that discourage its potential encroachment		Explore the use of fire in the control of <i>S. plumosum</i> encroachment and how fire influences its forage quality during different seasons.	
Management Implications	Development and adoption of management strategies that discourage <i>S. plumosum</i> encroachment in grassland communities		Develop management strategies that encourage strategic use of <i>S. plumosum</i> as feed for browsing animals, while controlling the rate and extent of its encroachment	

#### 1.4. Aims

The aim of this study was to investigate in the semi-arid grassland communities of South Africa the following research questions;

- Do local environmental factors contribute to cause and/or constrain *S. plumosum* L. encroachment?
- Do abiotic factors and grassland community have an effect on *S. plumosum* density and canopy sizes?
- Do *S. plumosum* L. canopies and fire influence components of soil fertility?
- How does season, fire and slope position influence *S. plumosum* L. forage quality?

#### 1.5. Objectives

The objectives were to explore;

1. The effect of environmental factors on *Seriphium plumosum* L. encroachment susceptibility in South African semi-arid grassland communities.
2. The effects of abiotic factors in South African semi-arid grassland communities on *Seriphium plumosum* L. density and canopy size.
3. The effects of *Seriphium plumosum* L. canopy cover, fire and soil depth on the components of soil fertility in South African semi-arid grassland communities.
4. The effect of season, fire and slope position on *S. plumosum* L. forage quality in South African semi-arid grassland communities.

The knowledge gained from this study will contribute some insight into factors that underlie *S. plumosum* encroachment and help to develop management strategies for increasing *S. plumosum* L. encroachment in semi-arid grassland communities, Gauteng province.

## **1.6. Outline of dissertation**

Each of the experimental chapters in this dissertation is structured as a paper for a specific journal. A certain level of repetition in some sections (introduction, materials and methods) of different paper chapters is unavoidable.

**Chapter 1:** Introduction and literature review.

**Chapter 2:** The effects of environmental factors on *S. plumosum* L. encroachment susceptibility in the semi-arid grassland communities of Gauteng Province, South Africa. Formatted for submission to the African Journal of Range and Forage Sciences.

**Chapter 3:** The effects of abiotic factors in South African semi-arid grassland communities on *Seriphium plumosum* L. density and canopy size. Published in PlosOne.

Pule H, Tjelele J & Tedder M. 2018. The Effects of Abiotic Factors in South African Semi-Arid Grassland Communities on *Seriphium plumosum* L. Density and Canopy Size. PLOS ONE 13(8): e0202809. <https://doi.org/10.1371/journal.pone.0202809>

**Chapter 4:** The effect of *Seriphium plumosum* L. canopy cover, fire and soil depth on the components of soil fertility in the semi-arid grassland community of Gauteng Province, South Africa. Formatted for submission to the African Journal of Range and Forage Science.

**Chapter 5:** The effect of season, fire and slope position on *S. plumosum* L. forage quality in the semi-arid grassland community of Gauteng Province, South Africa. Formatted for submission to the African Journal of Range and Forage Science.

**Chapter 6:** Synthesis

## 1.7. References

- Adams AS, Rieske L.K. 2003. Prescribed fire affects white oak seedling phytochemistry: implication for insect herbivory. In: Forest Ecology and Management. 176: 37 – 47.
- Anadón JD, Sala OE, Turner II BL, Bannett EM. 2014. Effect of woody-plant encroachment on livestock production in North and South America. PNAS. 35: 12984 – 12953.
- Archer SR, Anderson EM, Predick KI, Schwinning S, Steidl RJ, Woods SR. 2017. Woody plant encroachment: Causes and Consequences. In Briske DD, editor. Rangelands Systems. Springer Series on Environmental Management. pp 25 – 84.
- Archer SR, Boutton TW, Hibbard KA. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E.-D., Heimann, M., Harrison, S. et al. (eds.) Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego, pp. 39 – 46.
- Archer SR, Predick K. 2014. An ecosystem services perspective on brush management: Research priorities for competing land-use objectives. Journal of Ecology. 102 (6): 1394 – 1407.
- Archer SR. 2010. Rangeland conservation and shrub encroachment: new perspectives on an old problem. In: J.T. du Toit, R. Kock and J.C Deutsch eds): Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems.
- Asner GP, Elmore AJ, Olander LP, Martins RE, Harris AT. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources. 29: 261 – 299.
- Auld TD, Denham AJ. 2006. How much seeds remain in the soil after fire? Plant Ecology. 187: 15 – 24.
- Avenant P. 2015. Report on the national bankrupt bush (*Seriphium plumosum*) survey (2010 – 2012). Technical Report: Department of Agriculture, Forestry and Fisheries (DAFF).

- Ayres D, Melville G, Bean J, Beckers, D, Ellis M, Mazzer T, Freudenberger D. 2001. Woody weeds, biodiversity and landscape function in Western New South Wales. WEST 2000, Dubbo, Australia. P. 221.
- Baez S, Collins SL. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan desert plant communities. PlosOne. 3: 1 – 8.
- Bailey RG, Ropes L. 1998. Ecoregions: the ecosystem geography of the oceans and continents. Springer.
- Barger NN, Archer SR, Campell JL, Huang C, Morton, JA, Knapp AK. 2011. Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. Journal of Geophysical Research. 116: 1 – 17.
- Benhin JKA. 2006. Climate change and South African agriculture: Impacts and adaptation options, Centre for Environmental Economics and Policy in Africa (CEEPA), Discussion Paper no 21, University of Pretoria, Pretoria, South Africa.
- Bhark EW, Small EE. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6: 185 – 196.
- Bond WJ, Archibald S. 2003. Confronting complexity: fire policy choices in South African savanna parks. International Journal of Wildland Fire. 12: 381 – 389.
- Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO<sub>2</sub> and fire in promoting the spread of grasslands and savannas. Global Change Biology. 9: 973 – 982.
- Bond WJ, Midgley GF. 2000. A proposed CO<sub>2</sub> controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology. 6: 865 – 869.

- Bond WJ, Midgley GF. 2012. 'CO<sub>2</sub> and the uneasy interactions of trees and savanna grasses', *Philosophical Transactions of the Royal Society Biological Sciences*. 367: 601- 612.
- Bond WJ. 2008. What limits trees in C<sub>4</sub> grasslands and savannas? *Annual Review of Ecology, Evolution and Systematics*. 39: 641–659.
- Bond, W.J., Woodward, F.I. Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist*. 165: 525 – 538.
- Brando PM, During G. 2005. Changes in Cerrado vegetation after disturbance by frost (Sao Paulo State, Brazil).” *Plant Ecology* 175: 205 – 215.
- Brandt M, Rasmussen K, Peñuelas J, Tian F, Schurgers G, Verger A, Merts O, Palmer JRB, Fensholt R. 2017. Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa. *Nature Ecology and Evolution*. 1: 1– 6.
- Brown D, Raines T. 2002. Simulation of flow and effects of best management practices in the upper Seco Creek basin, south-central Texas, 1991 – 1998. *Water Resource Investigation Report 02-4249*. U.S. Geological Survey, Austin, Texas.
- Buitenwerf R, Bond WJ, Stevens N, Trollope WSW. 2012. Increased tree densities in South African savannas: 50 years of data suggest CO<sub>2</sub> as driver. *Global Change Biology*. 18: 675 – 684.
- Bumgarner J, Thompson F. 2012. Simulation of stream flow and the effects of brush management on water yields in the Upper Guadalupe River Watershed, South-central Texas. 1995 – 2010. *Scientific Investigations Report 2012 – 5051*, U.S, Geological Survey. Reston, Virginia.
- Burke IC, Reiners WA, Schimel DS. 1989. Organic matter turnover in a sagebrush steppe landscape. *Biogeochemistry*. 7: 11 – 31.

- Centritto, M., Lucas, M.E., Jarvis, P.G. 2002. Gas exchange, biomass, whole-plant water-use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. *Tree Physiology*. 22: 699 – 706.
- Chapman GA, Bork EW, Donkor NT. 2010. Effect of supplemental dietary tannins on the performance of white-tailed deer (*Odocoileus virginianus*). *Journal of Animal Physiology and Animal Nutrition*. 1: 65 – 73.
- Coetzee BWT, Tincani L, Wodu Z, Mwasi SM. 2008. Overgrazing and bush encroachment by *Tarchonanthus camphoratus* in semi-arid savanna. *African Journal of Ecology*. 46: 449 – 451.
- Criado MG, Myers-Smith IH, Bjorkman AD, Lehmann CER, Stevens N. 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography*. 29: 925 – 943.
- du Toit JCO, Sekwadi KP. 2012. Tebuthiuron residues remain active in the soil for at least eight years in the semi-arid grassland, South Africa. *African Journal of Range and Forage Science*. 29: 85 – 90.
- Eldridge DJ, Wilson BR, Oliver I. 2003. Regrowth and soil erosion in the semi-arid woodland of New South Wales. A report to the Native Vegetation Advisory Council. NSW Department of Land and Water Conservation.
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecological Letters*. 14: 709 – 722.
- Eldridge DJ, Soliveres S, Bowker MA, Val J. 2013. Grazing dampens the positive effect of shrub encroachment on ecosystem functions in a semi-arid woodland. *Journal of Ecology*. 50: 1028 – 1038.

- Eldridge DJ, Ding J. 2021. Remove or retain: ecosystem effect of woody encroachment and removal are linked to plant structural and functional traits. *New Phytologist*. 229: 2637 – 2646.
- Emmerich WE. 1999. Nutrient dynamics of rangelands burns in south-eastern Arizona. *Journal of Range Management*. 52: 606 – 614.
- Estell RE, Havstad KM, Cibis AF, Fredrickson EL, Anderson DM, Schrader TS, James DK. 2012. Increasing shrub use by livestock in a world with less grass. *Rangeland Ecology and Management*. 65: 553 – 562.
- Fensham RJ, Fairfax RJ, Archer SR. 2005. Rainfall, land use and woody vegetation cover in semi-arid Australian savanna. *Journal of Ecology*. 93: 596 – 606.
- Fryxell JM. 1991. Forage quality and aggregation by large herbivores. *American Naturalist*. 138: 478 – 498.
- Fuhlendorf SD, Archer SR, Smeins F, Engle DM, Taylor CA. 2008. The combined influence of grazing, fire and herbaceous productivity on tree-grass interaction. In van Auken O.W. (eds) *Western North American Juniperus communities*. Ecological studies, vol 196. Springer, New York, NY.
- Gillson L, Hoffman MT. 2007. Rangeland ecology in a changing world. *Science*. 315: 53 – 54.
- Gioria M, Osborne B. 2009. The impact of *Gunnera tinctoria* (Molina) Mirbel invasions on soil seed bank communities. *Journal of Plant Ecology*. 2: 153 – 167.
- Goheen JR, Young TP, Keesing F. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology*. 95: 129 – 138.
- Gordijn PJ, Rice E, Ward D. 2012. The effects of fire on woody plant encroachment are exacerbated by succession of trees of decreased palatability. *Perspectives in Plant Ecology, Evolution and Systematics*. 14: 411 – 422.

- Grellier S, Ward D, Janeau JL, Podwojewski P, Lorentz S, Abbadie L, Valentin C, Barot S. 2013. Positive versus negative environmental impacts of tree encroachment in South Africa. *Acta Oecologica*. 53: 1 – 10.
- Gross ME, Brune A, Walenciak O. 2008. Gut pH, redox conditions and oxygen levels in an aquatic caterpillar: potential effect on the fate of ingested tannins. *Journal of Insect Physiology*. 54: 462 – 471.
- Hatfield, J.L., Prueger, J.H. 2015. Temperature extremes: effect on plant growth and development. *Weather and Climate Extremes*. 10: 4 – 10.
- Hester AJ, Scogings PF, Trollope WSW. 2006. Long term impacts of goats browsing on bush-clump dynamics in a semi-arid subtropical savanna. *Plant Ecology*. 2: 277 – 290.
- Hibbard KA, Archer S, Schimel DS, Valentine DW. 2001. Biochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology*. 82: 1999 – 2011.
- Hoffman MT, Ashwell A. 2001. *Nature Divided: Land degradation in South Africa*, first ed. University of Cape Town Press, Cape Town, South Africa.
- Hoffmann WA, Haridasan AR, de Carvalho M, Geiger MT, Pereira EL, Gotsch MAB, Franco AC. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology*. 90: 1326 – 1337.
- Holdo R. 2006. Elephant Herbivory. Forst damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science*. 17: 509 – 518.
- Holdo RM. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications*. 17: 558 – 568.
- Holdo RM. 2013. Revisiting the two-layer hypothesis: Coexistence of alternative functional rooting strategies in savannas. *PLoSOne*. 8: 1 – 12.

- House J, Archer SR, Breshears DD, Scholes RJ, Nceas TGIP. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*. 30: 1763 – 1777.
- Huang Q, Liu X, Zhao G, Hu T, Wang Y. 2018. Potential and challenges of tannins as an alternative to in-feed antibiotics for farm animal production. *Animal Nutrition*. 4. 137 – 150.
- Huang Y, Wilcox BP, Stern L, Perotto-Baldivieso H. 2006. Springs on rangelands: runoff dynamics and influence of woody plant cover. *Hydrological Processes*. 20: 3277 – 3288.
- Hughes L. 2003. Climate change and Australia: Trends, projections and impacts. *Australian Journal of Ecology*. 28: 423 – 443.
- Huxman T E, Wilcox B P, Breshears DD, Scott R L, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody plant encroachment. *Ecology*. 86: 308 – 319.
- Jackson RB, Schenk HJ, Jobbagy EG, Canadell J, Colello GD, Field CB, Dickinson RE, Friedlingstein P, Heimann M, Kleidon A, Hibbard K, Kicklighter DW, Neilson RP, Parton WJ, Sala OE, Sykes MT. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* 10: 470 – 483.
- Joubert DF, Smit GN, Hoffman MT. 2012. The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. *Journal of Arid Environments*. 87: 1 – 7.
- Jung HG, Allen MS. 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. *Journal of Animal Science*. 73: 2774–90.
- Jurena PN, Archer S. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology*. 84: 907 – 919.

- Keeley JE, Fotheringham CJ. 2000. Role of fire in regeneration from seed. In *Seeds: The ecology of regeneration in plant communities*. 2<sup>nd</sup> edition (ed. M. Fenner).
- Kieft TL, White CS, Loftin SR, Aguilar R, Craig JA, Skaar DA. 1998. Temporal dynamics in soil carbon and nitrogen resource at a grassland-shrubland ecotone. *Ecological Society of America*. 79: 671 – 683.
- Knapp AK, Briggs JM, Collins SL, Archer, SR. 2008a. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*. 14: 615 – 623.
- Knapp AK, McCarron JK, Silletti AM, Hoch GA, Heisler JC, Lett MS, Blair JM, Briggs JM, Smith MD. 2008b. Ecological consequences of the replacement of native grassland by *Juniperus virginiana* and other woody plants. In *Western North American Juniperus communities: A dynamic vegetation type*, ed. O.W. Van Auken. New York: Springer. pp. 156 – 169.
- Koekemoer M. 2001. Systematics of the *Metalasia* group in the Relhaniinae (Gnaphalieae – Asteraceae). PhD thesis, Rand Afrikaans University, South Africa.
- Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RTW, Zotz G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Science*. 309: 1360 – 1362.
- Körner C. 2006. Plant CO<sub>2</sub> response: an issue of definition, time and resource supply. *New Phytology*. 172: 393 – 411.
- Kraaij T, Ward D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*. 186: 235 – 246.

- Kulmatiski A, Beard KH. 2013. Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change*. 3: 833 – 837. <https://doi.org/10.1038/nclimate1904>
- Kumar D, Pfeiffer, M, Gaillard C, Langan L, Martens C, Scheiter S. 2020. Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change. *Biological Conservation*. 241: 1 – 9.
- Kiswaga SAS, Mbwapbo JR, Shirima D, Mndolwa AS, Schaffner U, Eschen R. 2020. More widespread alien tree species do not have larger impacts on regeneration of native tree species in a tropical forest reserve. *Ecology and Evolution* 10: 5034–5044.
- Leakey ADB, Lau JA. 2012. Evolutionary context for understanding and manipulating plant responses to past, present and future atmospheric [CO<sub>2</sub>]. *Philosophical Transactions of the Royal Society Biology: Biological Sciences*. 367: 613 – 629.
- Liedloff AC, Cook GD. 2007. Modeling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the flames simulation model. *Ecological Modelling*. 201: 269 – 282.
- Liu F, Archer RS, Gelwick F, Bai E, Boutton TW, Ben Wu, X. 2013. Woody Plant Encroachment in to Grasslands: Spatial pattern of Functional Group Distribution and Community Development. *PloS ONE* 8: 1 – 13.
- Lohmann D, Tietjen B, Blaum N, Joubert DF, Jeltsch F. 2014. Prescribed fire as a tool for managing shrub encroachment in semi-arid savanna rangelands. *Journal of Arid Environments*. 107: 49 – 56.
- Maestre FT, Bowker MA, Puche MD, Hinojosa MB, Martinez I, Garcia-Palacios P, Castillo AP, Soliveres S, Luzuriaga AL, Sanchez AM, Carreira JA, Gallardo A, Escudero A. 2009. Shrub

- encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters*. 12: 930 – 941.
- MEA 2005. Millennium Ecosystem Assessment-Ecosystem and Human Well-being: Desertification Synthesis. World Resource Institute. Washington, D.C.
- Midgley JJ, Lawes MJ, Chamaille-Jammes S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*. 58: 1 – 11.
- Montane ´ F, Casals P, Dale MRT. 2011. How Spatial Heterogeneity of Cover Affects Patterns of Shrub Encroachment into Mesic Grasslands. *PLoS ONE* 6(12): e28652. doi:10.1371/journal.pone.0028652
- Moore BD, Andrew RL, Külheim C, Foley WJ. 2014. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. *New Phytology*. 201: 733 – 750.
- Morgan JA, Milchunas DG, LeCain DR, West M, Mosier AR. 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *PNAS*. 104: 14724 – 14729.
- [Munson](#) SM, [Sankey](#) TT, [Xian](#) G, [Miguel L. Villarreal](#) ML, [Homer](#) CG. 2016. Decadal shifts in grass and woody plant cover are driven by prolonged drying and modified by topo-edaphic properties. *Ecological Applications*. 26: 2480 – 2490.
- Naito AT, Cairns DM. 2011. Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. *Environmental Research Letters*. 6: 1 – 8.
- Nelson JA, Barnes PW, Archer S. 2002. Leaf demography and growth response to altered resource availability in woody plants of contrasting leaf habit in a subtropical savanna. *Plant Ecology*. 160: 193 – 205.

- Nkosi SE, Brown LR, Barrett SA. 2018. A baseline study for controlling the indigenous encroacher *Stoebe vulgaris* in natural grasslands of Southern Africa. *Agriculture, Ecosystems and Environments*. 265: 209 – 216.
- Noble JC. 1997. The delicate and noxious scrub: CSIRO studies on native tree and shrubs proliferation in the semi-arid woodlands of the eastern Australia. CSIRO, Lyneham.
- Oba G, Post E, Syvertsen PO, Stenseth NC. 2000. Bush cover and range condition assessment in relation to landscape and grazing in Ethiopia. *Landscape Ecology*. 15: 535 – 546.
- Oztas T, Koc A, Comakli B. 2003. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. *Journal of Arid Environments*. 55: 93 – 100.
- Padien DJ, Lajtha K. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. *International Journal of Plant Science*. 153: 425 – 433.
- Pierce NA, Archer SR, Bestelmeyer BT, James DK. 2018. Grass-shrub competition in arid lands: an overlooked driver in grassland-shrubland state transition? *Ecosystems*. Pp 1- 10
- Polley HW, Johnson HB, Tischler CR. 2003. Woody invasion of grasslands: evidence that CO<sub>2</sub> enrichment indirectly promotes establishment of *Prosopis glandulosa*. *Plant Ecology*. 164: 85 – 94.
- Pugnaire FI, Armas C, Mastre FT. 2011. Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradient, and ecosystem function. *Journal of Arid Environment*. 75: 1310 – 1320.
- Reynolds JF, Smith DMS, Lambin EF, Turner BL, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Fernandez RJ, Herrick JE, Huber-Sannwald E, Jiang H, Leemans R, Lynam

- T, Maestre FT, Ayarza M, Walker B. 2007. Global desertification: building a science for dryland development. *Science* 316, 847 – 851.
- Robinson NP, Allred BW, Naugle D.E, Jones MO. 2019. Plant available moisture is the function of the amount and timing of precipitation in combination with the effect of temperature on evaporative demand. *Ecological Applications*. 29: <https://doi.org/10.1002/eap.1862>.
- Roques KG, O'Connor TG, Watkinson AR. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*. 38: 268–280.
- Russell JM, Tedder MJ, Demmer S. 2019. *Vachellia sieberiana* var. *woodii*, a high-altitude encroacher: the effect of fire, frost, simulated grazing and altitude in the northwestern Kwazulu-Natal, South Africa. *African Journal of Range and Forage Science*. 36: 169 – 180.
- Russell JM, Tedder MJ. 2020. Frost tolerance in *Vachellia sieberiana* var. *woodii* in the high-altitude grasslands of southern Africa. *South African Journal of Botany*. 128: 239 – 245.
- Rutherford, M.C., Westfall, R.H. 1986. The biomes of Southern Africa - an objective categorization. *Memoirs of the Botanical Surveys of South Africa*. 51: 1 – 98.
- Safriel U, Adeel Z, Niemeijer D, Puigdefaregas J, White R, Lal R, Winslow M, Ziedler J, Prince S, Archer E, King C, Shapiro B, Wessels K, Nielsen T, Portnov B, Reshef I, Thonell J, Lachman E, McNab D. 2005. *Dryland Systems*. p. 636 – 653.
- Sanjuan Y, Arnaez J, Begueria S, et al. 2018. Woody plant encroachment following grazing abandonment in the subalpine belt: a case study in northern Spain. *Regional Environmental Change*. 18: 1103 – 1115.
- Sankaran, M. 2019. Drought and the ecological future of tropical savanna vegetation. *Journal of Ecology*. 107: 1531 – 1549.

- Sankaran M, Augustine DJ, Jayashree R. 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology*. 101: 1389 – 1399.
- Sankaran M, Augustine TM. 2009. Management and restoration in African savannas: Interactions and feedbacks. In: *New models for ecosystem dynamics and restoration* (eds): Hobbs, R.J. Suding, K.N. Island Press, Washington, Covelo, London.
- Sankaran M, Hanan NP, Scholes RJ, et al. 2005. Determinants of woody cover in African savannas. *Nature*. 438: 846 – 849.
- Sankey JB, Ravi S, Wallace CSA, Webb RH, Huxman TE. 2012. Quantifying soil surface change in degraded drylands: Shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical Research: Biogeosciences*, 117: G2, 1 – 11.
- Savadogo P, Savadogo L, Tiveau D. 2007. Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savanna woodlands of Burkina Faso. *Agriculture, Ecosystems and Environment*. 118: 80 – 92.
- Schimel DS. 2010. Drylands in the earth system. *Science*. 327: 418 – 419.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. *Science*. 247: 1043–1048.
- Schlesinger WH, Tartowski SL, Schmidt SM. 2006. Nutrient cycling within an arid ecosystem. *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site* (eds. K.M. Havstad, L. Huenneke & W.H. Schlesinger), pp. 133–149. Oxford University Press, New York.
- Schmidt E, Lotter M, McClelland W. 2002. *Tree and shrubs of the Mpumalanga and Kruger National Park*: Jacaranda Media Publisher, Pretoria.

- Schmidt E, Lötter M, McClelland W. 2007. Trees and Shrubs of Mpumalanga and Kruger National Park. Jacana Media, Johannesburg RSA.
- Scholes R J, Archer S R. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517 – 544.
- Scogings PF, Hjalten J, Skarpe C. 2011. Secondary metabolites and nutrients of woody plant in relation to browsing intensity in African savannas. *Oecologia*. 167: 1063 – 1073.
- Scogings PF. 1998. Impact of browser on woody plant in African savannas. In: *Proceedings of Research and training strategies for goat production systems in South Africa*. 76 – 77.
- Shackleton CM. 1999. Rainfall and topo-edaphic influences on woody community phenology in South African savannas. *Global Ecology and Biogeography*. 8: 125 – 136.
- Sharp BR, Whittaker RJ. 2003. The irreversible cattle-driven transformation of a seasonally flooded Australian savanna. *Journal of Biogeography*. 30: 783 – 802.
- Silva IA, Zambrano A, Farinas MR. 2001. Increase in woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela. *Journal of Biogeography*. 28: 977 – 983.
- Simmons MT, Windhager S, Power P, Lott J, Lyons RK, Schwope C. 2007. Selective and non-selective control of invasive plants: the short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. *Restoration Ecology*. 15: 662 – 669.
- Skarpe C. 1991. Impact of grazing on savanna ecosystems. *Ambio*. 20: 351 – 356.
- Skidmore AK, Ferwerda JG, Mutanga O, Van Wieren SE, Peel M, Grant RC, Prins HHT, Balcik FB, Venus B. 2010. Forage quality of savannas – Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environments*. 114: 64 – 72.

- Snyman H.A. 2015. Short-term responses of South African semi-arid rangelands to fire: A review of impact on plants. *Arid Land Research and Management*. 29: 237 – 254.
- Snyman HA. 2009a. A physiological approach to the distribution and spread of *Seriphium plumosum*. *Newsletter of the Grassland Society of Southern Africa*. 9: 29 – 37.
- Snyman HA. 2009b. Germination potential of *Seriphium plumosum* (bankrupt bush, slangbos or vaalbos). *Grassroots* 9: 43 – 48.
- Snyman HA. 2010. Allelopathic potential, seed ecology and germination of the encroacher shrub *Seriphium plumosum*. *African Journal of Range and Forage Science*. 27: 29 – 37.
- Snyman HA. 2011. Short-term response of the encroacher shrub *Seriphium plumosum* to fire. *African Journal of Range and Forage Science*. 28: 65 – 77.
- Snyman HA. 2012a. Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *South African Journal of Botany*. 81: 34 – 39.
- Snyman HA. 2012b. Control measures for the encroacher shrub *Seriphium plumosum*. *South African Journal of Plant and Soil*. 29: 157 – 163.
- Soliveres S, Palacios PG, Castillo-Monroy AP, Maestre FT, Escudero A, Valladares F. 2011. Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass-shrub interaction in semi-arid ecosystem. *Oikos*. 120 (5): 710 – 719.
- Stevens N, Lehmann CER, Murphy BP, Durigan G. 2016. Savanna woody encroachment is widespread across three continents. *Global Change Biology*. 23: 235 – 244.
- Stevens N, Swemmer AM, Ezzy L, Erasmus BFN. 2014. Investigating potential determinants of the distribution limits of a savanna woody plant: *Colophospermum mopane*. *Journal of Vegetation Science*. 25: 363 – 373.

- Stevens PW, Fox SL, Montague CL. 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management* 14:435–444.
- Styles CV, Skinner JD. 1997. Seasonal variations in the quality of mopane leaves as a source of browse for mammalian herbivores. *African Journal of Ecology*. 35: 254 – 265.
- Sun Y, Oba M. 2014. Effect of feeding a high-fibre by-product feedstuff as a substitute for barley grain on rumen fermentation and productivity of dairy cows in early lactation. *Journal of Dairy Sciences*. 97: 1594 – 1602.
- Tainton NM, Mentis M.T. 1984. Fire in grassland, pp 115 – 197. In P de V. Booysen, N.M. Tainton (Eds.), *Ecological effects of fire in South African ecosystems*. Springer-Verlag, Berlin/Heidelberg/New York.
- Tape K, Racine M.S. 2006. The evidence of shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*. 12: 686 – 702.
- Tews J, Jeltsch F. 2004. Modelling the impact of climate change on woody plant population dynamics in South African savanna. *BMC Ecology*. 4: 17.
- Thompson WA, Eldridge DJ. 2005. Plant cover and composition in relation to density of *Callitris glaucophylla* (white cypress pine) along a rainfall gradient in eastern Australia. *Australian Journal of Botany*. 53: 545 – 554.
- Throop HL, Archer SR. 2008. Shrub (*Prosopis velutina*) encroachment in the semidesert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. *Global Change Biology*. 14: 2420 – 2431.

- Throop LH, Reichmann LG, Sala OE, Archer S.R. 2012. Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. *Oecologia*. 169: 373 – 383.
- Tjelele T, Ward D, Dziba L. 2014. Diet quality modifies germination of *Dichrostachys cinerea* and *Acacia nilotica* seeds fed to ruminants. *Rangeland Ecology and Management*. 67: 423 – 428.
- Tjelele TJ, Ward D, Dziba LE. 2015a. The effect of passage through the gut of goats and cattle, and the application of dung as a fertilizer on seedling establishment of *Dichrostachys cinerea* and *Acacia nilotica*. *Journal of Australian Rangeland Society*. 37: 147 – 156.
- Tjelele TJ, Ward D, Dziba LE. 2015b. The effect of seed ingestion by livestock, dung fertilization, trampling, grass competition and fire on seedling establishment of two woody plant species. *Plos One*. 10: 1–13.
- Treydte AC, Grant CC, Jeltsch F. 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannas. *Biology and Conservation*. 18: 3989 – 4002.
- Van Auken OW, Smeins F. 2008. Western North American Juniperus Communities: Patterns and Causes of Distribution and Abundance. In: Van Auken O.W. (eds) *Western North American Juniperus Communities*. Ecological Studies, vol 196. Springer, New York, NY8.
- van Auken OW. 2009. Causes and consequences of woody plant encroachment into western North American grassland. *Journal of Environmental Management*. 90: 2931 – 2942.
- Venter ZS, Cramer MD, Hawkins HJ. 2018. Drivers of woody plant encroachment over Africa. *Nature communications*. 9: 1 – 7.
- Waghorn GC, McNabb WC. 2003. Consequences of plant phenolic compounds for productivity and health for ruminants. *Proceedings of the nutrition society*. 62: 383 – 392.

- Wakeling JL, Cramer MD, Bond WJ. 2012. The savanna-grassland 'treeline': why don't savanna trees occur in upland grasslands? *Journal of Ecology*. 100: 381 – 391.
- Ward D, Hoffmann MT, Collocott SJ. 2014. A century of woody plant encroachment in the dry Kimberley savanna of South Africa. *African Journal of Range and Forage Science*. 31 (2): 107 – 121.
- Ward D, Ngairorue BT. 2000. Are Namibia's grasslands desertifying? *Journal of Range Management*. 53: 138 – 144.
- Ward D, Wiegand K, Getzin S. 2013. Walter's two-layer hypothesis revisited: back to the roots! *Oecologia*. 172: 617 – 630.
- Ward D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*. 22: 101 – 105.
- Ward, D. 2010. A resource ration model of the effects of changes in CO<sub>2</sub> on woody plant invasion. *Plant Ecology*. 209: 147 – 152.
- Waterman RC, Vermeire LT. 2011. Grazing deferment effects on forage diet quality and ewe performance following summer rangeland fire. *Rangeland Ecology and Management*. 64: 18 – 27.
- Wepener JP, Kellner K, Jordaan D. 2008. The control of *Seriphium plumosum* encroachment in certain areas of the grassland biome in the North-West Province. *Proceedings of the Grassland Society of Southern Africa*. 43: 88 – 89.
- Whitford WG. 2002. *Ecology of desert systems*. Academic press, an Elsevier Science Imprint, San Diego, California. pp 343. ISBN 0-12-747261-4.

- Wiegand K, Saltz D, Ward D. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systems*. 7: 229 – 242.
- Wigley B J, Bond WJ, Hoffman MT. 2010 Thicket expansion in a South African savanna under divergent land use: local versus global drivers? *Global Change Biology*. 16: 964 – 976.
- Wiseman R, Page B, O’ Connor T. 2004. Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research*. 34: 25 – 37.
- Wilcox BP, Huang Y, and Walker JW. 2008. Long-term trends in streamflow from semiarid rangelands: uncovering drivers of change. *Global Change Biology* 14: 1676–89.
- World Resource Institute. 2002. Democratic Decentralization of natural resources: Institutionalizing popular participation. J. C. Ribot (Eds). In *Beyond structural adjustment*. Pp 159 – 182.
- Wu XB, Archer SR. 2005. Scale dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes. *Landscape Ecology*. 20: 733 – 742.
- Zafar A, Safriel U, Niemeijer D, White, R., Press, I. 2005. Millennium ecosystem assessment, ecosystems and human well-being: Desertification synthesis, Washington, D.C.

## CHAPTER 2

**The effects of environmental factors on *Seriphium plumosum* L. encroachment susceptibility in the semi-arid grassland communities of Gauteng Province, South Africa**

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## Abstract

A complex interaction of environmental factors is responsible for *Seriphium plumosum* L. encroachment in South African semi-arid grasslands. This complex interaction poses a major challenge to managing the rate and extent of *S. plumosum* encroachment. Although a broad understanding of *S. plumosum* ecology is required to develop an integrated approach to managing its encroachment, this area of research is still lacking. This study explored the effects of abiotic factors; aspect, rockiness, sand and fertility (soil organic carbon, phosphorus, magnesium and pH) and biotic (*S. plumosum* density, basal cover and veld condition) factors on *S. plumosum* encroachment susceptibility in grassland communities using logistic regression. There was a significant negative effect of basal cover (-0.0768;  $P = 0.0040$ ), sand (-0.1272;  $P = 0.0308$ ) and magnesium (-0.0362;  $P = 0.0329$ ) on the likelihood of *S. plumosum* encroachment. However, there were no significant effects of aspect, sward cover, rockiness, soil organic carbon, pH and phosphorus ( $P > 0.05$ ) observed on the likelihood of *S. plumosum* encroachment. Increases in basal cover had 0.926 times likelihood estimate of decreasing *S. plumosum* encroachment susceptibility, followed by sand and magnesium with 0.881 and 0.964, respectively. This study has shown that, overgrazing and/or veld burning on well-drained poor soils increases the likelihood of *S. plumosum* encroachment in the semi-arid grasslands communities of South Africa. Consequently, management that discourages overgrazing and accidental fires may contribute to manage *S. plumosum* encroachment in semi-arid grasslands of Gauteng Province, with result applicable to other Provinces where *S. plumosum* has encroached.

**Keywords:** catena gradient, regression analysis, soil fertility, veld condition

## **2.1. Introduction**

The arid and semi-arid grassland and savanna ecosystems cover more than 41% of the global terrestrial landscape (Chapin 2001), and support approximately 2.4 billion people (MEA 2005). These ecosystems are affected by woody plant encroachment (Archer 2010), a phenomenon that is synonymous to other wide-ranging terminologies such as desertification (Archer et al. 2017), woody weed invasion (Kiswaga et al. 2020), shrub invasion (Throop et al. 2012) and bush encroachment (Meik et al. 2002). Woody plant encroachment decreases grass productivity (Kulmatiski and Beard 2013), grass species richness (Knapp et al. 2008; van Auken 2009) and biodiversity (Ratajczak et al. 2012). Consequently, woody plant encroachment threatens the sustainability of ecosystems and the profitability of cattle and sheep production (Asner et al. 2004; Archer et al. 2017).

The causes of woody plant encroachment are still a subject of much debate worldwide (Ward 2005; Eldridge et al. 2011). This is because the relative importance of different drivers varies among species, land use history and climatic conditions (Buitenwerf et al. 2012; Archer et al. 2017). Climatic factors, soil disturbance and edaphic factors also interact to determine the relative abundance of trees, shrubs and grasses (Jurena and Archer 2003). The landscapes with varying slope positions vary on their ability to retain scarce water and nutrients, caused by differences in soil depth and texture (Oztas et al. 2003), which are important determinants of woody plant distribution (Wu et al. 2005).

The two-layer soil water hypothesis of tree-grass coexistence (Holdo 2013) posits that trees and grasses differ in their rooting depth, with grasses exploiting soil water in shallow layers, while trees have exclusive access to deep water (Nippert et al. 2012, Ward et al. 2013). This hypothesis suggests that sites on fine -textured soils may be resistant to woody plant encroachment while

those on coarse textured soils would be susceptible (Hughes et al. 2006). However, factors promoting or discouraging woody plant encroachment are difficult to understand (House et al. 2003). Consequently, the difficulty in understanding the factors that promote or discourage woody plant encroachment, complicate attempts to manage and/or control encroaching woody plant species.

In South Africa, an indigenous unpalatable fynbos shrub, *Seriphium plumosum* L (syn. *Stoebe vulgaris*) has recently increased its rate of spread in the semi-arid grassland communities, caused by among others, changes in environmental and/or ecological conditions (Snyman 2012b). *Seriphium plumosum* requires a summer rainfall of approximately 620 mm – 750 mm, which reflects a precipitation boundary between mesic and semi-arid grassland (Snyman 2012a). The area encroached by *Seriphium plumosum* is estimated to be approximately 11 million hectares of South Africa rangeland (Avenant 2015). Its encroachment reduces grass production by up to 65 % when *S. plumosum* densities reach a threshold of 2000 shrubs ha<sup>-1</sup>, converting grasslands into less productive shrubland-grasslands (Snyman 2012b). Consequently, its encroachment is viewed as a major threat to veld management (Snyman 2011), because it reduces carrying capacity of the rangelands (Snyman 2012a), especially in areas where sheep and cattle grazing is the primary land use.

*Seriphium plumosum* is sensitive to perennial and transient wet conditions, high soil clay content and fertile soils, particularly organic matter and phosphate (Snyman 2012a). The effects of overgrazing on *S. plumosum* encroachment are inconclusive. This is because *S. plumosum* encroachment is reported in both overgrazed and areas where grazing does not exist or is of light intensity (Snyman 2011; 2012b). The ability to predict where and how an ecosystem might change under different environmental conditions and management regimes is important for managing

woody plant encroachment (Liu et al. 2013). However, this research is lacking for *S. plumosum*, yet important in providing avenues for managing its encroachment in South African semi-arid grasslands.

There is a research consensus proposing multi-factorial experiments as possible ways to understand the causes of woody plant encroachment (Ward 2005; Kraaij and Ward 2006) that may assist in developing their management strategies in rangeland communities (Liu and Guan 2012). Snyman (2012a) proposed in-depth ecological research on *S. plumosum* to assist in controlling its encroachment on South African semi-arid rangeland communities. The objective of this study was to determine the environmental factors that contribute to *S. plumosum* encroachment susceptibility in South African semi-arid grassland communities.

## **2.2. Materials and methods**

### **2.2.1. Study Area**

The study was conducted in Gauteng Province (27° 30' to 29° 00' E, 25° 00' to 26° 30' S), South Africa. Gauteng Province covers approximately 17 010 km<sup>2</sup>, which is 1.4 % of South Africa's surface area. Altitude in Gauteng Province varies between 1081 m to 1899 m above sea level (Gauteng Department of Agriculture, Conservation and Environment, 2000). The vegetation is predominantly grassland and savanna, which comprises 71% and 21 % of the study area, respectively (Mucina and Rutherford 2006). The study area receives on average rainfall of 700 mm/annum in the southern areas of the Witwatersrand to approximately 600 mm/annum in the areas north of the Magaliesberg. The area has mean summer and winter temperatures of 25.6° C and 13.8° C (Weather Bureau 2000), respectively.

### **2.2.2. Data collection**

Data was collected from 34 randomly selected cattle farms with *Seriphium plumosum* encroached (n = 34) and un-encroached (n = 34) sites. These farms were selected from the Department of Agriculture, Fisheries and Forestry (DAFF), directorate; Land Use and Soil Management (LUSM) national database on *Seriphium plumosum* encroached farms. In Gauteng Province, the farms were from main mixed crop and livestock species farmers, who have been farming for at least five years on the property. Although not proven, all the farmers indicated that fire occurs almost once every three years during the dry season. At each of the farms, encroached and un-encroached sampling sites were chosen systematically to represent the extent of encroachment at each of these farms (Table 2.1), from which both abiotic and biotic variables were recorded.

**Table 2. 1.** The values of physical and chemical characteristics of the experimental sites in the semi-arid grassland communities of Gauteng Province.

No	Encroached farms	S.plumosum density(100m2)	Slope	LandUse	Altitude(m)	Aspect (°)	Veldcondition score ( % )	sand%	Silt%	Clay%	Org.C mg/kg	TotalN mg/kg	pHH2O	P mg/kg	Ca mg/kg	Mg mg/kg	K mg/kg	Na mg/kg	SANDSILT %	SILT %	CLAY %
1	Encroached	52	Mid	Grazing	1460	60	46,90	86	4	10	0,83	0,05	5,06	3,50	39,68	5,35	37,52	1,71	86,00	4,00	10,00
2	Encroached	147	Mid	Grazing	1414	120	40,00	76	6	18	1,02	0,06	4,74	3,06	52,67	10,67	41,71	1,10	76,00	6,00	18,00
3	Encroached	31	Mid	Grazing	1440	140	39,00	84	4	12	1,24	0,06	5,03	3,42	98,99	19,69	33,75	1,13	84,00	4,00	12,00
4	Encroached	214	Bottom	Grazing	1442	210	28,10	80	4	16	0,95	0,05	5,18	8,12	102,20	20,84	64,01	0,00	80,00	4,00	16,00
5	Encroached	140	Mid	Grazing	1632	140	52,90	70	10	20	1,24	0,07	4,91	11,80	73,21	19,82	122,69	0,23	70,00	10,00	20,00
6	Encroached	76	Mid	Grazing	1628	100	55,00	66	6	28	1,53	0,08	5,44	43,18	232,05	100,90	146,08	0,13	66,00	6,00	28,00
7	Encroached	96	Mid	Grazing	1606	25	41,50	74	10	16	1,25	0,07	5,18	7,79	151,06	38,63	53,45	5,85	74,00	10,00	16,00
8	Encroached	93	Top	Grazing	1614	220	44,50	50	20	30	2,24	0,10	4,78	4,63	66,75	19,37	98,81	2,17	50,00	20,00	30,00
9	Encroached	50	Mid	Grazing	1578	220	43,00	80	4	16	0,6	0,04	4,89	5,99	27,93	2,91	30,78	0,00	80,00	4,00	16,00
10	Encroached	241	Mid	Grazing	1597	170	48,20	84	4	12	1,48	0,06	5,42	6,95	146,29	54,03	62,24	2,14	84,00	4,00	12,00
11	Encroached	84	Mid	Grazing	1575	30	48,30	74	6	20	0,71	0,04	5,62	3,23	175,42	87,00	69,48	0,45	74,00	6,00	20,00
12	Encroached	191	Mid	Grazing	1534	190	54,70	78	6	16	1,07	0,06	5,98	1,15	436,37	139,34	68,61	5,56	78,00	6,00	16,00
13	Encroached	212	Bottom	Grazing	1519	10	44,50	82	4	14	0,85	0,06	5,03	2,55	95,29	22,61	29,30	0,04	82,00	4,00	14,00
14	Encroached	67	Mid	Grazing	1519	150	70,50	70	6	24	1,94	0,11	5,14	4,95	342,80	90,26	176,53	6,61	70,00	6,00	24,00
15	Encroached	51	Top	Grazing	1586	140	46,50	66	8	26	2,27	0,10	4,82	7,17	99,65	25,99	89,76	4,70	66,00	8,00	26,00
16	Encroached	132	Mid	Grazing	1632	260	43,60	36	18	46	1,67	0,10	4,81	1,21	223,91	103,08	0,10	5,11	36,00	18,00	46,00
17	Encroached	46	Mid	Grazing	1532	10	85,00	62	8	30	1,75	0,09	5,16	2,74	291,32	90,02	87,80	2,87	62,00	8,00	30,00
18	Encroached	107	Mid	Grazing	1484	180	67,60	74	4	22	0,94	0,06	5,12	3,33	156,56	47,29	69,31	0,04	74,00	4,00	22,00
19	Encroached	21	Bottom	Grazing	1455	340	65,70	74	10	16	2,44	0,12	5,39	9,00	454,12	118,41	200,95	1,28	74,00	10,00	16,00
20	Encroached	66	Mid	Grazing	1593	120	47,20	86	6	8	0,39	0,03	5,54	2,11	45,18	1,50	0,03	0,00	86,00	6,00	8,00
21	Encroached	17	Mid	Grazing	1619	200	39,70	78	4	18	0,60	0,04	5,32	5,34	67,36	11,56	26,81	0,56	78,00	4,00	18,00
22	Encroached	246	Mid	Grazing	1632	40	22,80	72	6	22	1,05	0,05	5,72	13,68	209,19	56,89	119,42	0,72	72,00	6,00	22,00
23	Encroached	237	Mid	Grazing	1527	325	37,80	80	0	20	1,72	0,10	5,81	116,23	674,59	112,69	303,21	3,88	80,00	0,00	20,00
24	Encroached	55	Mid	Grazing	1592	330	60,40	86	2	12	1,60	0,09	6,02	16,17	87,40	13,15	47,83	2,98	86,00	2,00	12,00
25	Encroached	87	Mid	Grazing	1633	230	34,60	64	8	28	1,77	0,09	5,92	34,81	457,84	74,80	140,74	1,67	64,00	8,00	28,00
26	Encroached	110	Mid	Grazing	1575	160	43,90	78	6	16	1,12	0,06	5,31	3,31	77,40	19,30	140,74	1,67	78,00	6,00	16,00
27	Encroached	105	Mid	Grazing	1611	180	50,20	72	10	18	1,41	0,06	5,81	2,35	139,90	40,82	27,22	1,10	72,00	10,00	18,00
28	Encroached	58	Mid	Grazing	1608	125	69,10	58	16	26	2,00	0,07	5,79	69,62	431,55	47,73	67,86	2,11	58,00	16,00	26,00
29	Encroached	100	Bottom	Grazing	1570	55	34,90	62	10	28	0,61	0,04	4,81	4,14	25,97	2,81	30,48	0,00	62,00	10,00	28,00
30	Encroached	119	Mid	Grazing	1505	60	55,90	86	2	12	0,89	0,05	5,03	5,29	28,11	2,10	55,84	0,00	86,00	2,00	12,00
31	Encroached	132	Bottom	Grazing	1469	130	43,30	82	4	14	1,00	0,06	5,12	8,61	95,02	16,11	73,95	0,00	82,00	4,00	14,00
32	Encroached	52	Mid	Grazing	1607	15	51,40	74	8	18	1,14	0,07	4,66	2,58	44,86	13,01	33,03	7,86	74,00	8,00	18,00
33	Encroached	97	Mid	Grazing	1615	260	61,80	66	12	22	2,72	0,11	5,71	20,27	292,80	89,20	180,33	6,21	66,00	12,00	22,00
34	Encroached	52	Mid	Grazing	1611	50	47,20	60	14	26	1,93	0,08	5,19	8,48	287,73	126,04	84,78	1,37	60,00	14,00	26,00

The abiotic variables recorded included; altitude, aspect (compass), catenal position (Soil Classification Working Group 1991), and soil depth using an extendable soil auger (Shackleton 1997). Five soil samples were taken to a depth of 30 cm every 20 m along a 2 m x 50 m belt transect orientated down the slope. The soil samples from each sampling site were pooled together, mixed and analyzed for soil texture (Bouyoucos hydrometer method), sand and rockiness (% volume), soil organic carbon (Walkley and Black 1934), pH and fertility (Ca, Mg, Na, K, P and TN) (Ambic I extraction followed by AA spectroscopy) at the Agricultural Research Council-Institute for Soil, Climate and Water (ARC-ISCW) laboratory. The ARC-ISCW laboratory is a member of AgriLASA proficiency scheme for soil, water, plants and fertilizer metrics.

The biotic variables recorded at each of the sampling sites included; grass species composition and basal cover following the spike-point method (Everson and Clarke 1987), revised as point to tuft and tuft diameter (Hardy and Tainton 1993). The plant nearest to the spike at 0.5 m intervals along each 2 m x 50 m belt-transect was identified and recorded. Nomenclature for each of the grass species followed Germishuizen and Meyer (2003). Grass basal cover was determined at 1 m intervals along each belt transect by measuring the distance from the spike to the centre of the nearest grass tuft, and their longest and shortest basal diameters. Grass species composition was determined using the number of individuals of different grass species recorded from 200 points at each of the 2 m x 50 m belt transects and expressed as species per unit area (100m<sup>2</sup>). Veld condition score (VCS) for each site was calculated using species attributes based on 200 records per sampling site (Tainton 1999). A hypothetical benchmark was used to serve as an index of the best possible range condition for comparison against the actual site assessed. Veld condition scores were converted into a percentage of the benchmark (actual score/ 2000 \* 100) to

derive a convenient value for comparisons (Goodall et al. 2011). The Hardy and Tainton (1993) equation was used to calculate basal cover;

$$BC = 19.8 + 0.39(D) - 11.87(\log_e D) + 0.64(d^2) + 2.93(\log_e d)$$

Where BC equals basal cover, D is the distance (cm) from the point to the nearest tuft of the grass plant, and d is the mean basal diameter (cm) of the tuft.

The degree of shading, sward cover and surface rockiness was determined using an eight-point scale based on aerial cover, with scale ranging from; 0 = no shading to 7 = 100 % shading, sward cover and rockiness as described by Walker (1976). The density of *S. plumosum* was determined for all encroached sites by counting the number of rooted *S. plumosum* plants in each of the 100 m<sup>2</sup> (2 m x 50 m) belt transects. *Seriphium plumosum* density was determined as the number of *S. plumosum* plants per hectare.

### 2.2.3. Statistical analysis

Data was analysed in two ways; first by identifying and removing redundancies between abiotic and biotic factors using a correlation analysis (SAS 2011). During this analysis, one of the closely correlated factors was removed, retaining only one as a surrogate to represent each group of associate variables (Tedder et al. 2015).

The second data analysis involved the development of a model, where the effect of abiotic and biotic variables on *S. plumosum* L. encroachment susceptibility were investigated using logistic regression (SAS 2011). Generally, the overall *Seriphium plumosum* L frequency of occurrence was skewed, as the species was present only in the encroached sites, resulting in the data being converted into presence and absence data. After removing redundant predictor variables, the final analysis examined only the surrogates; aspect, sward cover, rockiness, basal

cover, soil sand content, organic carbon, pH, phosphorus and magnesium on *S. plumosum* encroachment susceptibility.

### **2.3. Results**

The results of the correlation analysis of abiotic factors are presented in Table 2.2.

**Table 2. 2.** Correlation between abiotic and biotic variables of 68 sample plots in the Gauteng semi-arid grassland communities.

Significant correlations ( $P > 0.05$ ) are highlighted in bold.

Variables	S.plumosumdensity(100m2)	Altitude(m)	Aspect	Slope	Soildepth	Shading	Swardcover	Rockiness	Stones	Basalcover	Veldconditionscore	sand%	Silt%	Clay%	Org.C	TotalN	pHH2O	P	Ca	Mg	K	Na	SAND	SILT	CLAY
S.plumosumdensity(100m2)	<b>1</b>																								
Altitude(m)	-0,03	<b>1</b>																							
Aspect	-0,07	-0,10	<b>1</b>																						
Slope	0,01	0,19	0,05	<b>1</b>																					
Soildepth	0,14	-0,11	0,05	<b>-0,28</b>	<b>1</b>																				
Shading	-0,12	-0,15	0,09	-0,23	<b>0,24</b>	<b>1</b>																			
Swardcover	-0,09	-0,17	0,01	-0,22	0,12	<b>0,75</b>	<b>1</b>																		
Rockiness	-0,05	-0,03	-0,04	<b>0,28</b>	<b>-0,61</b>	-0,14	0,05	<b>1</b>																	
Stones	-0,04	0,04	0,00	<b>0,35</b>	<b>-0,64</b>	-0,17	-0,04	<b>0,90</b>	<b>1</b>																
Basalcover	<b>-0,28</b>	<b>0,33</b>	0,18	-0,14	-0,21	-0,09	-0,02	0,03	0,04	<b>1</b>															
Veldconditionscore	-0,17	-0,06	0,08	0,13	-0,19	0,04	0,10	<b>0,28</b>	<b>0,26</b>	-0,06	<b>1</b>														
sand%	0,03	<b>-0,36</b>	-0,10	-0,24	<b>0,30</b>	0,06	0,10	-0,13	<b>-0,25</b>	-0,05	<b>-0,24</b>	<b>1</b>													
Silt%	-0,03	<b>0,47</b>	-0,03	<b>0,41</b>	<b>-0,37</b>	-0,13	-0,17	<b>0,27</b>	<b>0,45</b>	0,14	0,10	<b>-0,81</b>	<b>1</b>												
Clay%	-0,01	0,24	0,15	0,07	-0,21	-0,01	-0,05	0,01	0,09	-0,01	<b>0,26</b>	<b>-0,93</b>	<b>0,55</b>	<b>1</b>											
Soil Org.C	-0,12	<b>0,26</b>	0,18	<b>0,46</b>	<b>-0,48</b>	-0,11	-0,09	<b>0,43</b>	<b>0,49</b>	0,18	0,13	<b>-0,38</b>	<b>0,51</b>	<b>0,25</b>	<b>1</b>										
TotalN	-0,14	0,15	<b>0,26</b>	<b>0,38</b>	<b>-0,43</b>	-0,10	-0,07	<b>0,35</b>	<b>0,39</b>	0,11	0,09	<b>-0,26</b>	<b>0,34</b>	0,18	<b>0,91</b>	<b>1</b>									
pHH2O	-0,11	0,08	<b>0,35</b>	-0,20	0,14	0,23	0,16	-0,14	-0,18	0,22	0,12	-0,07	-0,06	0,13	-0,06	0,01	<b>1</b>								
P	0,07	0,05	0,18	-0,15	0,04	-0,14	-0,08	-0,02	-0,04	<b>0,32</b>	-0,10	0,04	-0,10	0,00	0,20	<b>0,34</b>	0,20	<b>1</b>							
Ca	-0,21	-0,09	0,24	-0,05	-0,06	0,14	0,11	-0,01	-0,07	0,01	0,18	<b>-0,46</b>	0,17	<b>0,50</b>	<b>0,29</b>	<b>0,26</b>	<b>0,39</b>	<b>0,27</b>	<b>1</b>						
Mg	-0,15	-0,15	0,20	-0,07	-0,02	0,18	0,15	0,01	-0,02	-0,07	0,04	<b>-0,44</b>	0,18	<b>0,49</b>	0,15	0,10	0,22	0,02	<b>0,76</b>	<b>1</b>					
K	-0,07	-0,04	0,08	0,12	-0,23	-0,01	0,03	0,08	0,08	0,05	0,07	<b>-0,25</b>	0,09	<b>0,26</b>	<b>0,44</b>	<b>0,41</b>	0,07	<b>0,46</b>	<b>0,68</b>	<b>0,41</b>	<b>1</b>				
Na	-0,12	-0,03	<b>0,33</b>	0,13	-0,08	0,15	0,10	0,11	0,10	0,02	0,13	<b>-0,45</b>	<b>0,28</b>	<b>0,42</b>	0,21	0,17	<b>0,38</b>	-0,04	<b>0,67</b>	<b>0,82</b>	<b>0,29</b>	<b>1</b>			
SAND	0,03	<b>-0,36</b>	-0,10	-0,24	<b>0,30</b>	0,06	0,10	-0,13	<b>-0,25</b>	-0,05	<b>-0,24</b>	<b>1,00</b>	<b>-0,81</b>	<b>-0,93</b>	<b>-0,38</b>	<b>-0,26</b>	-0,07	0,04	<b>-0,46</b>	<b>-0,44</b>	<b>-0,25</b>	<b>-0,45</b>	<b>1</b>		
SILT	-0,03	<b>0,47</b>	-0,03	<b>0,41</b>	<b>-0,37</b>	-0,13	-0,17	<b>0,27</b>	<b>0,45</b>	0,14	0,10	<b>-0,81</b>	<b>1,00</b>	<b>0,55</b>	<b>0,51</b>	<b>0,34</b>	-0,06	-0,10	0,17	0,18	0,09	<b>0,28</b>	<b>-0,81</b>	<b>1</b>	
CLAY	-0,02	<b>0,24</b>	0,15	0,11	-0,22	-0,01	-0,05	0,03	0,11	0,00	<b>0,28</b>	<b>-0,95</b>	<b>0,59</b>	<b>0,99</b>	<b>0,26</b>	0,18	0,13	-0,01	<b>0,54</b>	<b>0,51</b>	<b>0,29</b>	<b>0,47</b>	<b>-0,95</b>	<b>0,59</b>	<b>1</b>

The results showed that basal cover ( $P = 0.004$ ), sand ( $P = 0.031$ ) and magnesium ( $P = 0.033$ ) were significant predictors of *S. plumosum* encroachment susceptibility. However, aspect, sward cover, rockiness, soil organic carbon, pH and phosphorus did not show a significant likelihood of predicting *S. plumosum* encroachment susceptibility ( $P > 0.05$ ; Table 2.3.).

**Table 2. 3.** Summary of the initial single parameter logistic regression models of the presence/absence of *Seriphium plumosum* L. in the semi-arid grassland of Gauteng Province, South Africa. Significant parameters ( $p < 0.05$ ) are highlighted in bold.

Parameter	Df	Odd Ratio	Estimate	SE	P
Aspect	1	0.999	-0.00132	0.00384	0.7311
Sward cover	1	1.127	0.1198	0.4270	0.7791
Rockiness	1	1.143	0.1332	0.3277	0.6843
Basal cover	1	0.926	-0.0768	0.0267	<b>0.0040</b>
Sand	1	0.881	-0.1272	0.0589	<b>0.0308</b>
Soil organic carbon	1	0.936	0.0663	0.7293	0.9276
Ph	1	1.917	0.6506	0.8469	0.4423
Phosphorus	1	1.027	0.0269	0.0185	0.1455
Magnesium	1	0.964	-0.0362	0.0169	<b>0.0329</b>

The odds ratio (exponentiated value of the estimate in Table 2.3.) has shown that, a decrease in percentage basal cover, sand, and soil magnesium content increased the likelihood of *S. plumosum* encroachment by 0.926, 0.881 and 0.964 times.

## **2.4. Discussion**

The study showed that basal cover, sand and soil magnesium content are the best predictors of *S. plumosum* L. encroachment susceptibility. Generally, when these variables increase, the likelihood of *S. plumosum* encroachment in semi-arid rangelands decreases and visa versa. Other studies have also shown a positive relationship between grass production loss and *S. plumosum* encroachment (Snyman 2012). Grazing reduces the ability of grasses to outcompete woody plant seedlings, thus making grasslands susceptible to woody plant encroachment (Jurena and Archer 2003). The removal of grass by grazing and/or fire had a positive effect on *Acacia* recruitment in savanna (Grellier et al. 2012). Grazing herbivores dominate most of the African rangelands, reducing grass competition with woody plants and fuel loads for fire (Ward 2009). The overgrazing hypothesis also proposes that sustained heavy grazing reduces above- and below-ground grass biomass, thus increasing resource availability for the establishment and recruitment of shrubs (Coetzee et al. 2008). Annual net primary productivity (ANPP) of grasses has also been found to respond positively to shrub removal, but more so in years with above-average rainfall (Pierce et al. 2018). This confirms the findings that when basal cover decreases, the likelihood of *S. plumosum* encroachment increases accordingly. Furthermore, it explains the significant effect of basal cover as one of the factors determining *S. plumosum* encroachment susceptibility in the semi-arid grassland communities of Gauteng Province, South Africa. Clearly, disturbances such as heavy

grazing and fire that reduce grass sward cover may contribute to causing woody plant encroachment, either independently or in combination with other factors (Ward 2009).

*Seriphium plumosum* L. encroaches mostly on relatively sandier soils (Snyman and Le Roux, 2009). However, soils with a clay content of up to 24% could still be encroached if the drainage is sufficient and favours the establishment of this woody plant species (Wepener 2007). Trees occurs on sandy soils with a lower range of rainfall than on clayey soils due to higher percolation rates (van Langevelde et al. 2003). Archer et al. (2017) also found that *Prosopis velutina* in North American deserts occurs mostly on Holocene-age sandy soils, thus confirming the susceptibility of sandy soils to woody plant encroachment (Booth and Barker 1981). In addition, it was found that, soil sand content under shrubs canopy microsites is higher relative to interspace microsites (Sankey et al. 2012). Clearly, coarse-textured soils support trees and shrubs with deeper, more extensive root systems that allow percolation of rainfall to deeper depths (Nippert et al. 2012). It is probably the same reason among many that bush encroachment occurred in sandy soil in the Kalahari sands of Botswana (Kgosikoma et al. 2012). This is consistent with the general hypothesis that sandy soils should be prone to woody plant encroachment than clayey soils (Browning et al. 2008). Contrary to these results, this study found that a decrease in soil sand content increased the likelihood of *S. plumosum* encroachment susceptibility. These results suggest that even fine textured soils may provide suitable conditions for *S. plumosum* encroachment, provided the soil is welldrained. Snyman (2009a) also found that *S. plumosum* seldom occurs in dump soils. The study also suggest that *S. plumosum* is adapted to a wide-range of environmental conditions. Consequently, its adaption may contribute to decreased likelihood estimate for its encroachment with decreasing only soil sand content. Models of woody plant abundance in savannas based on regional and sub-continental assessment, predict a decline in

woody plant cover and density with decreasing rainfall and increasing topsoil clay content (Williams et al. 1996).

The regression analysis in chapter 3 in this study revealed a non-significant relationship between *S. plumosum* L. density, canopy size and soil magnesium. These results imply that an increase or decrease in *S. plumosum* density or cover have a neutral or no effect on soil magnesium content. In this study, we found an increasing likelihood of *S. plumosum* encroachment with decreasing soil magnesium content. In contrast, soil magnesium content was three times higher in the soils collected from under the canopy than in the inter-shrub patches (Bachar 2012). These results suggest that the outcome of woody plant encroachment on ecosystem functioning is non-universal. Magnesium is not a nutrient compound limiting plant growth (Jobbagy and Jackson 2001) and probably not required for *S. plumosum* encroachment to occur. In addition, *S. plumosum*, unlike other woody or shrubby plant species, prefer mostly well-drained poor soils. Consequently, this explains an increased *S. plumosum* encroachment likelihood with decreasing soil magnesium content found in this study. The results in this study have demonstrated that soil responses to woody plant encroachment depend on among others, the stage of encroachment, land use and other disturbance factors such as fire and grazing.

## **2.5. Conclusion**

The study revealed that basal cover, sand and magnesium are the best predictors of *S. plumosum* encroachment susceptibility in the semi-arid grassland communities of Gauteng Province. A decrease in herbaceous basal cover, soil sand and magnesium content would increase the likelihood of *S. plumosum* encroachment susceptibility in semi-arid grassland communities of Gauteng Province. A decrease in basal cover is a result of anthropogenic-induced disturbances

such as overgrazing and fire, which alone or in combinations with other factors contribute to *S. plumosum* encroachment. Consequently, the interaction of overgrazing and fire may be creating conditions suitable for *S. plumosum* to recruit and establish, thus leading to its encroachment.

The fact that an increase in soil sand content increases the likelihood of *S. plumosum* encroachment susceptibility in the semi-arid grassland communities was not expected. However, the results showed that *S. plumosum* is adapted to a wide variety of well-drained soils. Furthermore, fine soils alone or in combination with poor herbaceous basal cover and soil magnesium content contribute to increasing *S. plumosum* encroachment susceptibility in grassland communities. Clearly, the rate of *S. plumosum* encroachment may be reduced by among others, rangeland management strategies that discourage loss of vegetation cover such as decreased grazing intensity and recurring fires. Furthermore, improving soil fertility, by increasing soil magnesium content, may contribute to reducing *S. plumosum* encroachment susceptibility, thus contributing to preventing it from spreading. To understand the drivers of *S. plumosum* encroachment, there is a need for more controlled experiments with varying levels of soil fertility including magnesium concentrations, soil texture and water. This research may provide valuable information necessary for validating the pattern exhibited under natural conditions, where control for other confounding factors is impossible.

## **2.6. Research Implications**

This research has shown that management strategies that encourages reduced herbaceous basal cover and soil magnesium content on well-drained sandy soil increases the likelihood of *S. plumosum* encroachment susceptibility. Clearly, there is a need for management interventions that discourage *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng

Province. These management interventions include rangeland management strategies that promote and maintain good grass cover, while discouraging loss of soil nutrients. The loss in herbaceous basal cover may increase soil erosion, which contributes to the reduction of soil nutrients. This study also proposes more ecological research on *S. plumosum* encroachment to understand its causes and consequences in rangeland communities.

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## **2.7. References**

- Archer, S.R. 2010. Rangeland conservation and shrub encroachment: new perspectives on an old problem. In: (J.T. du Toit, R. Kock and J.C Deutsch eds): Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems.
- Archer, S.R., Anderson, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., Woods, S.R. 2017. Woody plant encroachment: Causes and Consequences. In Briske DD, editor. Rangelands Systems. Springer Series on Environmental Management. pp 25 – 84.

- Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T. 2004. Grazing systems, ecosystem response, and global change. *Annual Review of Environmental Resources*. 29: 261 – 299.
- Avenant, P. 2015. Report on the national bankrupt bush (*Seriphium plumosum*) survey (2010 – 2012). Technical Report: Department of Agriculture, Forestry and Fisheries (DAFF).
- Bachar, A., Soares, M.I.M., Gillor, O. 2012. The effect of Resource Island on abundance and diversity of bacteria in arid soils. *Microbial Ecology*. 63: 694 – 700.
- Booth, C.A., Barker, P.J. 1981. Shrub invasion on sand plain country west of Wanaaring, New South Wales. *Soil Conservation Service of New South Wales*. 37: 65 – 70.
- Browning, D.M., Archer, S.R., Asner, G.P., McClaran, M.P., Wessman, C.A. 2008. Woody plants in grasslands: Post-encroachment stand dynamics. *Journal of Applied Ecology*. 18: 928 – 944.
- Buitenwerf, R., Bond, W.J., Stevens, N., Trollope, W.S.W. 2012. Increased tree densities in South African savannas: > 50 years of data suggest CO<sub>2</sub> as a driver. *Global Change Biology*. 18: 675 – 684.
- Chapin III, F. S., Sala, O.E., Huber-Sannwald, E., Leemans, R (eds). 2001. The future of biodiversity in a changing world. In: *Global biodiversity in a changing environment: scenarios for 21<sup>st</sup> century*. Springer.
- Coetzee, B.W.T., Tincani, L., Wodu, Z., Mwasi, S.M. 2008. Overgrazing and bush encroachment by *Tarchonanthus camphoratus* in semi-arid savanna. *African Journal of Ecology*. 46: 449 – 451.
- Colgan, M.S., Asner, G.P., Levick, S.R., Martin, R.E., Chadwick, O.A. 2012. Topo-edaphic controls over woody plant biomass in South African savannas. *Biogeosciences*. 9: 1809 – 1821.

- Eldridge, D.J., Bowker M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G. 2011. Impact of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecological Letters*. 14: 709 – 722.
- Everson, C.S., Clarke, G.P.Y. 1987. A comparison of six methods of botanical analysis in the montane grasslands of Natal. *Plant Ecology*. 73: 47 – 51.
- Gauteng Department of Agriculture, Conservation and Environment. 2000. Spatial Development Framework. Gauteng Provincial Government: Development Planning and Local Government. Unpublished report, APS PlanAfrica in association with Labat-Anderson Africa, Johannesburg.
- Germishuizen, G., Meyer, N.L., (eds). 2003. Plants of Southern Africa: an annotated checklist. National Botanical Institute, Pretoria.
- Goodall, J., Ed. Witkowski, T.F., Morris, C.D., Henderson, L. 2011. Are environmental factors important facilitators of pompom weed (*Campuloclinium macrocephalum*) invasion in South African rangelands? *Biological Invasions*.
- Grellier, S., Barot, S., Janeau, J. L., Ward, D. 2012. Grass competition is more important than seed ingestion by livestock for Acacia recruitment in South Africa. *Plant Ecology*. 213: 899 – 908.
- Hardy, M.B., Tainton, N.M. 1993. Towards a technique for determining basal cover in tufted grasslands. *African Journal of Range Forage Sciences*. 10: 77 – 81.
- House, J., Archer, S., Breshears, D.D., Scholes, R.J., Nceas, T.G.I.P. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*. 30: 1763 – 1777.
- Holdo, R.M. 2013. Revisiting the twolayer hypothesis: Coexistence of alternative functional rooting strategies in savannas. *PLoSOne*. 8: 1 – 12.

- Hughes, R.F., Archer, S.R., Asner, G.P., Wessman, C.A., McMurtry, C., Nelson, J., Ansley, R.J. 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. *Global Change Biology* 12: 1733 – 1747.
- Jobbagy, E.G., Jackson, R.B. 2001. The nutrient distribution with soil depth: Global patterns and imprint of plants. *Biogeochemistry*. 53: 51 – 77.
- Jurena, P.N., Archer, S.R. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology*. 84: 907 – 919.
- Kgosikoma, O, Mojeremane W, Harvie B A. 2012. Pastoralists' perception and ecological knowledge on savanna ecosystem dynamics in semi-arid Botswana. *Ecology and Society*. 17: 27.
- Kiswaga, S.A.S., Mbwambo, J.R., Shirima, D., Mndolwa, A.S., Schaffner, U., Eschen, R. 2020. More widespread alien tree species do not have larger impacts on regeneration of native tree species in a tropical forest reserve. *Ecology and Evolution* 10: 5034–5044.
- Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*. 14: 615 – 623.
- Kulmatiski, A., Beard, K.H. 2013. Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change*. 3: 833 – 837.
- Liu, F., Archer, R.S., Gelwick, F., Bai, E., Boutton, T.W., Ben, Wu, X. 2013. Woody Plant Encroachment in to Grasslands: Spatial pattern of Functional Group Distribution and Community Development. *PloS ONE*. 8: 1 – 13.
- Liu, Y., Shang, Q., Wang, L., Liu, X. 2019. Effects of understory shrub biomass on variation of

- soil respiration in a temperate-subtropical transitional oak forest. *Forest*. 10, 88; doi: 10.3390/f10020088.
- Liu, N., Guan, L. 2012. Linkages between woody plant proliferation dynamics and plant physiological traits in southwestern North America. *Journal of Plant Ecology*. 5: 407 – 416.
- MEA. 2005. Millennium Ecosystem Assessment. Ecosystems and Human well-being: Desertification Synthesis. World Resources Institute, Washington D.C.
- Meik, J.M., Jeo, R.M., Mendelson, L.H., J.R., Jenks, K.E. 2002. Effect of bush encroachment on an assemblage of diurnal lizard species in central Namibia. *Biological Conservation*. 106: 29 – 36.
- Mucina, L., Rutherford, M.C. 2006. The Vegetation of Southern Africa, Lesotho and Swaziland. *Strelitzia* 19, South African National Botanical Institute, Pretoria, South Africa;
- Nippert J.B., Wieme R.A., Ocheltree T.W., Craine J.M. (2012) Root characteristics of C4 grasses limit reliance on deep soil water in tallgrass prairie. *Plant and Soil* 355: 385–394.
- O' Connor, T.G., Puttick, J.R., Hoffman, M.T. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range and Forage Science*. 31: 67 – 88.
- Oztas, T., Koc, A., Comakli, B. 2003. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. *Journal of Arid Environments*. 55: 93 – 100.
- Pierce, N.A., Archer, S.R., Bestelmeyer, B.T., James, D.K. 2018. Grass-shrub competition in arid lands: an overlooked driver in grassland-shrubland state transition? *Ecosystems*. 22: 619 – 628.
- Ratajczak, Z.R., Nippert, J.B., Hartman, J.C., Ocheltree, T.W. 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere*. 2: 1–14.

- Roques, K.G., O' Connor, T.G., Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*. 38: 268 – 280.
- Sankey J.B., Ravi, S., Wallace, C.S.A., Webb, R.H., Huxman, T.E. 2012. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical research*. 117: 1 – 11.
- SAS Institute. SAS/STAT User's Guide. Version 9.3. SAS Institute, Cary: NC, USA; 2011.
- Shackleton, CM. 1997. The prediction of woody plant productivity in the savanna biome, South Africa. PhD thesis, University of the Witwatersrand, Johannesburg.
- Snyman HA. 2012b. Control measures for the encroacher shrub *Seriphium plumosum*. *South African Journal of Plant and Soil*. 29: 157–163.
- Snyman, H.A. 2009a. A physiological approach to the distribution and spread of *Seriphium plumosum*. *Newsletter of the Grassland Society of Southern Africa*. 9: 29–37.
- Snyman, H.A. 2009b. Germination potential of *Seriphium plumosum* (bankrupt bush, slangbos or vaalbos) *Newsletter of the Grassland Society of Southern Africa*. 9: 43 – 48.
- Snyman, H.A. 2011. Short-term response of the encroacher shrub *Seriphium plumosum* to fire. *African Journal of Range and Forage Science*. 28: 65 – 77.
- Snyman, H.A., 2012a. Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *South African Journal of Botany*. 81: 34 – 39.
- Snyman, H.A., le Roux, P.A.L. 2009. Wat bepaal die voorkoms van slangbos? *Ons Eie*. 44: 55 – 57.

- Soil Classification Working Group. 1991. Soil classification – a Taxonomic System for South Africa. Memoirs on the Agricultural Natural Resources of South Africa, No 15. Department of Agricultural Development, Pretoria.
- Tainton, N.M., (ed). 1999. Veld management in South Africa. University of Natal Press, Pietermaritzburg.
- Tedder, M.J., Kirkman, K.P., Morris, C.D., Trollope, W.S.W., Bonyongo, M.C. 2015. Determinants of the occurrence of a native encroacher species, *Pechuelloeschea leubnitziae* (wild sage), in the eastern Okavango Delta, Botswana. African Journal of Range and Forage Sciences. 32: 253 – 259.
- Throop, L.H., Reichmann, L.G., Sala, O.E., Archer S.R. 2012. Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. Oecologia. 169: 373 – 383.
- van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grassland. Journal of Environmental Management. 90: 2931 – 2942.
- Van Langevelde, F., Van De Vijver, C. A. D. M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., and Bond, W. J. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology. 84: 337 – 350.
- Walker, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. South African Journal of Wildlife Research. 6:1 – 32.
- Walkley, A., Black, I.A. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Science. 37: 29 – 38.

- Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*. 22: 101 – 105.
- Ward, D. 2009. A resource ration model of the effect of changes in CO<sub>2</sub> on woody plant invasion. *Plant ecology*. 209: 147 – 152.
- Ward, D., Wiegand, K., Getzin, S. 2013. Walter's two-layer hypothesis revisited: back to the roots! *Oecologia*. 1723: 617 – 630.
- Weather Bureau. 2000. Prints of the climate statistics of the Johannesburg Leeukop, Pretoria Forum WB and Johannesburg Kroningspark weather station. Department of Environmental Affairs and Tourism.
- Wepener, J.P. 2007. The control of *Stoebe vulgaris* encroachment in the Hartebeesfontein area of the North West Province. MSc Thesis, North-West University, Potchefstroom, South Africa. Pp. 135.
- Williams R.J., Duff G.A., Bowman D., Cook G.D. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a largescale
- Wonkka, C L., Twidwell D., West, J B., Rogers, W E. 2016. Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecological Applications* 26: 128 – 145.
- Wu, X.B., Archer, S.R. 2005. Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes. *Landscape Ecology* 20: 733 – 742.

## CHAPTER 3

### **The Effects of Abiotic Factors in the Semi-Arid Grassland Communities of Gauteng Province on *Seriphium plumosum* L Density and Canopy Size**

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## Abstract

Most studies suggest that multiple factors are responsible for woody plant encroachment, but are inconclusive on its causes. Woody plant encroachment is modified by local patterns of disturbance, topography, soil texture and fertility, and their relative importance and interaction strength varies among locations. We used grassland communities, Carletonville Dolomite Grassland (CDG), Rand Highveld Grassland (RHG) and abiotic factors (Soil Organic Carbon (SOC), Total nitrogen (TN), Phosphorus (P), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg) and pH) to investigate habitat preferences of *Seriphium plumosum* L. in the semi-arid grassland of Gauteng Province, South Africa. Grassland community had a significant effect on *S. plumosum* density, canopy size, and on components of soil fertility ( $P < 0.05$ ). Slope position had a significant effect on *S. plumosum* density and canopy size ( $P < 0.05$ ). *Seriphium plumosum* density was significantly lower ( $23 \text{ plants}/50 \text{ m}^2 \pm 2.39 \text{ (SEM)}$ ) in CDG than in RHG ( $40 \text{ plants}/50 \text{ m}^2 \pm 4.19$ ). By contrast, *S. plumosum* canopy size was significantly higher ( $1.39 \text{ m}^2 \pm 0.11$ ) at CDG than at the RHG ( $1.06 \text{ m}^2 \pm 0.08$ ). The interaction of grassland community and slope position had a significant effect on *S. plumosum* density and soil sodium content ( $P < 0.05$ ). Bottom slope regions in RHG ( $59.00 \text{ plants}/50 \text{ m}^2 \pm 8.62$ ) had higher *S. plumosum* density than bottom slope regions ( $19.75 \text{ plants}/50 \text{ m}^2 \pm 3.01$ ) in CDG. Soil sodium content was similar in CDG slopes and higher than in RHG slopes. *Seriphium plumosum* density was positively related to components of soil fertility; P ( $r^2 = 0.1270$ ;  $P 0.0036$ ), K ( $r^2 = 0.0786$ ;  $P 0.0237$ ), Na ( $r^2 = 0.0686$ ;  $P 0.0350$ ), Ca ( $r^2 = 0.0681$ ;  $P 0.0358$ ), and SOC content ( $r^2 = 0.0669$ ;  $P 0.0374$ ). However, *Seriphium plumosum* canopy size did not show any relationship with components of soil fertility. This study revealed that *S. plumosum* density in grassland communities increased with increasing soil texture and fertility.

**Keywords:** herbaceous layer, invasion, landscape, transect, veld type

### **3.1. Introduction**

Woody plant encroachment is an increase in density, cover and biomass of trees or shrubs, especially in the arid and semi-arid grassland and savanna biomes (van Auken 2000). Causes of woody plant encroachment have been widely documented (Kerley and Whitford 2009, Tjelele et al. 2012, Bond et al. 2003), however, the problem persists. This is probably because the interaction of different factors such as species adaptations, land-use history, and climate trends alone or in combination may lead to woody plant encroachment (Archer et al. 2017). Woody plant encroachment is associated with declines in forage productivity (Coetzee et al. 2008), species richness (Price and Morgan 2008), biodiversity (Trollope 1984) and increased erosion (Grover and Musiek 1990). Consequently, it decreases pastoral productivity, particularly in dryland ecosystems (Oba et al. 2000) where grazing by cattle and sheep is the primary land use (Wingley et al. 2009, Archer et al. 2017). Understanding causes of woody plant encroachment is important because arid and semi-arid lands or dry lands cover about 41% of the terrestrial surface of the earth with approximately 2.4 billion people living in these habitats (MEA 2005).

Woody plant encroachment has global and local drivers. The global drivers includes climate change and increased atmospheric carbon dioxide (Archer et al. 2017). The prime causes of woody plant encroachment at local scales are heavy grazing pressure, animal seed dispersal (Tjelele et al. 2015), fire suppression (Trollope 1984), and their interactions (Van Wilgen et al. 2009). Grazing pressure reduces fuel load and fire frequency, which may contribute to increasing woody plant dominance (Van Wilgen et al. 2009). This is consistent with the overgrazing hypothesis, which proposes that sustained heavy grazing reduces above- and below-ground grass biomass, thus

increasing resource availability for the establishment and recruitment of shrubs (Coetzee et al. 2008). However, woody plant encroachment is also widespread in areas where grazing is infrequent and light (Tjelele et al. 2015, Ward 2005). Woody plants seeds that pass through digestive tracks of browser also have a potential to germinate and recruit, thus facilitating woody plant encroachment (Tjelele et al. 2012). Elevated atmospheric carbon dioxide (Bond and Midgley 2000, Shaver et al. 2001) and increased temperatures (Ward et al. 2014) caused by increasing industrialization (Morgan et al. 2007) may also contribute to cause woody plant encroachment (Schlesinger and Pilmanis 1998).

Soil properties (texture, depth and fertility) and topography interact to influence the pattern of woody plant abundance and distribution (McAuliffe et al. 1994). The extent to which portions of a landscape may differentially capture or retain scarce water and nutrient resources (e.g. top to the bottom of the slope) is an important determinant of vegetation patterns, particularly with respect to the distribution of woody plants (Wu and Archer 2005). Woodlands occur on coarse-textured soils and savannas on fine-textured soils (Knoop and Walker 1985). The two-layer soil water hypothesis of tree-grass coexistence (Walker and Noy-Meir 1982) posits that trees and grasses differ in rooting depth, with grasses exploiting soil water in shallow layers, while trees have exclusive access to deep water (Walker et al. 1981, Walker and Noy-Meir 1982, Ward et al. 2013). Soil texture regulates the infiltration and percolation of rainwater, suggesting that the deep sandy soils often on bottom slopes are more suitable for woody or shrubby plant encroachment compared to the shallow, fine textured soils on top slopes, which are dominated by grasses (Jackson et al. 1996). The rainfall dependence of dry savanna and grasslands obscures the importance of edaphic factors in determining community structure and functioning (Scholes and Archer 1997). In areas where climate and soils are capable of supporting increased woody plant

densities, the occurrence of periodic fires or higher densities of browsers utilizing woody plants can prevent woody plants from encroaching (Archer et al. 2017). Generally, there is a complex interaction of local-scale factors (soil properties and topography) with grazing pressure and browsers through dispersing viable seeds that contribute to causing woody plant encroachment (Tjelele et al. 2015). However, most of these factors are studied individually (Ward 2005). Consequently, this study addresses how complex interaction of these local factors and other drivers may contribute to the development of management strategies for woody plant encroachment in rangeland communities.

The study also aims to clarify the effect of *S. plumosum* encroachment on soil fertility. This is because woody or shrubby plant encroachment can also create “islands of fertility”, by increasing nutrient availability below the shrubs, thus providing habitat for species that are sensitive to low nutrient availability (Pugnaire et al. 2011). Nutrient concentration and organic matter are positively and negatively associated with woody or shrubby plant canopy cover and interspaces, respectively (Van Wilgen 2009). In South African semi-arid savannas, the soil nutrient status (Total Nitrogen (TN), Soil Organic Carbon (SOC), and Calcium (Ca) under woody plant canopies was higher than between canopy areas (Hagos and Smit 2004). Thus, woody plant encroachment may obstruct surface flows of water and wind, thereby capturing, concentrating and conserving water and nutrient runoff (Hagos and Smit 2005). Although in doing so, woody plant encroachment may mitigate disturbances caused by intense grazing and high fire intensities (Ratajczak et al. 2011), thus enhancing woody plants persistence and development more than grasslands (Whitford 2002). However, little research exist on how *S. plumosum* encroachment affects soil fertility, yet important to understand its general role on ecosystems.

Generally, the outcomes of woody plant encroachment in semi-arid grassland and savanna communities are not universal (Eldridge et al. 2011). There is little consensus on the consequences of woody plant encroachment for soil nutrient enrichment (Browning et al. 2008, Hobbs and Hoenneke 1992, Maestre et al. 2009). This is because the outcomes of woody plant encroachment depend on soil properties, topographic position (Liu et al. 2013), rainfall (Hoekstra et al. 2005), plant functional traits and their interactions (Liu et al. 2013). Understanding woody plant encroachment is critical because grassland and savanna communities are undergoing widespread degradation (Hoekstra et al. 2005) caused by among others, reduction in grass productivity (Wingley et al. 2009).

In South Africa, *Seriphium plumosum* L., an indigenous, unpalatable shrub in the Asteraceae family, has increased in abundance within its historic range in the fynbos biome and expanded its geographic range in to the grassland biome (du Toit and Sekwadi, 2012). *Seriphium plumosum* encroachment has converted extensive grazing areas into less productive rangelands (Snyman 2012), through displacing palatable grass species (Roux 1969), and reducing carrying capacities of grazing lands. Control methods, including chemical and mechanical options have failed to control *S. plumosum* encroachment and have proven to be prohibitively expensive. Consequently, solutions that integrate knowledge of the ecology of *S. plumosum* species, such as soil –water relationships in rangelands communities, will probably improve our ability to control its encroachment in grasslands.

This study is aimed at determining; 1) the effect of grassland communities, slope position (top, mid and bottom) and their interactions on *S. plumosum* density, cover and soil fertility (Total nitrogen (TN), Phosphorus (P), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg) and Soil Organic Carbon (SOC) and pH). 2) The type of association found between *S. plumosum*

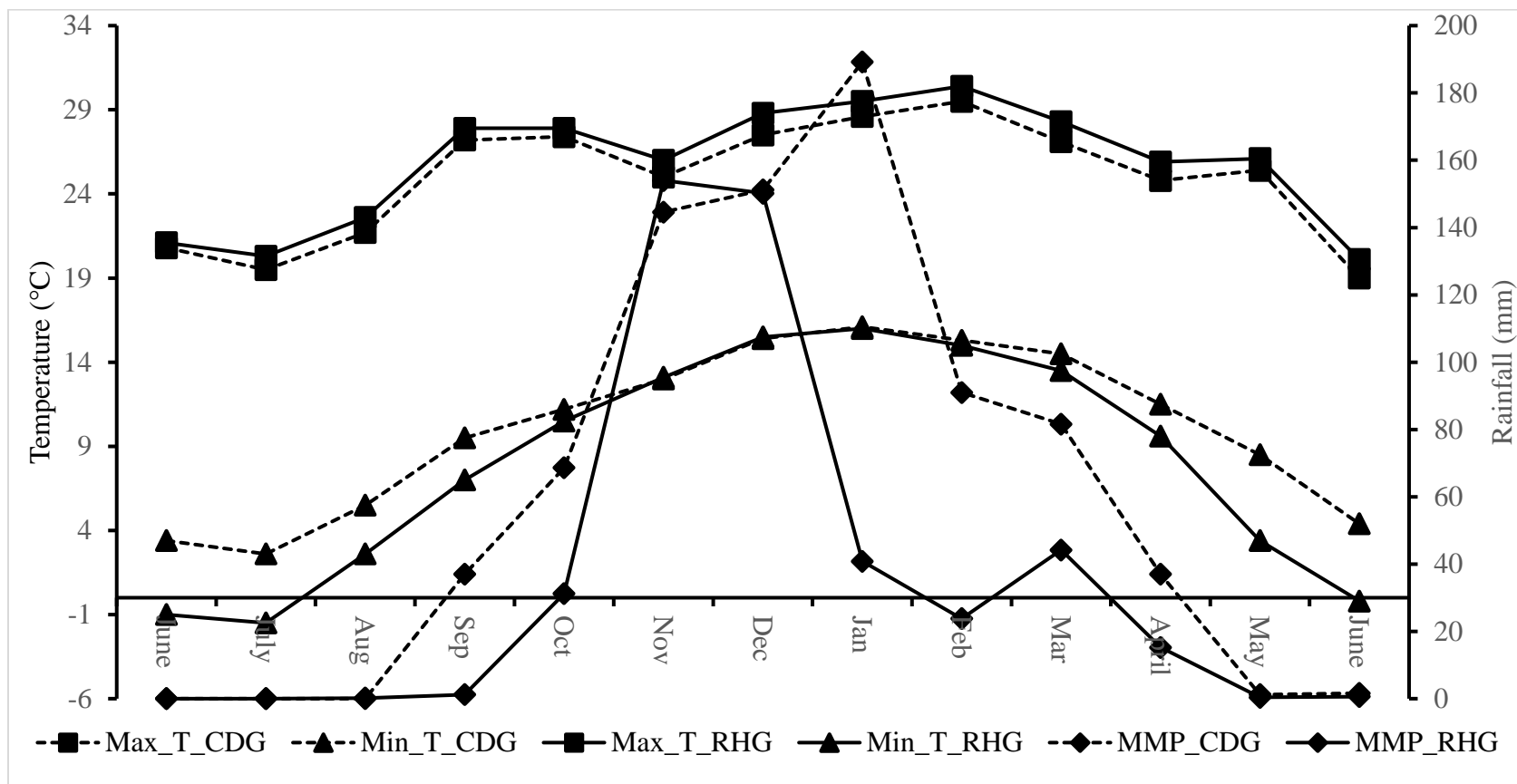
densities, cover, and soil fertility. We predicted that 1) *Seriphium plumosum* density, size and soil fertility will be high at bottom slopes due to run-on of nutrients and rain water. 2) *Seriphium plumosum* density will vary between grassland communities, because of local differences in environmental factors and disturbance regimes, among others.

## **3.2. Materials and Methods**

### **3.2.1. Study area**

The study was conducted on Kaalfontien and Schietfontein private owned farms situated in Gauteng, South Africa. The farm owners gave us permission to do field work on their farms and there was no specific permission required for each locations, since both farms were private owned and the study did not involve any endangered or protected species. These farms are located in Carletonville Dolomite Grassland (Gh15) and Rand Highveld Grassland (Gm 11) veld types, respectively (Mucina and Rutherford 2006). Kaalfontein farm is situated approximately 40 km, west of Johannesburg (27.46738° E, 26.08041° S), and Schietfontein farm approximately 40 km east of Pretoria (28.67918° E, 25.76907° S). In both veld types, *S. plumosum* coexisted with a diversity of herbs, many of which also belong to Asteraceae family. *Seriphium plumosum* occurs in predominantly disturbed and overgrazed areas (Roux 1969, Snyman 2009) of the Eastern Cape, Free State, Mpumalanga, North West and Gauteng Province (Snyman 2009) of South Africa. It also occur in Africa (Koekemoer 2001), Madagascar and in the USA (Schmidt et al. 2001). Both farms used in this study had a history of livestock grazing with accidental fire occurring approximately every second year. These farms are also encroached by the unpalatable, fynbos shrub, *Seriphium plumosum*.

Generally, the sites on Carletonville Dolomite Grassland (CDG) are higher (mean 1614.28 m  $\pm$  0.78 (SEM)) in altitude compared to the Rand Highveld Grassland (RHG) sites (1457.24 m  $\pm$  0.85). Similarly, soils in the CDG had higher silt (8.66 %  $\pm$  0.96) and clay (28 %  $\pm$  0.29) than silt (2.66 %  $\pm$  0.96) and clay (11 %  $\pm$  0.20) in RHG. Rain in both veld types where the farms are located falls almost exclusively in summer (October- April), with means of 593 mm and 654 mm per annum for CDG and RHG, respectively (Mucina and Rutherford 2006). However, during the experiment (2015), the mean annual rainfall of 803 mm and 461.8 mm for CDG and RHG was recorded, respectively. The minimum and maximum summer and winter temperatures for CDG are 11.44 °C and 26.43 °C and in RHG are 9.99 °C and 27.62 °C (Mucina and Rutherford 2006), respectively. However, during the experiment, the mean monthly minimum and maximum summer and winter temperatures for CDG was 10.06 °C and 24.88 °C and in RHG was 7.00 °C and 25.80 °C (Figure 3.1), respectively.



**Figure 3. 1.** Mean monthly precipitation (a), minimum (Min) and maximum (Max) temperature (b), for June 2014 to June 2015 in CDG and RHG.

Carletonville Dolomite Grassland has a complex mosaic pattern of grasses such as *Aristida congesta*, *Brachiaria serrata*, *Eragrostis chloromelas* and *Alloteropsis semialata*. The soils are mostly from the Dolerite and chert of the Malmani Subgroup, which support mostly shallow Mispah and Glenrosa soil forms (Mucina and Rutherford 2006). The RHG is species-rich, with wiry, sour grassland alternating with low, sour shrublands on rocky outcrops and steep slopes. The most common species belong to the genera; *Themeda*, *Eragrostis*, *Heteropogon* and *Elionurus*. The soils are from the Quartzite ridges of the Witwatersrand Super group such as Glenrosa and Mispah, along rocky ridges (Mucina and Rutherford 2006), which support soils of various quality.

### **3.2.2. Sampling design**

A factorial design consisting of two grassland communities (CDG and RHG) x three slope positions (bottom, mid and top slopes) with twelve replicates was used in this study. The sampling sites at each grassland community had six replicates and two subplots at each of the three slope positions (top, mid and bottom) on the north-facing slopes. The two subplots at each slope position were chosen randomly from four previously established subplots. There were 10 m buffer zones between subplots and slope positions. The distance (measured from the center of each subplot) between the two subplots used in this study ranged between 35 m (i.e. for adjacent subplots) and 75 m (i.e. for nonadjacent subplots) apart within slope positions and 35 m (i.e. for adjacent subplots) and 130 m (i.e. nonadjacent subplots) between slope positions (Table 3.1).

**Table 3. 1.** Schematic representation of a replicate used at each of the grassland community.

<b>Slope position</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>
<b>Top</b>	<b>X</b>	<b>X</b>		
<b>Mid</b>		<b>X</b>		<b>X</b>
<b>Bottom</b>	<b>X</b>		<b>X</b>	

**X** represents randomly selected subplots within and between slope positions at each of the six replicates at each grassland community.

There were 50 m buffer zones between the replicates at each of the grassland communities. The centers of the replicates were approximately 150 m apart from each other. The variables measured included *S. plumosum* density and canopy size, and components of soil fertility: Soil organic carbon (SOC), Total Nitrogen (TN), Phosphorus (P), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg) and pH.

### **3.2.3. Vegetation and soil sampling**

*Seriphium plumosum* density, canopy size and soil samples were collected from March to June 2015 at both veld type-sites. *Seriphium plumosum* density was determined by counting all individuals rooted in a 50 m<sup>2</sup> (25 m x 2 m) belt-transect, running downhill, at the center of each 625 m<sup>2</sup> (i.e. 25 m x 25 m) subplots. Density was expressed as mean individual plants per unit area (50 m<sup>2</sup>). Canopy size was determined by measuring horizontal diameter (to the nearest 2 cm) of the long and short axis of the canopy of individuals whose canopy intercepted the 25 m line transect placed down slope in each of the subplots and slope positions. Canopy size was calculated

using an ellipse function ( $C = ab\pi / 4.0$ ), where  $a$  represents the long axis and  $b$  represents the short axis of the canopy (Smith and Grant 1986), and expressed as mean individual canopy size per unit area ( $m^2$ ). Since *S. plumosum* requires water and nutrients to germinate, recruit and survive, but reported to dislike fertile soils (Snyman 2012), the soil samples were taken from 5 cm depth at five random points, irrespective of their proximity to (i.e. below or between) *S. plumosum* plants in each belt transect. The soils were analyzed for eight components of fertility using Ambic I extraction followed by AA spectroscopy. The sub-sample of soils from each of the two subplots at each slope position in each replicate were pooled together and analysed for texture (silt and clay) at the Agricultural Research Council-Institute for Soil, Climate and Water (ARC-ISCW) soil analyses accredited laboratory.

#### **3.2.4. Statistical analyses**

*Seriphium plumosum* density, canopy size and soil fertility at the two grassland communities and three slope positions was analysed as a completely randomised design with a  $2 \times 3$  factorial analysis of variance (ANOVA) using SAS GLM procedures (SAS 2011). Data for *S. plumosum* density, size and soil fertility for each slope position were averaged before the analysis. Data met the assumption of ANOVA concerning homogeneity of variance before being analysed for the effect of grassland community, slope position and their interaction on *S. plumosum* density, canopy size, and components of soil fertility using SAS (2011). When the ANOVA produced significant results, the effect of grassland community, slope position, their interactions on *S. plumosum* density, cover, and components of soil fertility were compared using the Turkey's HSD test, and the differences declared significant at  $P < 0.05$ . Using linear regression analyses in SAS

(2011), we explored the relationship between *S. plumosum* density, individual size and the eight components of soil fertility.

### 3.3. Results

#### 3.3.1. Vegetation parameters

The results on the main factors of grassland community and slope position, as well as their interaction on *S. plumosum* density and canopy size are presented below (Table 3.2).

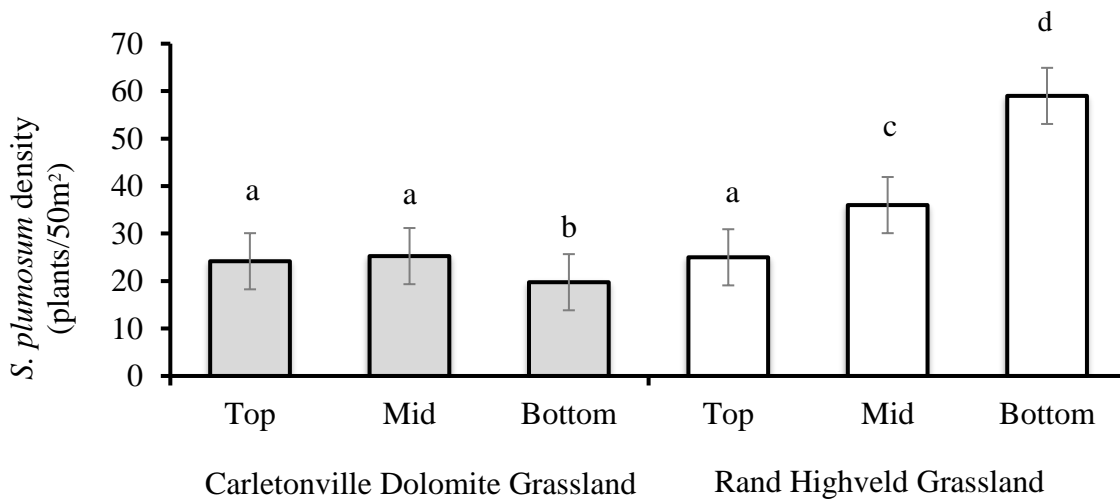
**Table 3. 2.** F values and P values for the effects of grassland community and slope position and their interaction on *Seriphium plumosum* L density and canopy size.

Factors	Vegetation parameters				
	<i>S. plumosum</i> density			<i>S. plumosum</i> canopy size	
	DF	F	P	F	P
Grassland community	1	16.11	<b>0.0002</b>	5.83	<b>0.0186</b>
Slope position	2	3.97	<b>0.0236</b>	3.67	<b>0.0307</b>
Grassland community x slope position	2	7.08	<b>0.0016</b>	0.05	0.9521

Values in bold are significant (P <0.05).

*Seriphium plumosum* density was significantly lower in CDG (23 plants/50 m<sup>2</sup> ± 2.39) than in the RHG (40 plants/50 m<sup>2</sup> ± 4.19). *Seriphium plumosum* density at bottom slopes (39 plants/50 m<sup>2</sup> ±

6.06) was significantly higher than at the top slopes ( $25 \text{ plants}/50 \text{ m}^2 \pm 2.88$ ). *Seriphium plumosum* density at the mid slopes ( $31 \text{ plants}/50 \text{ m}^2 \pm 3.61$ ) was not significantly different from the bottom and top slopes. Grassland community x slope position had a significant interaction effect on *S. plumosum* density ( $P < 0.0016$ ) (Figure 3.2).



**Figure 3. 2.** *Seriphium plumosum* density at CDG (n = 36) and RHG (n = 36) slopes sites.

Bars represent standard error (SEM). Bars with different letters are not significantly different ( $P > 0.05$ )

Bottom slope regions in RHG ( $59.00 \text{ plants}/50 \text{ m}^2 \pm 8.62$ ) had significantly higher *S. plumosum* density than in the mid slopes ( $36 \text{ plants}/50 \text{ m}^2 \pm 4.88$ ) and top slopes ( $25 \text{ plants}/50 \text{ m}^2 \pm 3.94$ ) as well as all slope positions in the CDG. Canopy size of *S. plumosum* was larger in CDG ( $1.39 \text{ m}^2 \pm 0.11$ ) than in RHG ( $1.06 \text{ m}^2 \pm 0.09$ ). In general, *S. plumosum* individual canopy size were bigger at the top slopes ( $1.42 \text{ m}^2 \pm 0.13$ ) than at the bottom slopes ( $0.99 \text{ m}^2 \pm 0.12$ ), while canopy size at the mid slopes ( $1.29 \text{ m}^2 \pm 0.11$ ) was similar to both top and bottom slopes.

### **3.3.2. Components of soil fertility**

Grassland community differed significantly in soil organic carbon ( $P < 0.0001$ ), total nitrogen ( $P < 0.0001$ ), phosphorus ( $P < 0.0001$ ), potassium ( $P < 0.0001$ ), sodium ( $P < 0.0001$ ), calcium ( $P < 0.0001$ ) and magnesium ( $P < 0.0001$ ) content. However, these differences were not observed for soil pH content (Table 3.3).

**Table 3. 3.** F values and P values for the effects of grassland community and slope position and their interaction on components of soil fertility.

Factors	Components of soil fertility																
	SOC			TN		P		K		Na		Ca		pH		Mg	
	DF	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
GC	1	164.47	< 0.0001	36.43	< 0.0001	98.19	< 0.0001	53.02	< 0.0001	80.15	< 0.0001	104.70	< 0.0001	0.32	0.5759	55.47	< 0.001
SP	2	1.28	0.2845	1.76	0.1799	1.26	0.2915	0.04	0.9622	2.38	0.1006	0.45	0.6412	0.10	0.9041	0.56	0.5716
GC X SP	2	0.84	0.4376	1.54	0.2231	158	0.2145	0.54	0.5854	4.28	0.0181	0.11	0.8978	2.90	0.0619	0.80	0.4552

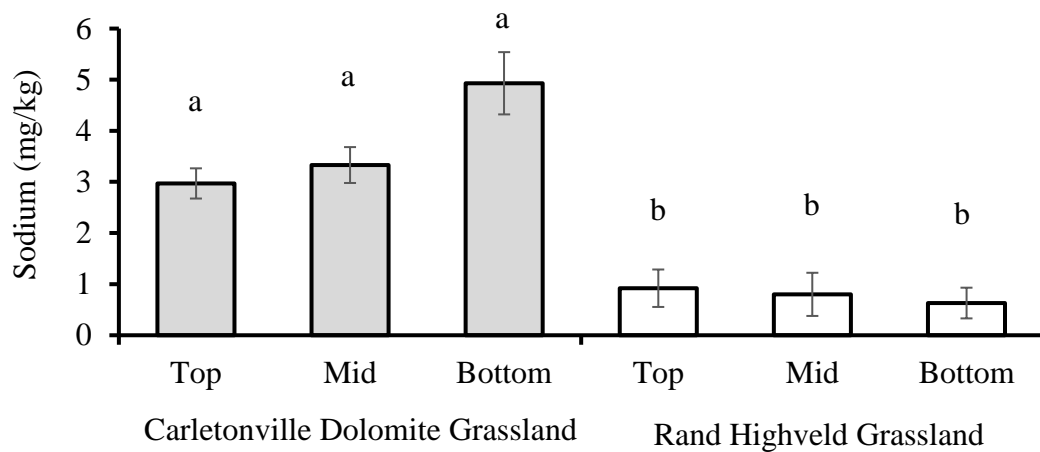
Significant values shown in bold. GC, Grassland Community; SP, Slope position; SOC, Soil Organic Carbon; TN, Total Nitrogen; P, Phosphorus; K, Potassium; Na, Sodium, Ca; Calcium, Mg; Magnesium.

All the components of soil fertility were significantly higher in CDG than in RHG, except pH that was similar at both grassland communities (Table 3. 4).

**Table 3. 4.** Components of soil fertility in Carletonville Dolomite Grassland (CDG) and Rand Highveld Grassland (RHG).

	<b>CDG</b>			<b>RHG</b>		
<b>Components of soil fertility</b>	<b>N</b>	<b>Mean</b>	<b>SE</b>	<b>N</b>	<b>Mean</b>	<b>SE</b>
<b>SOC (%)</b>	36	1.52	0.06	36	0.77	0.03
<b>TN (%)</b>	36	0.05	0.00	35	0.00	0.00
<b>P (%)</b>	36	4.14	0.26	36	1.13	0.16
<b>K (mg/kg)</b>	36	115.04	7.09	36	52.71	4.47
<b>Ca (mg/kg)</b>	35	136.97	11.62	36	15.71	1.06
<b>Mg (mg/kg)</b>	34	49.14	4.25	36	8.39	4.41
<b>pH (mg/kg)</b>	36	5.0	0.04	36	9.90	2.22
<b>Na (mg/kg)</b>	33	3.79	0.30	35	0.79	0.20

No effect of slope position in any soil fertility components was found ( $P = 0.1006$ ). The interaction of grassland community and slope position had significant effect on soil sodium content ( $P = 0.0181$ ). Although Na content did not differ significantly at each site and slope position, there was a tendency of Na to increase from top to bottom slope at CDG and decreasing from top to bottom at RHG (Figure. 3.3).



**Figure 3. 3.** Soil sodium content at CDG (n = 33) and RHG (n = 35) slopes sites.

Bars represent standard error (SEM). Bars with different letters are significantly different ( $p < 0.05$ )

The relationship between *S. plumosum* density and soil fertility was weak but significant ( $P < 0.05$ ). Canopy size did not show any significant relationship with the components of soil fertility ( $P > 0.05$ ; Table 3.5).

**Table 3. 5.** Regression analysis for the relationship between *Seriphium plumosum* density, canopy size and components of soil fertility;  $P < 0.05$  significance level

Components of Soil fertility	<i>S. plumosum</i> density		<i>S. plumosum</i> canopy size	
	$R^2$	$P$	$R^2$	$P$
Soil organic carbon (%)	0.0669	<b>0.0374</b>	0.0302	0.1660
Total Nitrogen (%)	0.0112	0.4010	0.0009	0.8170
Phosphorus (mg/kg)	0.1270	<b>0.0036</b>	0.0207	0.2530
Potassium (mg/kg)	0.0786	<b>0.0237</b>	0.0158	0.3182
Sodium (mg/kg)	0.0686	<b>0.0350</b>	0.0153	0.3270
Calcium (mg/kg)	0.0681	<b>0.0358</b>	0.0398	0.1112
Magnesium (mg/kg)	0.0548	0.0605	0.0324	0.1513
pH (H <sub>2</sub> O)	0.0390	0.1149	0.0125	0.3762

### 3.4. Discussion

*Seriphium plumosum* density was significantly higher at the RHG than in the CDG. This difference between grassland communities suggests that variation in the rate and extent of encroachment may be mediated by, among others, the differences in environmental factors between locations (Archer et al. 2017, Wiens 1999). The RHG bottom slopes had higher *S. plumosum* density than the top slopes. This supports our prediction that, *S. plumosum* density will be high at bottom slopes due to run-on of nutrients and rain water. Ben-Shahar (1990) also found that bottom slopes with high woody vegetation density had high soil nutrient content. In addition, Ludwig et al. (1999) proposed a decrease in ratio of open areas, free from woody plants to run-on areas of woody plants with increasing rainfall, particularly at the bottom

slopes. Woody or shrubby plant encroachment in dryland ecosystems is influenced by, among other factors, high rainfall, which may enhance the establishment of woody or shrubby plant seedlings (O' Connor 1999). Consequently, the higher rainfall and nutrients accumulation at bottoms slopes may explain the higher *S. plumosum* density at the RHG bottom slopes found in this study.

Contrary to our prediction, the bottom slopes in CDG had significantly lower *S. plumosum* density than mid slopes and top slopes. These results are however, consistent with the research finding reporting a decrease in *S. plumosum* density down the slope, with no plants occurring on bottom slope areas (Snyman 2012). It is reported that the top slopes contains on average less water compared to bottom slopes (Ben-Shahar 1990). The fact that *S. plumosum* density was lower at the bottom slopes of CDG may also suggests that multiple factors are responsible for *S. plumosum* germination and recruitment and not only water and nutrients deposited at the bottom slopes. Furthermore, it may suggest that the rate of encroachment stage varies between grassland communities, with RHG being encroached recently relative to CDG. This is because the rate of encroachment is high in the early stages of encroachment, and then declines (Fensham et al. 2005) or fluctuates (Browning et al. 2008), as maximum cover thresholds are approached. Since the CDG had relatively higher soil silt (8.66 %) and clay (28 %) than silt (2.66 %) and clay (11 %) content in the RHG also suggests that CDG bottom slopes may be water logged, and *S. plumosum* is sensitive to water logging conditions (Browning et al. 2008). Contrary to our results, other studies showed a negative correlation between *S. plumosum* density and soil nutrients, i.e., lower density of *S. plumosum* when the soil nutrients are higher, which resulted in decreased *S. plumosum* density at the bottom slope (Snyman 2012). The inconsistency in *S. plumosum* densities between grassland communities and slope positions observed in this study suggest that no single driving factor may explain woody plant

encroachment, but rather a combination of interacting factors (Jackson et al. 1996). Furthermore, it may also suggest that woody plants are generally well suited to a broad range of grassland topographic settings (Liu et al. 2013). The results from this study propose that there may be a number of factors either alone or in combination that have an effect on *S. plumosum* density. Although nutrient and water transported to the bottom slopes may facilitate woody plant seeds germination and assist in explaining *S. plumosum* density at bottom slopes, this condition alone may not adequately explain its encroachment, but a combination of multiple interacting factors (Van Auken 2000). Furthermore, because shrubs act as fertility islands, different management actions may be required at different stages of encroachment because of shrub mediated changes in soil fertility.

*Seriphium plumosum* density was inversely related to individual plant canopy size at the bottom and top slopes of both grassland communities. The RHG had significantly higher *S. plumosum* density and lower canopy size. These results suggest that there is a tradeoff between density and plant canopy size. The higher neighborhood densities in plants may result in density dependent mortality or compensate by shifting the crown centers away from the trunks or neighbours (Getzin and Wiegand 2006). This density dependent mortality or shifting the crown away from the trunks or neighbours could also mean that *S. plumosum* is sensitive to shading by other co-existing species in the same communities.

The fact that CDG had a higher percentage of soil silt and clay content than soils in the RHG, might explain the fewer *S. plumosum* density observed in CDG than in the RHG (Fig 3.2). Many other differences observed between CDG and RHG in this study might result in the differences in density, such that a higher percentage of certain soil textures may not be the only explanation for observed *S. plumosum* densities. The difference in rooting depth between

woody and herbaceous species suggests that the fine-textured soils should be more resistant to woody plant encroachment compared to the coarse-textured soils (Bond and Midgley 2000). Previous research (Hanna et al. 1982), predicted an inverse relationship between woody plant abundance and soil clay content. The higher *S. plumosum* density observed in relatively sandier soils in this study support this prediction. *Seriphium plumosum* encroachment in the CDG suggests that the species is able to spread in soils with greater than the 24% clay encroachment threshold, provided they are deep and well drained. The high silt and clay content found in CDG soils, suggests that *S. plumosum* is sensitive to fine textured soils and probably water logging conditions. Generally, *S. plumosum* prefers slightly deep sandy soils, which are periodically subjected to water stress (Snyman 2012). These results further suggest that soil texture is a primary factor influencing *S. plumosum* density, with slope position being a secondary factor.

Carletonville Dolomite Grassland had fertile soils and lower *S. plumosum* density compared to the marginal soils and higher *S. plumosum* density at the RHG. This finding confirms the research reporting *S. plumosum* encroachment of mostly soils low in fertility (Koekemoer 2001) and withdrawn from cash-crop cultivation. The lower soil sodium content and higher *S. plumosum* density on the bottom slope regions of CDG, may suggests that *S. plumosum* cannot tolerate high soil sodium content (Fig 3.3). This finding suggests that sodium chloride application may assist in controlling *S. plumosum* spread on rangeland communities (Roux 1969, Snyman 2012), and probably increase grass production.

Interestingly, components of soil fertility (SOC, P, K, Na, and Ca) were positively correlated with *S. plumosum* density, but not canopy sizes. These results could not explain whether the “fertility island effect” was caused by woody plant encroachment and not an intrinsic

condition of the soils. However, these results confirm reports that the rate of encroachment is highest in the early stages of encroachment and declines or fluctuates as maximum cover thresholds are reached (Archer et al. 2017) and/or when nutrients and water are depleted due to intraspecific competition (Scholes and Archer 1997). It is also proposed that while some attributes increased and others declined as woody plant encroachment occurs (Eldridge et al. 2011). The findings by Snyman (2012) that *S. plumosum* encroaches first on marginal soils (low in fertility), requires further investigation. The fact that, as woody plants encroach, grass productivity declines, causing soil erosion and reducing the amount of soil nutrients (Stevens et al. 2016) may apply in certain circumstances and not others. Some authors reported that, as woody plants encroach, soil fertility might increase (Hanna 1982, Eldridge et al. 2011), due to patches of woody vegetation obstructing surface flows of water and wind, thereby capturing, concentrating and conserving runoff water and nutrients (Pugnaire et al. 2011). This creates “islands of fertility”, which increase nutrient availability below the shrubs. These “islands of fertility” will in turn provide habitat for species that are sensitive to low nutrient availability (Jackson et al. 1996). The positive relationship between *Seriphium plumosum* density and components of soil fertility, and *S. plumosum* relative abundance in the bottom slope may suggest the sensitivity of *S. plumosum* to low soil nutrient availability. Although this finding confirms our predictions that, *S. plumosum* encroachment would be positively correlated with some components of soil fertility, which would facilitate its germination and recruitment, other research has found the opposite. Consequently, it is suggested in this study that the effects of woody plant encroachment are not universal (Eldridge et al. 2011). Furthermore, it may suggest that woody plant traits also determine the causes and outcomes of encroachment (Liu et al. 2013).

### 3.5. Future Directions

This study shows *S. plumosum* encroachment of mostly, fine textured and fertile soils. Previous research found that, *S. plumosum* occurs mainly in coarse-textured, nutrient poor soils, often with relatively low sodium content. These results are consistent with others on the occurrence of *S. plumosum* on coarse textured soils, but inconsistent on the soil nutrient status. The fact that in this study, *S. plumosum* density has shown a weak positive correlation with components of soil fertility and negative correlation reported in the other study, suggests a need for controlled research on manipulation of soil nutrient resources, especially soil organic carbon (SOC), Phosphorus (P) Potassium (K), and Sodium (Na). This could contribute to understanding how *S. plumosum* responds to soil fertility. Furthermore, an interaction of abiotic factors at grassland communities found in this study, suggests that *S. plumosum* encroachment is influenced by a complex interaction of multiple abiotic factors. Consequently, a better understanding of the complex interaction of these abiotic factors on *S. plumosum* encroachment is needed to aid in its control and management on semi-arid grassland communities of Gauteng Province. The relationship between the changes in abiotic factors and the extent, rate and the occurrence of *S. plumosum* encroachment on the semi-arid grassland communities of Gauteng Province is also lacking. Consequently, more research to understand these relationships is needed to aid in the development of management and control methods for its encroachment in South African semi-arid grassland communities.

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### 3.7. References

- Archer SR, Anderson EM, Predick KI, Schwinning S, Steidl RJ, Woods SR. Woody plant encroachment: Causes and Consequences. In Briske DD, editor. Rangelands Systems. Springer Series on Environmental Management; 2017. pp 25 – 84. [https://doi: 10.1007/978-3-319-46709-2\\_2](https://doi.org/10.1007/978-3-319-46709-2_2).
- Ben-Shahar R. Soil nutrients distribution and moisture dynamics on upper catena in a semi-arid nature reserve. *Plant Ecol.* 1990; 89: 69–77. [https://doi:10.1007/BF00134435](https://doi.org/10.1007/BF00134435).
- Bond WG, Midgley GF. A proposed CO<sub>2</sub> controlled mechanism of woody plant invasion in grassland and savannas. *Glob Change Biol.* 2000; 6: 865–869. [https://doi: 10.1046/j.1365-2486.2000.00365.x](https://doi.org/10.1046/j.1365-2486.2000.00365.x)
- Bond WJ, Midgley GF, Woodward FI. The importance of low atmospheric CO<sub>2</sub> and fire in promoting the spread of grasslands and savannas. *Glob Change Biol.* 2003; 9: 973–982. [https://doi: 10.1046/j.1365-2486.2003.00577.x](https://doi.org/10.1046/j.1365-2486.2003.00577.x).
- Browning DM, Archer SR, Asner GP, McClaran MP, Wessman CA. Woody plants in grasslands: Post-encroachment stand dynamics. *Ecol Appl.* 2008; 18: 928–944. [https://doi:10.1890/07-1559.1](https://doi.org/10.1890/07-1559.1).
- Coetzee BWT, Tincani L, Wodu Z, Mwasi SM. Overgrazing and bush encroachment by *Tarchonanthus camphoratus* in semi-arid savanna. *Afr J Ecol.* 2008; 46: 449–451. <https://doi.org/10.1111/j.1365-2028.2007.00842.x>
- du Toit JCO, Sekwadi KP. Tebuthiuron residues remain active in the soil for at least eight years in the semi-arid grassland, South Africa. *African J of Range and Forage Sci.* 2012; 29: 85–90. <https://doi.org/10.2989/10220119.2012.705325>

- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. Impact of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett.* 2011; 14: 709–722. <https://doi.org/10.1111/j.1461-0248.2011.01630.x>
- Fensham RJ, Fairfax RJ, Acher AR. Rainfall, land use and woody vegetation cover change in semi-arid Australia savanna. *J of Ecol.* 2005; 596 – 606. <https://doi.org/10.1111/j.1365-2745.2005.00998>.
- Getzin S, Wiegand K. Asymmetric tree growth at the stand level: Random crown patterns and the response to slope. *Forest Ecol and Manag.* 2006; 242: 165-174. <http://dx.doi.org/10.1016/j.foreco.2007.01.009>.
- Grover HD, Musick HB. Shrublands encroachment in southern New Mexico, USA: An analysis of desertification processes in the American Southwest. *Climate Change.* 1990; 17: 305 – 330. <http://dx.doi.org/10.1007/BF00138373>
- Hagos MG, Smit GN. Soil enrichment by *Acacia Mellifera* subsp. *detinens* on nutrient poor sandy soil in a semi-arid southern African savanna. *J Arid Environ.* 2004; 61: 47–49. <https://doi.org/10.1016/j.jaridenv.2004.08.003>.
- Hanna AY, Harlan PW, Lewis DT. Soil available water as influenced by landscape position and aspect. *Agronomy Journal.* 1982; 74: 999 – 1004. doi:10.2134/agronj1982.000219620074000600016x
- Hobbs RJ, Hoenneke LF. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conserv Biol.* 1992; 6: 324–337. <https://doi.org/10.1046/j.1523-1992.06030324.x>
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C. Confronting a biome crisis: global disparities of habitat loss and protections. *Ecol Lett.* 2005; 8: 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>

- Jackson RB, Canadell J, Ehleringer JR, Mooney H.A, Sala OE, Schulze ED. A global analysis of roots distributions for terrestrial biomes. *Oecologia* 1996; 108: 389–411. <https://doi.org/10.1007/BF0033371>.
- Kerley GIH, Whitford WG. Can Kangaroo rat graminivory contribute to the persistence of desertified shrublands? *J Arid Environ.* 2009; 73: 651–657. <http://dx.doi.org/10.1016/j.jaridenv.2009.01.001>.
- Knoop WT, Walker BH. Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecol.* 1985; 235 – 253. <https://doi.org/10.2307/2259780>.
- Koekemoer M. Systematics of the Metalasia group in the Relhaniinae (Gnaphalieae – Asteraceae). PhD thesis. 2001; Rand Afrikaans University, South Africa.
- Liu F, Archer RS, Gelwick F, Bai E, Boutton TW, Ben Wu X. Woody Plant Encroachment in Grasslands: Spatial pattern of Functional Group Distribution and Community Development. *PloS ONE*. 2013; 8: 1–13. <https://doi.org/10.1371/journal.pone.0084364>.
- Ludwig JA, Tongway DJ, Eager RW, Williams RJ, Cook GD. Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landsc Ecol.* 1999; 14: 557–566. <https://doi.org/10.1023/A:10081122193>
- Maestre FT, Bowker MA, Puche MD, Hinojosa MB, Martinez I, Garcia-Palacios P, et al. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecol Lett.* 2009; 12: 930–941. <https://doi.org/10.1111/j.1461-0248.2009.01352.x>.
- McAuliffe JR. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs.* 1994; 64: 112–148. <https://doi.org/10.2307/2937038>.
- MEA. Millennium Ecosystem Assessment- Ecosystems and Human Well-being: Desertification Synthesis. World Resource Institute, Washington, D.C; 2005.

- Morgan JA, Milchunas DG, LeCain DR, West M, Mosier AR. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. PNAS. 2007; 104: 14724–14729. <https://doi.org/10.1073/pnas.0703427104>.
- Mucina L, Rutherford MC. The Vegetation of Southern Africa, Lesotho and Swaziland. Strelitzia 19, South African National Botanical Institute, Pretoria, South Africa; 2006.
- O' Connor TG. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. Oecologia. 1995; 103: 214–223. <https://doi.org/10.1007/BF00329083>.
- Oba G, Post E, Syvertsen PO, Stenseth NC. Bush cover and range condition assessment in relation to landscape and grazing in southern Ethiopia. Landsc Ecol. 2000; 15: 535 – 546. <https://link.springer.com/article/10.1023/A:1008106625096>
- Price JN, Morgan JW. Woody plant encroachment reduces species richness of herd-rich woodlands in southern Australia. Austral Ecol. 2008; 33: 278 – 289. <https://doi.org/10.1111/j.1442-9993.2007.01815.x>
- Pugnaire FI, Armas C, Mastre FT. Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradient, and ecosystem function. J Arid Environ. 2011; 75: 1310–1320. <http://dx.doi.org/10.1016/j.jaridenv.2011.01.016>.
- Ratajczak ZR, Nippert JB, Hartman JC, Ocheltree TW. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. Ecosphere. 2011; 2: 1–14. <https://doi.org/10.1890/ES11-00212.1>.
- Roux E. Bankrotbos. In: Roux WM, editor. Grass: a story of Frankenwald. Cape Town: Oxford University Press; 1969. pp. 153–159.
- SAS Institute. SAS/STAT User's Guide. Version 9.3. SAS Institute, Cary: NC, USA; 2011.
- Schlesinger WH, Pilmanis AM. Plant – soil interactions in desert. Biogeochemistry. 1998; 42: 169–187. <https://doi.org/10.1007/978-94-017-2691-79>.

- Schmidt E, Lotter M, McClelland W. Tree and shrubs of the Mpumalanga and Kruger National Park: Jacaranda Media Publisher, Pretoria; 2002.
- Scholes RJ, Archer RS. Tree-grass interaction in savannas. *Annu Rev Ecol Syst.* 1997; 28: 517–544. <https://doi.org/10.1146/annurev.ecolsys.28.1.517>
- Shaver GR, Bret-Harte MS, Jones MH, Johnston J, Gough L, Laundre J, et al. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology.* 2001; 82: 3163–3181. [https://doi.org/10.1890/0012-9658\(2001\)082\[3163:SCIWFT\]2.0.CO2](https://doi.org/10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO2).
- Smith TM, Grant K. The role of competition in the spacing of trees in a *Burkea africana-Terminalia sericea* savanna. *Biotropica.* 1986; 18: 219–223. <https://doi:10.2307/2388488>.
- Snyman HA. A physiological approach to the distribution and spread of *Seriphium plumosum*. *Newsletter of the Grassland Society of Southern Africa.* 2009a; 9: 29–37.
- Snyman HA. Control measures for the encroacher shrub *Seriphium plumosum*. *South Afri J of Plant and Soil.* 2012; 29: 157–163. <https://doi:10.1080/02571862.2012.745905>.
- Snyman HA. Habitat preference of the encroacher shrub, *Seriphium plumosum*. *J Botany.* 2012; 81: 34–39. <https://doi:10.1016j.sajb.2012.05.001>.
- Stevens N, Lehmann CER, Murphy BP, Durigan G. Savanna woody encroachment is widespread across three continents. *Glob Chang Biol.* 2016; 23: 235 – 244. <https://doi:10.1111/gcb.13409>.
- Tjelele JT, Dziba LE, Pule HT. Recovery and germination of *Dichrostachys cinerea* seeds fed to goats (*Capra hircus*). *Range Ecol and Man.* 2012; 65(1): 105 – 108. <https://doi.org/10.2111/REM-D-09-00161.1>

- Tjelele TJ, Dziba LE, Pule HT. Recovery and germination of *Dichrostachys cinerea* seeds fed to goats (*Capra hircus*). *Rangeland Ecol and Manag.* 2012; 65: 105–108. [https://doi: 10.2111/REM-D-09-00161.1](https://doi.org/10.2111/REM-D-09-00161.1).
- Tjelele TJ, Ward D, Dziba LE. The effect of seed ingestion by livestock, dung fertilization, trampling, grass competition and fire on seedling establishment of two woody plant species. *Plos One.* 2015; 10: 1–13. e0117788.[doi:10.1371/journal.pone.0117788](https://doi.org/10.1371/journal.pone.0117788).
- Trollope WSW. Fire in Savanna. In de Booyesen PV, editor. *Ecological effects of fire in South African Ecosystems. Ecological Studies (Analysis and Synthesis).* Vol 48. Springer, Berlin, Heidelberg; 1984. pp 149 – 175.
- van Auken OW. Shrub invasion of North American semi-arid grasslands. *Annu Rev Ecol Syst.* 2000; 71: 197–215. <https://doi.org/10.1146/annurev.ecolsys.31.197>.
- Van Wilgen BW. The evolution of fire and invasive alien plant management practices in fynbos. *S Afr J Sci.* 2009; 105: 335–342. <http://hdl.handle.net/10204/3795>.
- Walker BH, Ludwig D, Holling CS, Peterman RM. Stability of semi-arid savanna grazing systems. *J. Ecol.* 1981; 473 – 493. <http://www.jstor.org/stable/2259679>.
- Walker BH, Noy-Meir I. Aspects of the stability and resilience of savanna ecosystem. In: Huntley BJ, Walker BH, editors. *Ecology of Tropical Savannas.* Springer-Verlag, Berlin; 1982. pp. 556–590. [https://doi: 10.1007/978-3-68786-0\\_26](https://doi.org/10.1007/978-3-68786-0_26).
- Ward D, Wiegand K, Getzin S. Walter’s two-layer hypothesis revisited: Back to the roots! *Oecologia.* 2013; 617–630. <https://doi.org/10.1007/s00442>.
- Ward D. Do we understand the causes of bush encroachment in African savannas? *Afr J Range and Forage Sci.* 2005; 22: 101–105. [https:// doi 10.2989/10220110509485867](https://doi.org/10.2989/10220110509485867).
- Ward DW, Hoffman MT, Collocott SJ. A century of woody plant encroachment in the dry Kimberly savanna of South Africa. *Afr J Range and Forage Sci.* 2014; 31: 107–121. [https://doi: 10.2989/10220119.2014.914974](https://doi.org/10.2989/10220119.2014.914974).

- Whitford WG. Ecology of desert systems. Academic press, an Elsevier Science Imprint, San Diego, California. 2002; pp 343. ISBN 0-12-747261-4.
- Wiens JA. Spatial scaling in Ecology. *Funct Ecol.* 1989; 3: 385–397. [https://doi: 10.2307/2389612](https://doi.org/10.2307/2389612).
- Wingley BJ, Bond WJ, Hoffman MT. Thicket expansion in South African savanna under divergent land use: local vs. global drivers? *Glob Change Biol.* 2009; 16: 964–976. [https://doi: 10.1111/j.1365-2486.2009.02030.x](https://doi.org/10.1111/j.1365-2486.2009.02030.x)
- Wu XB, Archer SR. Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes. *Lands Ecol.* 2005; 20: 733 – 742. [https://doi: 10.1007/s10980-005-0996-x](https://doi.org/10.1007/s10980-005-0996-x)

## CHAPTER 4

**The effect of *Seriphium plumosum* L. canopy cover, fire and soil depth on components of soil fertility in the semi-arid grassland community of Gauteng Province, South Africa**

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## Abstract

The causes of an indigenous unpalatable shrub, *Seriphium plumosum* L., encroachment in the semi-arid grasslands of Gauteng Province are numerous, but its encroachment effects on grassland ecosystem functioning are still not clearly understood. This limits the ability of land users to evaluate trade-offs that must be considered as the extent of *S. plumosum* encroachment increases. The aim of this study was to investigate the interactive effect of *S. plumosum* canopy cover, fire and soil depth on components of soil fertility [Potassium, Phosphorus, Magnesium, Total nitrogen (TN), Sodium, Calcium, Soil organic carbon (SOC) and pH]. Soil samples were collected from two different microhabitats (under *S. plumosum* canopies and between canopied areas), fire (pre- and post-fire) treatment areas at different depth [topsoil (5 cm) and subsoil (10 cm)] using randomly selected subplots (25 m x 25 m), located at top, mid and bottom slope positions and replicated six times. Data was analysed as a completely randomised design with a 2 x 2 x 2 factorial analysis of variance using Generalised Linear Model (GLM) procedure. There were significant main effects of fire and soil depth ( $P < 0.05$ ), but not microhabitat ( $P > 0.05$ ) on the components of soil fertility. There was a significant interaction effect of fire x soil depth on K, P, Mg, TN, Ca, SOC and pH ( $P < 0.05$ ). However, there were no significant interaction effects of habitat x fire, habitat x soil depth and habitat x fire x soil depth found on the components of soil fertility ( $P > 0.05$ ). All the components of soil fertility measured showed a significant decrease with soil depth and increase with fire treatment ( $P < 0.05$ ). The results showed that *S. plumosum* encroachment contributes to accelerate rather than reverse rangeland degradation. Furthermore, fire alone is not a recommended management tool to control *S. plumosum* encroachment in grassland, because it might stimulate *S. plumosum* to resprout from the basal areas, exacerbating its encroachment.

**Key words:** burning, veld degradation, shrub invasion, microclimate

#### **4.1. Introduction**

Drylands cover over 40% of the terrestrial land surface (Schimel 2010) and are home to 2.3 million people (World Resource Institute, 2002). In these ecosystems, one of the most striking land cover changes over the past 150 years is the proliferation of trees and shrubs at the expense of perennial grasses - a phenomenon referred to as woody plant encroachment (Ward 2005). This phenomenon occurs particularly in the semi-arid savannas and grasslands of North America (Barger et al. 2011), South America (Stevens et al. 2016), Africa (Hudak and Wessman 2001), and Australia (Sharp and Whittaker 2003). Woody plant encroachment is regarded as a form of land degradation (Golubiewski and Hall-Beyer 2010; MEA 2005; Archer et al. 2017). It increases runoff and soil erosion (Parizek et al. 2002; Puttock et al. 2014), with resultant reductions in soil fertility (Puttock et al. 2014), soil moisture (Schade and Hobbie 2005; Bonan, 2008) and infiltration rate. Woody plant encroachment reduces productivity, density, cover and recruitment of grasses (Gibbens et al. 2005). It threatens grassland biodiversity and the sustainability of pastoral, subsistence and commercial livestock farming (Ayalew and Mulualem 2018).

Some ecosystem attributes (organic C, total N and potential N mineralization) may increase in the soil (Reynolds et al. 2007), but others (grass cover and soil pH) may decrease with encroachment (Eldridge et al. 2011), while some remain unchanged (House et al. 2003). Clearly, woody plant encroachment effects on ecosystem functioning depend on the woody plant species functional traits (Maestre et al. 2009) its encroachment stage (Archer et al. 2017) and local rainfall. To understand the causes and consequences of woody plant encroachment requires multi-factorial experiments that recognize woody plant encroachment as a complex socio-ecological system (Wilcox et al. 2018). Furthermore, understanding the causes and consequences of woody plant encroachment may help evaluate trade-offs that must be considered as woody species abundance changes (Archer et al. 2017).

*Seriphium plumosum* L., previously known as *Stoebe vulgaris* (Clark et al. 2020), is a multi-stemmed, unpalatable shrub in the Asteraceae family and indigenous to South Africa (Snyman 2011). *Seriphium plumosum* L has increased its geographic range from the fynbos biome into the semi-arid grassland biome (Mucina and Rutherford 2006), where it occupies mostly nutrient poor sandy soils. Its encroachment in South Africa is predominantly in the Eastern Cape, Free State, Mpumalanga, North West and Gauteng Provinces (Snyman 2009a). *Seriphium plumosum* also occurs in other African countries such as Angola, Namibia, Mozambique and Zimbabwe (Koekemoer 2001) and farther afield in the USA (Badenhorst 2009; Schmidt et al. 2002).

*Seriphium plumosum* encroachment has converted large parts of the semi-arid grassland into less productive shrubland-grasslands (Snyman 2012a; Avenant 2015). Grass productivity decreases by up to 65 % when *S. plumosum* densities reaches 2000 plants/ ha (Snyman 2012a). This reduction in grass production may result in grassland communities being unable to support large populations of grazers and the pastoral economy as in the past (Reynolds et al. 2007). Chemical and mechanical control measures for *S. plumosum* have been proposed (Wepener et al. 2007; Snyman 2011), but because of their cost factor, these control measures are regarded as unsustainable. Consequently, more ecological research is required to aid in controlling its encroachment in rangeland communities (Snyman 2012; Clark et al. 2020).

In the semi-arid regions, soil fertility beneath tree canopies is frequently higher than in the inter-canopy zones (Treydte et al. 2010). Woody and/or shrubby plant canopies may have a positive effect on soil fertility, species richness and biomass production of the understorey plant communities (Hagos and Smit 2005; Soliveres and Eldridge 2014). Their canopies may also alter the microenvironment, soil physical and chemical (fertility) properties (Ding and Eldridge 2019). This often occurs when sediments, nutrients and water are transported by wind and water, and are obstructed underneath woody plant canopies (Ludwig et al. 2005), thus

creating localised nutrient enrichment (Hugos and Smit 2005). Shading also reduces direct losses of C from surface litter via photo-degradation (Austin and Vivanco, 2006), altering soil microbes, temperature, and moisture conditions, all of which affect organic matter mineralisation rates and soil C stores (Thomas et al. 2018).

Fire is recognized as a disturbance that maintains grasslands and savannas (Neary and Leonard 2018). It may prevent woody plant species encroachment (Archer et al. 2001) or woody plants species may recruit en masse in the patches opened up by fire. Fire has the potential to influence ecosystem carbon storage and dynamics by changing plant species diversity and dominance, plant tissue chemistry, primary productivity, decomposition of soil organic matter and characteristics of the physical environment (Dai et al. 2006). Furthermore, fire can increase surface runoff and erosion rates by removing vegetation, changing the soil's hydrologic properties and providing a readily erodible layer of sediment and ash (Shakesby et al. 2007; Shakesby 2011).

The most intuitive change the soil experiences during fire is loss of organic matter (Certini, 2005). Burned soils have lower nitrogen than unburned soils, higher calcium, and largely unchanged potassium, magnesium, and phosphorus stocks (Neff et al. 2005). The lower nitrogen during prescribed burning is due to nitrogen volatilization (Caldwell et al. 2002). Soil nutrients enhancement by fire occurs largely on the surface soil (0-5 cm), with only soluble N increasing in the subsurface soil (5-10 cm). There is a large body of evidence that heat penetration in the soil is limited to the soil surface areas (i.e., 0 to 5 cm depth: Mondal and Sukumar 2014). Low-intensity prescribed fire usually results in little change in soil carbon, while intense fire can result in a huge loss of soil carbon (Certini 2005) caused by soil carbon's low temperature threshold 500° C (Verma and Jayakumar 2012). Although fire may change soil nutrient status by direct addition of nutrients and by indirectly altering the soil environment (Verma and Jayakumar 2012), there is a lack of information on the effect of fire on soil nutrients

in *S. plumosum* encroached areas. The development of *Seriphium plumosum* management strategies need a sound understanding of their ecology (Snyman 2012), particularly on the effect of post- fire on *S. plumosum* encroachment.

This study explored how *S. plumosum* L. encroachment and prescribed fire interact to accelerate or reverse rangeland degradation. Specifically, we investigated the effect of *S. plumosum* canopy areas and prescribed fire on the components of soil fertility at different soil depths in the semi-arid grassland communities in Gauteng Province. We hypothesize that, soils, particularly topsoils, will be more fertile under *S. plumosum* canopies post fire. The knowledge gained in this study will be relevant for other ecosystems where encroaching woody plants are fire adapted such as with *S. plumosum* encroached semi-arid grassland communities.

## **4.2. Materials and Methods**

### **4.2.1. Study site**

The experiment was conducted in Gauteng Province (27.46738° E, 26.08041° S), South Africa. The vegetation forms part of the Carletonville Dolomite Grassland (CDG) (Gh15) veld type (Mucina and Rutherford 2006), with the experimental site facing the north at an elevation of 1614 m above sea level. Rain falls almost exclusively in summer (October- April), with a mean of 593 mm per annum (Mucina and Rutherford 2006). However, an above average rainfall of 803 mm/ annum was recorded during the year (2015) of data collection. The minimum and maximum summer and winter temperatures for CDG are 15.4 °C and 30 °C and 6 °C and 21 °C (Mucina and Rutherford 2006), respectively. The experimental site is encroached by *S. plumosum* shrubs that coexist with a diversity of grasses species and herbs, many of which belong to the Asteraceae family. *Seriphium plumosum* L. density and canopy size at the experimental site were 23 plants / 50 m<sup>2</sup> ± (2.39 (SEM)) and 1.39 m<sup>2</sup> ± (0.11), respectively. The soils had a mean silt and clay content of 8.66 % ± (0.96) and 28 % ± (0.29), respectively.

The farm had a history of livestock grazing with accidental fire occurring approximately once in every three years.

#### **4.2.2 Sampling design**

The study used a factorial design, consisting of habitat (under canopy areas and inter-canopy areas), fire (pre- and post-fire) and soil depth (topsoils and subsoils), replicated six times at each of the three slope positions (top, mid and bottom). Soil samples collected pre-fire treatment were from two subplots of 25 m x 25 m each, randomly located at each of the three slope positions. During post-fire treatment, soil samples were collected from one randomly selected subplot located at each of the three slope positions in each of the six replicates. These subplots were chosen from a pool of four previously established subplots at each of the three slope positions in each of the six replicates. There were 10 m buffer zones between subplots in different and at the same slope positions. The distance (measured from the center of each subplot) between the two subplots ranged between 35 m (i.e. for adjacent subplots) and 75 m (i.e. for nonadjacent subplots) apart within slope positions and 35 m (i.e. for adjacent subplots) and 130 m (i.e. nonadjacent subplots) between slope positions for the pre-fire sampling.

#### **4.2.3. Soil sampling**

Individual *S. plumosum* plants ( $n = 5$ ) were randomly selected in each of the experimental subplots during pre-fire treatment. Soil samples were collected under the canopy of these plants (i.e. 20 cm from the stem, but under its canopied areas) at 5 cm and 10 cm depth, and between their canopied areas (i.e. approximately 50 cm away from nearest *S. plumosum* canopied areas in the inter spaces) during both pre- and post-fire treatment. The soils collected pre-fire treatment are from the same sampling point for both 5 cm (topsoil) and 10 cm depth (subsoil) and were extracted using a soil auger. The same sampling procedure was followed during post-

fire treatment, except that new soil sampling areas were used. The soils collected at each depth and subplot were pooled together and stored pending analysis. This sampling procedure was followed pre- (n = 144) and post-fire (n = 72) treatment. These soils were analysed for; potassium (K), phosphorus (P), magnesium (Mg), total nitrogen (TN), sodium (Na), calcium (Ca), soil organic carbon (SOC) and pH. Soil phosphorus was determined using a P Bray No1, following Mallarino and Blackmer (1992). Soil K, Ca, Mg and Na content were determined using soil ammonium acetate extraction method (Schollenberger and Dreiselbis 1930). Soil organic carbon was determined following the Walkley Black (1934) procedure, while TN was determined using a Total Nitrogen digester. Soil pH was determined using water, with a 2:5 soil: water ratio (Jackson 1982). Soil analysis were conducted at the Agricultural Research Council: Institute for Soil, Climate and Water (ARC: ISCW).

#### **4.2.4. Statistical analysis**

The effect of microhabitat, fire treatment, soil depth and their interactions on components of soil fertility was analysed as a randomised complete block design, with a 2 x 2 x 2 factorial analysis of variance (ANOVA) using generalised linear model (GLM) procedures. Microhabitat (under canopied and between canopied areas), fire (pre- and post-fire treatment) and soil depth (topsoil (5 cm) and subsoil (10 cm)) areas are independent variables and components of soil fertility (K, P, Mg, TN, Na, Ca, SOC and pH), as dependent variables. Components of soil fertility at Carletonville Dollomite Grassland slope positions were not significantly different. Consequently, the effect of slope position on components of soil fertility were excluded during the analysis. The data met the assumptions of ANOVA concerning normality and homogeneity of variance before being analysed using SAS (2011). When the ANOVA produced significant results, means were compared using the Turkey's HSD test, and the differences declared significant at  $P < 0.05$ .

### 4.3. Results

There was no significant main effect of microhabitat on any of the components of soil fertility observed in this study ( $P > 0.05$ ). However, there was a significant main effect of fire on soil K, P, Mg, Na, Ca and pH concentrations ( $P < 0.05$ ). Soil K content were significantly lower ( $94.74 \pm 3.36$  (SEM)) during pre-fire treatment compared to post-fire treatment ( $116.20 \text{ mg/kg} \pm 6.74$ ). Soil P content was a significantly lower ( $3.23 \text{ mg/kg} \pm 0.15$ ) during the pre-fire treatment than during post-fire treatment ( $4.34 \text{ mg/kg} \pm 0.27$ ). Similarly, soil Mg content was lower ( $46.49 \text{ mg/kg} \pm 2.15$ ) during pre-fire treatment compared to post-fire treatment ( $57.67 \text{ mg/kg} \pm 3.68$ ). We found a significantly lower ( $4.33 \text{ mg/kg} \pm 0.21$ ) soil Na content during pre-fire treatment than during post-fire treatment ( $6.27 \text{ mg/kg} \pm 0.41$ ). Furthermore, soil calcium content was significantly lower ( $117.20 \text{ mg/kg} \pm 5.12$ ) during pre-fire treatment than during post fire treatment ( $142 \text{ mg/kg} \pm 8.89$ ). Soil pH content was lower ( $4.78 \pm 0.01$ ) during the pre-fire treatment, but not significantly different from pH content ( $4.87 \pm 0.03$ ) during the post fire treatment.

The main factor of soil depth had a significant effect on soil K, P, Mg, Ca, TN, SOC and pH concentrations ( $P < 0.05$ ). Soil K content was significantly higher ( $127.64 \text{ mg/kg} \pm 4.77$ ) on topsoil compared to subsoil ( $76.15 \text{ mg/kg} \pm 2.65$ ). Similarly, soil P content was significantly higher ( $4.99 \text{ mg/kg} \pm 0.01$ ) on topsoil than on subsoil ( $2.29 \text{ mg/kg} \pm 0.13$ ). There was a significant higher ( $60.70 \text{ mg/kg} \pm 3.08$ ) soil Mg content at the topsoil compared to subsoil ( $39.72 \text{ mg/kg} \pm 1.78$ ). Total nitrogen on topsoil was significantly higher ( $0.06 \% \pm 0.0009$ ) than in the subsoil ( $0.05 \% \pm 0.00067$ ). In addition, soil calcium content was significantly higher ( $154.88 \text{ mg/kg} \pm 7.02$ ) at the top soil compared to the subsoil ( $90.37 \text{ mg/kg} \pm 4.28$ ). Soil organic carbon was similar on topsoil ( $1.54 \text{ mg/kg} \pm 0.02$ ) than subsoil ( $1.28$

mg/kg  $\pm$  0.01). Soil pH content was higher on the topsoil ( $4.91 \pm 0.022$ ) than at the subsoil ( $4.71 \pm 0.01$ ).

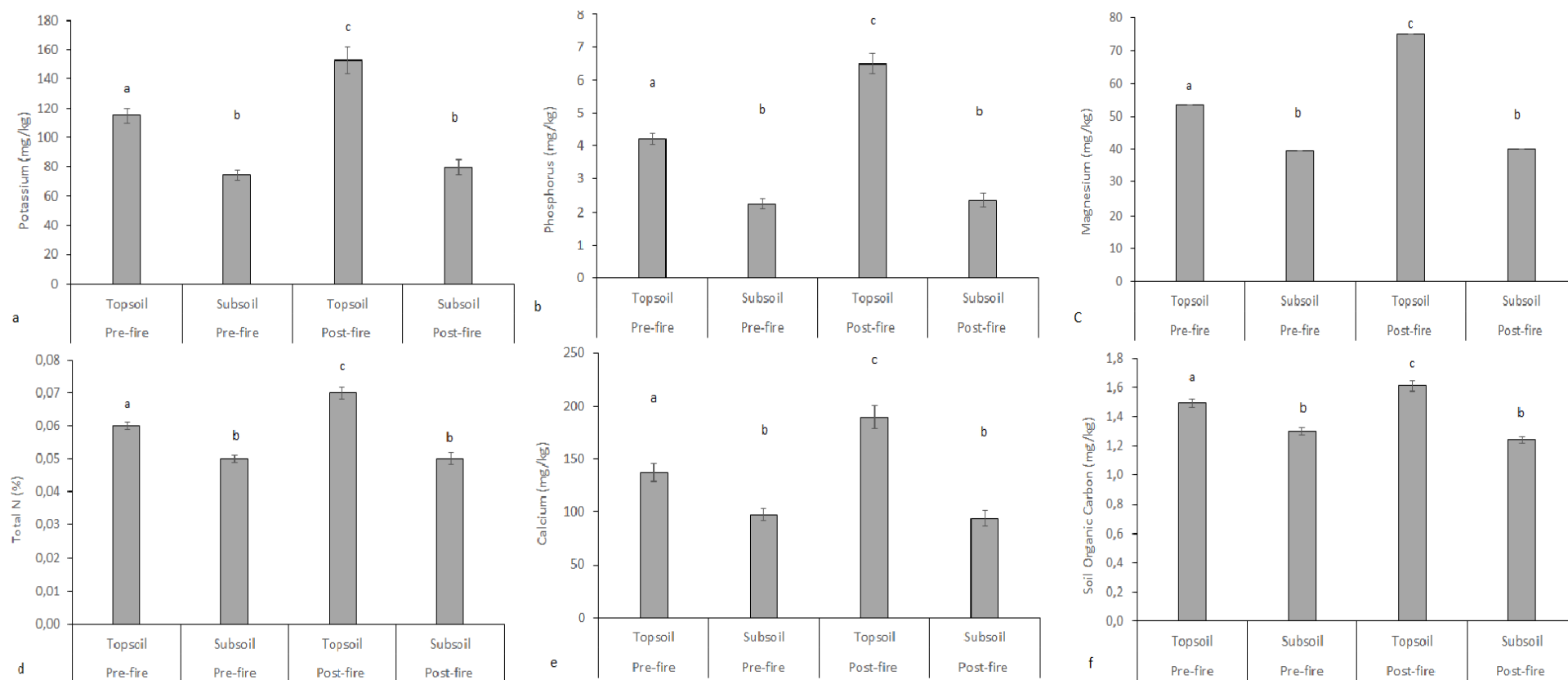
The interaction of microhabitat x fire and habitat x soil depth had no significant effect on any components of soil fertility in this study ( $P > 0.05$ ; Table 4.1). However, there was a significant interaction effect of fire x soil depth on soil K, P, Mg, TN, Ca, SOC and pH ( $P < 0.05$ ). Soil pH content was significantly lower ( $4.87 \pm 0.03$ ) on topsoils, pre-fire treatment than during post fire treatment ( $5.02 \pm 0.03$ ). Furthermore, there were no significant differences between the subsoil pH during pre-fire treatments ( $4.70 \pm 0.02$ ) and post-fire treatment ( $4.74 \pm 0.02$ ). Generally, there was a significant effect of fire on topsoil fertility parameters (K, P, Mg, TN, Ca and SOC), but not on subsoil fertility parameter ( $P > 0.05$ ; Figure 4.1).

**Table 4. 1.** ANOVA results for main effects of microhabitat, fire and soil depth and their interaction on components of soil fertility

Factors		Components of soil fertility															
		K		P		Mg		Total N		Sodium		Calcium		SOC		pH	
	DF	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Microhabitat	1	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00
Fire	1	14.00	< 0.001	31.56	< 0.001	9.25	< 0.001	0.30	0.58	21.59	< 0.001	8.71	< 0.001	1.04	0.31	12.06	< 0.001
Soil depth	1	96.32	< 0.001	177.73	< 0.001	36.62	< 0.001	134.18	< 0.001	0.03	0.87	54.02	< 0.001	71.25	< 0.001	67.46	< 0.001
Microabitat x Fire	1	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00
Microhabitat x Soil depth	1	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00
Fire x Soil depth	1	8.60	< 0.001	26.48	< 0.001	8.33	< 0.001	4.99	0.03	1.33	0.25	11.06	< 0.001	6.66	0.01	4.38	0.04
Microhabitat x Fire x Soil depth	1	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00

Significant values are shown in bold. K: Potassium; P: Phosphorus; Mg: Magnesium; TN: Total nitrogen; Na: Sodium; Ca: Calcium; SOC: Soil

Organic Carbon.



**Figure 4. 1.** Interaction effect of fire x soil depth on the concentration of soil potassium (a), phosphorus (b), magnesium (c), total N (d), calcium (e) and soil organic carbon (f) concentrations. Same letters on the bars means that  $P > 0.05$ .

#### 4.4. Discussion

The presence of *Seriphium plumosum* canopy did not affect the components of soil fertility. This finding contradicted our prediction that soils will be more fertile under *S. plumosum* canopies. The soils under woody plant canopies generally have higher levels of organic matter, calcium, magnesium, potassium, total exchangeable bases, cation exchange capacity and pH than those in open grasslands (Eldridge et al. 2011). Woody plant encroachment produces resource poor and rich patches between and under shrub canopies, respectively (Waring et al. 2015), especially in arid and semi-arid areas. Shrubs establishing in degraded rangelands often create “islands of fertility” under individual shrub canopies (Shade and Hobbie 2005; Mudrak et al. 2014), which enhances vascular plant richness, microbial biomass, soil fertility, and nitrogen mineralization (Archer et al. 2017). Consequently, shrubs may reverse, rather than cause, desertification. Certain woody plant species may lead to the formation of fertile shrub patches interspaced with nutrient-depleted bare soil patches (Sankey et al. 2012).

Generally, there are positive effects of individual shrub canopies on the understorey plant communities and soil condition in semi-arid environments (Maestre and Cortina 2005; Holzapfel et al. 2006; Soliveres and Eldridge 2014). However, the positive effect of *S. plumosum* shrubs canopies on the understorey plant community and soil condition, was not observed in this study. Although the effect of allelopathy was not explored in this study, Snyman (2010) reported that *S. plumosum* contains allelopathic compounds that deter growth of other dicot and herbaceous species. This may suggest that *S. plumosum* encroachment in semi-arid grassland communities may be accelerating rather than reversing rangeland degradation and/or unchanged soil fertility under *S. plumosum* canopies was an inherent characteristic of the site and not a result of encroachment. Other studies also found a link between woody or shrubby plant encroachment with land degradation and desertification processes (MEA 2005; Ravi et al. 2009). There are other factors such as species functional

traits which also influence the outcome of woody plant encroachment (Li et al. 2007; Eldridge et al. 2011; Archer et al. 2017), thus making woody/shrubby plant encroachment outcomes on ecosystem functioning non-universal (Maestre et al. 2009; Eldridge et al. 2011).

The components of soil fertility were relatively higher in the topsoils, especially post-fire treatment. These results suggest that fire improves topsoil nutrients concentration. Consistent with our findings, Certini (2005) found that soil nutrient concentrations in burned areas are generally higher than in unburned areas. Soil K and P, increase with fire (Duguy et al. 2007), especially in the topsoil. Ando et al. (2014) reported an increased level of available nutrients such as ammonium nitrogen, phosphorus, exchangeable potassium and calcium following the decomposition of soil organic matter and microbial mortality following fire. Fire might contribute to the control of woody plant encroachment (Hoffmann et al. 2003; Gignoux et al. 2009). However, it might also improve soil nutrient status and the conditions for *S. plumosum* seedbank germination (Snyman 2011).

The components of soil fertility (K, P, Mg, TN, Ca, SOC, and pH) have shown a general trend of decreasing with soil depth and increasing post-fire. The soils in the coastal fynbos ecosystem has showed a distinct gradient of decreasing quantities of organic matter and total nitrogen with soil depth (Bond 2010). Furthermore, Duguy et al. (2007) found the largest amounts of available soil nutrients within the top few centimetres of the soil. These results corroborate our hypothesis that, soil fertility will be higher in the topsoil, especially post-fire. Soil P, K, SOC, TN and Mg concentrations were reported to be higher in the topsoil than in the subsoil (Jobbágy and Jackson 2000; Adugna and Abegaz 2015). In contrast, Certini (2005) found that the most intuitive change the soil experiences during burning is the loss of organic matter. Low-intensity prescribed fire usually results in little change in soil organic carbon, while an intense accidental or wildfire can significantly reduce soil organic carbon (Davies et al. 2008) caused by its low temperature threshold of 500° C (Verma and Jayakumar 2012).

This result suggests that, the prescribed fire used during the experiment had a relatively lower temperature below the soil organic carbon volatilization threshold, which resulted in soil carbon accumulation in the soil post-fire. The increased topsoil fertility post-fire observed in this study, could potentially improve the conditions for *S. plumosum* survival and eventually its recruitment.

#### **4.5. Conclusion**

The fact that we did not find any significant differences between *Seriphium plumosum* canopied and between canopied areas has shown that *S. plumosum* encroachment is not improving components of soil fertility as previously proposed. This study has also shown that the formation of a fertile island is dependent on species-specific traits, among other factors, hence this phenomenon was not observed under *S. plumosum* canopies. The fact that the formation of a fertile island was not observed under individual *S. plumosum* canopies confirms that, *S. plumosum* encroachment of grassland communities accelerates, rather than reverses rangeland degradation. Although fire has the potential to control woody plant encroachment, its use in the control of *S. plumosum* encroachment in semi-arid grassland communities still needs more research. This is because fire improves components of soil fertility, potentially leading to improved condition for its recruitment and encroachment. Furthermore, the ability of *S. plumosum* to coppice after disturbances such as fire nullifies its effectiveness as a management tool for its encroachment.

Fire, which occurs both naturally and anthropogenically in the semi-arid grasslands, may, in combination with other factors, contribute to *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng Province. A clear understanding of the role of fire intensity and severity on the control of *S. plumosum* encroachment is still lacking. Furthermore, evidence on how these fires influence the soil physical and chemical properties is inadequate,

yet key to understanding how soil dynamics might change when using fire in the control of *S. plumosum* encroachment. There is a need for more research into how multiple interacting factors in space and time contribute to cause *S. plumosum* encroachment in South African grassland communities. Furthermore, grasslands previously affected by accidental wildfires need more research attention to aid in their rehabilitation.

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#### **4.7. References**

- Adugna, A., Abegaz, A. 2015. Effect of soil depth on the dynamics of selected soil properties among the highlands resources of Northeast Wollega, Ethiopia: are these sign of degradation? Solid Earth Discussions. 7: 2011 – 2035.
- Ando, K., Shinjo, H., Noro, Y., Takenaka, S., Miura, R., Sekotela, S.B., Funakawa, S. 2014. Short-term effects of fire intensity on soil organic matter and nutrients release after slash-and-burn in Eastern Province, Zambia. Journal of Soil Science and Plant Nutrition. 60: 173 – 182.
- Archer, SR, Boutton TW, Hibbard KA. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E.-D, Heimann, M, Harrison, S. et

- al. (eds.) Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego, pp. 39 – 46.
- Archer, S.R., Anderson, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., Woods, S.R., 2017. Woody plant encroachment: Causes and Consequences. In Briske DD, editor. Rangelands Systems. Springer Series on Environmental Management, pp 25 – 84.
- Ayalew, S., Mulualem, G. 2018. A review on bush encroachment effect on cattle rearing in rangelands. Journal of Rangeland Science. 8: 403 – 415.
- Austin, A.T., Vivanco, L. 2006. Plant litter decomposition in semi-arid ecosystem controlled by photodegradation. Nature. 442: 555 – 558.
- Avenant P. 2015. Report on the national bankrupt bush (*Seriphium plumosum*) survey (2010 – 2012). Technical Report: Department of Agriculture, Forestry and Fisheries (DAFF).
- Badenhorst, L, 2009. *Seriphium plumosum*. South African National Biodiversity Institute's PlanZAfrica.com website. Available at <http://www.plantzafrica.com/plantqrs/Seriphium.htm> [accessed August 2009].
- Barger, N.N., Archer, S.R., Champbell, J.L., Huang, C., Morton, J.A., Knapp, A.K. 2011. Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. Journal of Geophysical Research. 116: 1 – 17.
- Bond, W.J. 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. Plant and Soil. 334: 47 – 60.
- Caldwell, T.G., Johnson D.W., Miller, W.W., Qualls, R.G. 2002. Forest floor carbon and nitrogen losses due to prescription fire. Soil Science Society of America Journal. 66: 262 – 267.
- Clark, M.D., Wonkka, C.L., Kreuter, U.P., Rogers, W.E. 2020. Interactive effect of prescribed fire and livestock grazing on *Seriphium plumosum* in South African sour bushveld. African Journal of Range and Forage Science. 37, 278 – 285.

- Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia*. 143: 1 – 10.
- Davies, M.G., Gray, A., Hamilton, A., Legg, C.J. 2008. The future of fire management in the British uplands. *International Journal of Biodiversity Science and Management*. 4: 127 – 147.
- Dai, X., Boutton, T.W., Hailemiccheal, M., Ansley, R.J., Jessup, K.E. 2006. Soil carbon and nitrogen storage in response to fire in a temperate mixed-grass savanna. *Journal of Environmental Quality*. 35: 1620 – 1628.
- Eldridge, DJ, Ding, J. 2021. Remove or retain: ecosystem effect of woody encroachment and removal are linked to plant structural and functional traits. *New Phytologist*. 229: 2637 – 2646.
- Duguy, D., Rovira, P., Valleja, R. 2007. Land-use history and fire effects on soil fertility in eastern Spain. *European Journal of Soil Science*. 58: 83 – 91.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G. 2011. Impact of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecological Letters*. 14: 709 – 722.
- Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F., Nolen, B. 2005. Vegetation changes in the Jornada Basin from 1958 to 1998. *Journal of Arid Environment*. 61: 651 – 668.
- Gignoux, J., Lahoreau, G., Julliard, R., Barot, S. 2009. Establishment and early persistence of tree seedling in an annually burned savanna. *Journal of Ecology*. 97: 484 – 495.
- Golubiewski, N., Hall-Beyer M. 2010. Woody encroachment in the southwestern United States. In: CJ Cleveland (ed) *Encyclopedia of Earth*. Environmental Information Coalition, National Council for Science and the Environment). Washington.
- Hagos, M.G., Smit, G.N. 2005. Soil enrichment by *Acacia mellifera* subsp. *Detinens* on nutrients poor sandy soil in a semi-arid southern African savanna. *Journal of Arid Environments*. 61: 47 – 59.

- Hoffmann, W.A., Franco, A.C. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology*. 91: 475 – 484.
- Holzappel, C., Tielbörger, K., Parag, H.A., Kigel, J., Sternberg, M. 2006. Annual plant –shrub interaction along an aridity gradient. *Basic and Applied Ecology*. 268 – 279.
- House, J., Archer, S.R., Breshears, D.D., Scholes, R.J., Nceas, T.G.I.P. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*. 30: 1763 – 1777.
- Hudak, A.T., Wessman, C.A. 2001. Textural analysis of high-resolution imagery to quantify bush encroachment in Madikwe Game Reserve, South Africa, 1955 – 1996. *International Journal of Remote Sensing*. 22: 2731 – 2740.
- Jackson, P.R. 1982. Pale fire and Sherlock Holmes. *Studies in American fictions*. Johns Hopkins University Press. 10: 101 – 105.
- Koekemoer, M. 2001. Systematics of the Metalasia group in the Relhaniinae (Gnaphalieae – Asteraceae). PhD thesis. Rand Afrikaans University, South Africa.
- Li, J., Zhao, C., Zhu, H., Li, Y., Wang, F. 2007. Effect of plant species on shrub fertile island at an oasis-desert ecotone in the South Junggar Basin, China. *Journal of Arid Environments*. 71: 350 – 361.
- Ludwig, F., Kroon, H., Berendse, F., and Herbert, H. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170: 93 –105.
- Maestre, F.M., Bowker, M.A., Puche, M.D., Hinojosa, M.B., Martínez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sánchez, A.M., Carreira, J.A., Gallardo, A., Escudero, A. 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters*. 12: 930 – 940.

- Maestre, F.T., Cortina, J. 2005. Remnants shrubs in Mediterranean semi-arid steppes: effect of shrub size, abiotic factors and species identity on understorey richness and occurrence. *Acta Oecologica- International Journal of Ecology*. 27: 161 -169.
- Mallarino, A.P., Blackmer, A.M. 1992. Comparison of methods for determining critical concentrations of soil test phosphorus for corn. *Journal of Agronomy*. 84: 850 – 856.
- MEA. 2005. Millennium Ecosystem Assessment – Ecosystem and Human Well-being: Desertification Synthesis. World Resource Institute, Washington, DC.
- Mondal, N., Sukumar, R. 2014. Characterising weather patterns associated with fire in a seasonally dry tropical forest in southern India. *International Journal of Wildland fire*. 23: 196 – 201.
- Mucina, L., Rutherford, M.C. 2006. The Vegetation of Southern Africa, Lesotho and Swaziland. *Strelitzia* 19, South African National Botanical Institute, Pretoria, South Africa.
- Mudrak, E.L., Schafer, J.L., Fuentes-Ramirez, A., Holzapfel, C., Kirk A. Moloney, K.A. 2014. Predictive modeling of spatial patterns of soil nutrients related to fertility islands. *Landscape Ecology*. 29: 491 – 505.
- Neary, D.G., Leonard, J.M. 2018. Effect of fire on grassland soils and water: a review. *Grasses and Grassland Aspects*. DOI: 10.5772/intechopen.90747.
- Neff, J.C., Harden, J.W., and Gleixner, G. 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. *Canadian Journal of Forest Research*. 35: 2178 – 2187.
- Parizek, B., Rostagno, C.M. & Sottini, R. 2002. Soil erosion as affected by shrub encroachment in northeastern Patagonia. *Journal of Rangeland Management*. 55: 43 – 48.
- Puttock, A., Dungait, J. A. J., Macleod, C. J. A., Bol, R., Brazier R. E. 2014. Woody plant encroachment into grasslands leads to accelerated erosion of previously stable organic

- carbon from dryland soils, *Journal of Geophysical. Research and Biogeosciences*. 119: 2345 – 2357.
- Ravi, S., D’Odorico, P., Wang, L., White, C. S., Okin, G. S., Macko, S. A., Collins S. L. 2009. Post-fire resource redistribution in desert grasslands: A possible negative feedback on land degradation. *Ecosystems*. 12: 434 – 444.
- Reynolds, J.F., Mark Stafford Smith, D., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J., Downing T.E., Dowlatabadi, H., Fendandez, R. J., Hendrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B. 2007. Global desertification: Building a Science for dry development. *Science*. 316: 847 – 851.
- Sankey, J.B., Ravi, S., Wallace, C.S.A., Webb, R.H., Huxman, T.E. 2012. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical research*. 117: 1 – 11.
- SAS Institute. SAS/STAT User’s Guide. Version 9.3. SAS Institute, Cary: NC, USA; 2011.
- Schade, J.D., Hobbie, S.E. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry*. 73: 541–553.
- Schimel, D. S. 2010. Drylands in the Earth system. *Science* 327, 418–419.
- Schmidt, E., Lotter, M., McClelland, W. 2002. Tree and shrubs of the Mpumalanga and Kruger National Park: Jacaranda Media Publisher, Pretoria.
- Schollenberger, C.J., Driebelbis, E.R. 1930. Analytical methods in base-exchangeable investigations on soils. *Soil science*. 30: 161 – 174.
- Scott, J.D. 1966. Veld burning in South Africa. *African Wildlife*, 20: 93 – 102.
- Shakesby, R.A., 2011. Post-wildfire soil erosion in the Mediterranean: Review and future research directions. *Earth Science Reviews* 105: 21 – 100.

- Shakesby, R.A., Wallbrink, S.H., Doerr, S.H., English, P.M., Chafer, C.J., Humphreys G.S., Blake, W.H., Tomkins, K.M. 2007. Distinctiveness of wildfire effects on soil erosion in south-east Australian eucalypt forests assessed in a global context. *Forest Ecology and Management*. 238: 347 – 364.
- Sharp, B.R., Whittaker, R.J. 2003. The irreversible cattle driven transformation of a seasonally flooded Australian savanna. *Journal of Biogeography*. 30: 783 – 802.
- Snyman, H.A. 2009a. A physiological approach to the distribution and spread of *Seriphium plumosum*. *Newsletter of the Grassland Society of Southern Africa*. 9: 29–37.
- Snyman, H.A. 2009b. Germination potential of *Seriphium plumosum* (bankrupt bush, slangbos, vaalbos). *Grassroots*. 9: 43 – 48.
- Snyman, H.A. 2011. Short-term response of the encroacher shrub *Seriphium plumosum* to fire. *African Journal of Range and Forage Science*. 28: 65 – 77.
- Snyman, H.A., 2012a. Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *South African Journal of Botany*. 81: 34 – 39.
- Snyman, H.A., 2012b. Control measures for the encroacher shrub *Seriphium plumosum*. *South African Journal of Plant and Soil*. 29: 157–163.
- Soliveres, S., Eldridge, D. 2014. Do changes in grazing pressure and the degree of shrub encroachment alter the effect of individual shrubs on understorey plant communities and soil function? *Functional Ecology*. 28: 530 – 537.
- Stock, W.D., Lewis, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *Journal of Ecology*. 74: 317 – 328.
- Thomas, A.D., Elliott, D.R., Dougill, A.J., Stringer, L.C., Hoon, S.R., Sen, R. 2018. The influence of trees, shrubs, and grasses on microclimate, soil carbon, nitrogen, and CO<sub>2</sub> efflux: Potential implications of shrub encroachment for Kalahari rangelands. *Land Degradation and Development*. 29: 1306 – 1316.

- Treydte, A.C., Riginos, C., Jeltsch, F. 2010. Enhanced use of beneath-canopy vegetation by grazing ungulates in African savannas. *Journal of Arid Environments*. 74: 1597 – 1603.
- Verma, S., Jayakamur, S. 2012. Impact of forest fire on physical, chemical and biological properties of soil: a review. *Proceedings of International Academy of Ecology and Environmental Science*. 2: 168 – 176.
- Von Holle, B., Neill, C., Largay, E.F., Katherine A. Budreski, K.A., Ozimec, B., Sara A. Clark, S.A., Lee, K. 2013. Ecosystem legacy of the introduced N<sub>2</sub>-fixing tree *Robinia pseudoacacia* in a coastal forest. *Oecologia*. 172: 915 – 924.
- Walkley, A., Black, I.A. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science*. 37: 29 – 38.
- Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*. 22: 101 – 105.
- Waring, B.G., Alvarez-Cansino, L., Barry, K.E., Becklund, K.K., Dale, S., Gei, M.G., Keller, A.B., Lopez, O.R., Markesteijn, I., Mangan, S., Riggs, C.E., Rodriguez-Ronderos, M.E., Segnitz, R.M., Schnitzler, S.A., Powers, J.S. 2015. Pervasive and strong effect of plants on soil chemistry: a meta-analysis of individual plants “Zinke” effects. *Proceedings of Biological Sciences*. 282: 20151001. doi: 10.1098/rspb.2015.1001.pmid:26224711.
- Wilcox, B.P., Birt, A., Fuhlendorf, S.D., Archer, S.R. 2018. Emerging framework for understanding and mitigating woody plant encroachment in grassy biomes. *Current Opinion in Environmental Sustainability*. 32: 46 – 52.
- World Resource Institute (WRI). 2002. Drylands, people, and ecosystem goods and services: A web-based geospatial analysis.

## CHAPTER 5

### **The effect of season, fire and slope position on *Seriphium plumosum* L. forage quality in the semi-arid communities of Gauteng Province, South Africa**

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## Abstract

Research on the encroacher shrub, *Seriphium plumosum* L. forage quality is lacking, yet important for managing its encroachment in the semi-arid grassland communities of South Africa. To control woody plant encroachment using browsing animals, there is a need to understand the interaction effect of season and fire on its forage quality. *Seriphium plumosum* crude protein (CP), neutral detergent fibre (NDF), total phenolics (TPs) and condensed tannins (CTs) concentrations were determined from combined leaves and fine stems collected during the dry and wet seasons, from burned and unburned areas at the upper and bottom slope positions. *Seriphium plumosum* CP and CTs concentrations were significantly higher in the wet season, when TP and NDF concentrations were lower. In contrast, TPs and CTs were significantly higher in the dry season, when CP and CTs were lower. Crude protein from burned sites was significantly higher than unburned sites ( $P < 0.05$ ). Slope position had no effect on *S. plumosum* CT, TP, CP and NDF concentrations ( $P > 0.05$ ). *Seriphium plumosum* CP concentrations were lower during the dry season on burned and unburned sites, than during the wet season in unburned sites, which were also lower than in burned sites ( $P < 0.05$ ). These results suggest strategic use of fire as cost effective management tools for *S. plumosum* encroachment on grassland communities. More research attention is required on fire and browser interaction on *S. plumosum* control programmes and on post-fire herbaceous vegetation recovery period for sustaining rangeland productivity, while controlling *S. plumosum* encroachment.

**Key words:** Browsers quality, bush encroachment, chemistry, condensed tannins, edible material

## 5.1. Introduction

Woody plant increases in the savannas and grasslands is a global concern (Ward, 2005; Britz and Ward, 2007), especially in the arid and the semi-arid areas (Archer and Predick, 2014). It reduces rangeland carrying capacity by displacing herbaceous forages (Ward, 2005; Venter et al. 2018), thus affecting livestock production (Joubert et al. 2012). Although woody plant encroachment is generally viewed in the context of pastoral production systems (Eldridge et al. 2011), conservationists are also concerned about the loss of biodiversity as grassland habitat is lost to woody plant encroachment (Bond and Archibald, 2003). The mechanisms behind woody and herbaceous species coexistence are not yet clear (Sankaran et al. 2004; Ward, 2005). Furthermore, the existing models and hypotheses on woody and herbaceous species coexistence cannot account for their interaction and coexistence of tree-grass systems (House et al. 2003). Consequently, experiments that explore the role of multiple interacting factors on woody plant encroachment are key to understanding grassland to woodland dominated state transition (Kraaij and Ward, 2006; Archer and Predick, 2014).

In South Africa, encroachment by the indigenous, unpalatable shrub such as *Seriphium plumosum* L (syn. *Stoebe vulgaris*) is a major concern for land users. Its encroachment converts extensive semi-arid grassland and savanna areas into less productive shrubland-grassland and woodland areas (Snyman, 2010). This compromises the potential of rangelands ecosystems to support a large population of grazers and the pastoral economy (Clark et al. 2020). *Seriphium plumosum* has encroached on approximately 150202 ha of South African rangelands (Avenant, 2015), where it occupies relatively disturbed and nutrient poor sandy soils (Snyman, 2012). Control of *S. plumosum* encroachment using a variety of chemical and mechanical methods have been proposed (Snyman, 2009a), but because of their cost and labour implications; more ecologically (Snyman, 2012a, b) and economically sustainable control measures are still

needed (Snyman, 2011, Clark et al. 2020). The interaction of fire and grazing is widespread throughout fire dependent landscapes worldwide (Allred et al. 2011). These factors, either alone or in combination have shown potential to mitigate woody plant encroachment (Fuhlendorf et al. 2009; Venter et al. 2018). Although these factors are effective in controlling woody plant encroachment, their individual or combined role in managing *S. plumosum* encroachment in South African semi-arid grasslands, remain less explored. Furthermore, there has been widespread failure to restore grasslands using these factors after woody encroachment has occurred (Twidwell et al. 2013). The lack of research on the role of fire and browsers in managing woody plant encroachment limits the development of cost effective control measures for their encroachment.

Resource availability (Endara and Coley 2011) cause many woody plant species to produce secondary defensive compounds that are highly diverse within and between populations (Speed et al. 2015). Generally, woody plant species that are adapted to resource poor environments, grow inherently more slowly and invest in constitutive defences that may reduce feed intake by herbivores (Stamp 2003; Endara and Coley, 2011). However, herbivores do not only forages selectively for plants high in protein content (Somers et al. 2008; Seccombe-Hett and Turkington, 2008), but they also avoid feeding on forage with high levels of plant secondary metabolites that may be toxic (Sorensen et al. 2005a; Skidmore et al. 2010). An increased knowledge on how nutrients and plant secondary metabolite concentrations vary seasonally and annually could contribute to understanding variations in herbivore populations and nutrients cycling (Covelo and Gallardo, 2001). Knowledge of these aspects for *S. plumosum* might help in the development of a cost effective control measure that includes it in diet formulations for herbivores, while reducing rate and extent of its encroachment.

There are two major classes of tannins; the hydrolysable tannins (HT) and condensed tannins (CTs), collectively known as proanthocyanidins (Barbehenn and Constabel, 2011). Of these two groups, condensed tannins (CTs) are among the most abundant group of chemical defences produced by woody plants (Gross, 2008; Barbehenn and Constabel, 2011). Condensed tannins can influence diet choice and food consumption of animals by either making the food taste astringent or by reducing nutrients availability after ingestion (Freeland, 1992). The maximum tolerable level of CTs for ruminants in forages is 55 g/kg DM (Min et al. 2003). However, their concentration in woody plant species is highly variable depending on plant genotype, tissue developmental stage and in response to seasonal variations and resources availability (Barbehenn and Constabel, 2011; Moore et al. 2014). This research area is lacking for *S. plumosum*, yet required for development of cost effective ways for managing its encroachment.

The slope aspect is one of the main factors that determines soil diversity in semi-arid regions (Bayat et al. 2017). Landscapes with varying slope positions differ in their ability to retain water and nutrients due to the differences in soil depth and texture (Oztas et al. 2003) which may influence forage quality. Soil nutrients, especially nitrogen availability change along the topographic sequence and decrease up the slope (Tateno et al. 2004). Furthermore, lower and mid slopes had higher soil nutrient levels relative to upper slopes (Liu et al. 2019). Although environmental conditions influence plant secondary metabolites, this does not always occur in predictable ways (Endara and Coley, 2011). Consequently, understanding how edaphic factors mediate nutrients and plant secondary metabolites concentrations in *S. plumosum* is crucial for development of cost effective management strategies.

Burning appears to be a desirable follow-up treatment to mechanical and chemical woody plant encroachment control; because it temporarily increases nutritional value of shrub sprouts and

decreases physical defences, while suppressing growth of shrub species with low palatability to browsing animals (Schindler et al. 2004). Burning increases nutrients content of the understory vegetation (Hu et al. 2018). It removes old, dead vegetation and replaces it with young regrowth that attracts herbivore (Johnson et al. 2018). Herbivores feeding on post-fire regrowth gain relatively greater mass compared to those feeding on unburned vegetation (Eby et al. 2014). Although fire may have the potential to control *S. plumosum* encroachment, it may also improve its forage quality and its acceptability to domestic and wild animals.

This study assessed the effect of season, slope position, fire, and their interaction on *S. plumosum* L. crude protein (CP), neutral detergent fibre (NDF), condensed tannins (CTs) and total phenolics (TPs) concentration in the semi-arid grassland communities of Gauteng Province. The resource driven hypothesis of plant defences proposes that plant species growing on resource poor environment grow inherently more slowly and invest more in constitutive defences that may reduce forage intake by herbivory (Endara and Coley, 2011). In light of this hypothesis, we predicted that; 1) *S. plumosum* CT, TP and NDF concentrations will be less during wet season when its CP concentration is higher as a result of resources availability and actively growing plant. 2) Fire will increase and reduce *S. plumosum* CP and NDF concentrations, respectively. 3) *Seriphium plumosum* CP concentrations at the bottom slope positions will be higher, with lower constitutive defences (i.e. CTs and TPs) compared to the top slope positions.

## **5.2. Materials and Methods**

### 5.2.1. Study Area

The study was conducted in the Rand Highveld Grassland veld type (Mucina and Rutherford, 2006), approximately 40 km east of Pretoria (28.67918° E, 25.76907° S), South Africa. The study site is part of the Mesic Highveld Grassland (Gm 11), situated approximately 1457 m above sea level on relatively poor sandy soils. The average rainfall at the site is 654 mm per annum, ranging between 570 mm – 730 mm and falling almost exclusively from October to April (Mucina and Rutherford, 2006). The RHG receives mean minimum (9.99° C) and maximum (27.62° C) temperatures in winter and summer seasons, respectively (Mucina and Rutherford, 2006). The soils are from the Quartzite ridges of the Witwatersrand Super group, which support the soils of varying quality such as Glenrosa and Mispah, especially along the rocky ridges (Mucina and Rutherford, 2006).

This experimental site is encroached by an unpalatable encroacher shrub, *S. plumosum* L that coexist with a variety of herbaceous species, and a diversity of herbs, many of which also belong to the Asteraceae family. The experimental site has a history of livestock grazing, with unplanned fires occurring almost every second year, probably caused by accumulation of dry fuel load during the dry season. A year before vegetation sampling, almost half of the experimental site experienced unplanned fires, while the other half remained unburned. The fire and no fire treatments were separated by a road, with each site located approximately 50 m away from the road in opposite directions. The experimental site is located on the north-facing slope, with altitude varying from 1469 m (top slope), 1461 m (mid slope) and 1454 m (bottom slope) above sea level. The distance between sampling areas in different slope positions was approximately 60 m apart and 120 m between fire and no fire treatment.

### 5.2.2. Data Collection

*Seriphium plumosum* L. individual plants ( $n = 5$ ) with an average height and width of 45 cm were identified randomly at the bottom, mid and top slope positions, in fire and no fire treatments, and during both dry and wet season. During vegetation sampling, a combination of *S. plumosum* fine leaves and twigs were harvested at approximately 10 cm aboveground. The minimum distance between sampled plants at each sampling area was 10 m apart. Due to the unplanned fire that occurred on half of the experimental site during the dry season of 2014, plant samples during the wet season of 2015 were collected from the previous and current season's growth for no-fire and fire treatment sites, respectively. Although analysed for only dry and wet season, respectively, the *Seriphium plumosum* sampling during both wet and dry season was done during early, mid and late seasons. These sampling times were appropriate because condensed tannins and total phenolics are thought to accumulate as the season progresses (Barton and Koricheva 2010).

*Seriphium plumosum* samples (combined fine leaves and twigs) were pooled together per sampling area and oven dried at 60 °C for 24 hours before being analysed for crude protein (CP), neutral detergent fibre (NDF), condensed tannins (CTs) and total phenolics (TPs) concentrations. Condensed tannins were determined using the acid-butanol assay method (Porter et al. 1985), with purified *Sorghum* as a standard for CT estimation (Hattas and Julkunen-Tiitto, 2012). Total phenolics concentrations were determined using a Prussian blue assay (Price and Butler, 1977), with a gallic acid standard (Scogings et al. 2013).

### 5.2.3. Data Analysis

The effect of season, slope position, fire and their interactions on *Seriphium plumosum* CP, NDF, CT and TP were analysed as a factorial analysis of variance (ANOVA) using GLM

procedures. Data met the assumption of ANOVA concerning homogeneity and normality of variance before being analysed. In instances where ANOVA produced significant results, the effect of season, slope position, fire and their interaction on *S. plumosum* CP, NDF, CT and TP were compared using Turkey's HSD test. The differences between means were declared significant at  $P < 0.05$ .

### 5.3. Results

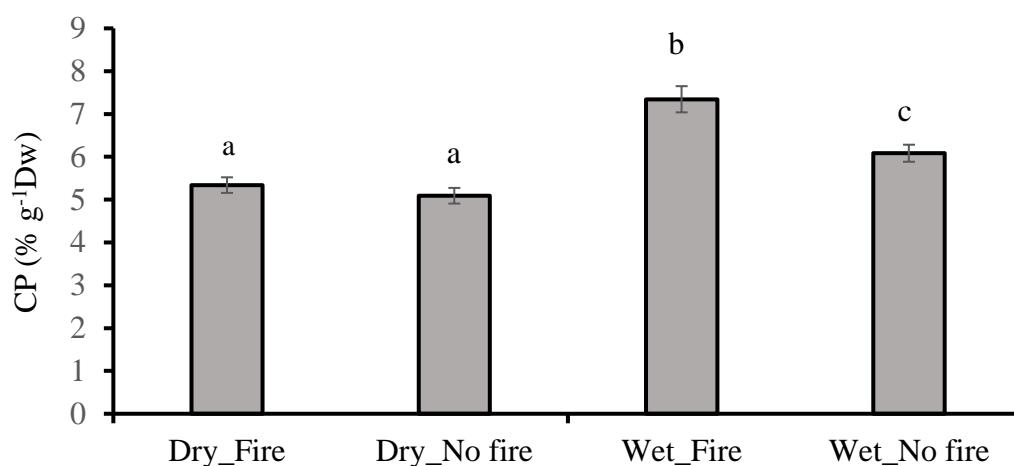
The main effect of season had a significant effect on *Seriphium plumosum* total phenolics (TPs;  $P = 0.0262$ ), condensed tannins (CTs;  $P < 0.0001$ ), crude protein (CP;  $P < 0.0001$ ) and neutral detergent fibre (NDF;  $P < 0.0001$ ) concentrations. The mean TP concentrations in *S. plumosum* was significantly higher ( $14.44 \pm 1.03 \text{ mg g}^{-1}$  dry weight (DW)) during the dry season than during the wet season ( $11.08 \pm 1.07 \text{ mg g}^{-1}\text{DW}$ ). In contrast, CTs concentrations were significantly higher ( $1.56 \pm 0.13 \text{ mg g}^{-1}\text{DW}$ ) during the wet season than during the dry season ( $1.00 \text{ mg} \pm 0.03 \text{ g}^{-1}\text{DW}$ ). Crude protein concentrations in *S. plumosum* was significantly higher ( $6.69 \% \pm 0.20 \text{ g}^{-1}\text{DW}$ ) during the wet season than during the dry season ( $5.22 \% \pm 0.13 \text{ g}^{-1}\text{DW}$ ). Neutral detergent fibre concentrations were significantly higher ( $58.01 \% \pm 0.41 \text{ g}^{-1}\text{DW}$ ) during the dry season than during the wet season ( $53.17 \% \pm 0.34 \text{ g}^{-1}\text{DW}$ ). Fire had a significant effect on *S. plumosum* CP concentrations ( $P = 0.0010$ ). Crude protein concentrations from fire treated sites were significantly higher ( $6.31 \% \pm 0.22 \text{ g}^{-1}\text{DW}$ ) than from no fire untreated sites ( $5.60 \% \pm 10.5 \text{ g}^{-1}\text{DW}$ ). Slope position did not have significant effects on TP, CTs, CP and NDF ( $P > 0.05$ ). The interaction of season x slope position; fire x slope position as well as season x slope position x fire had no significant effects on TPs, CTs, CP and NDF concentrations ( $P > 0.05$ ; Table 5.1).

**Table 5. 1.** Analysis of variance for the effects of season, fire, slope position and their interaction on *S. plumosum* L. total phenolics, condensed tannins, crude protein and neutral detergent fibre.

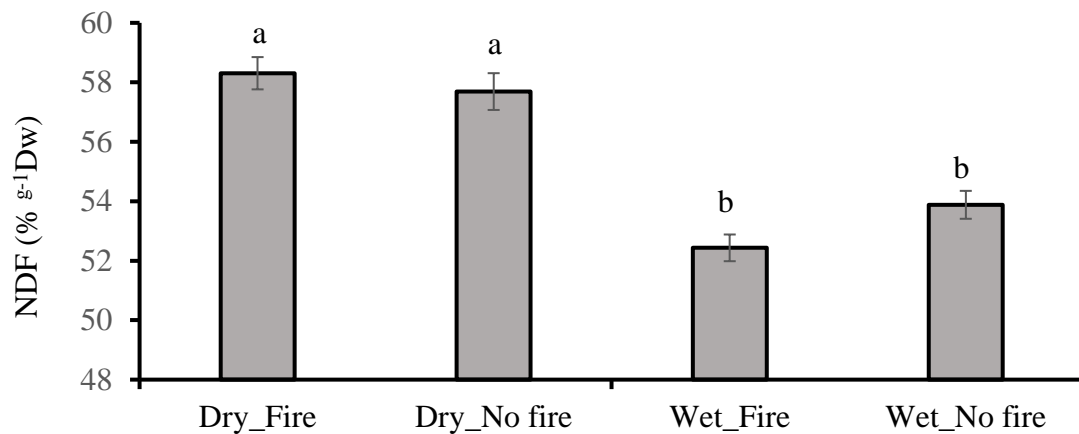
Factors	Total Phenolics			Condensed Tannins		Crude Protein		Neutral Detergent Fibre	
	DF	F	P	F	P	F	P	F	P
Season	1	5.08	<b>0.0262</b>	18.04	<b>&lt; 0. 0001</b>	43.45	<b>&lt;.0001</b>	84.91	<b>&lt;0.0001</b>
Fire	1	3.56	0.0619	0.03	0.8535	11.40	<b>0.0010</b>	0.60	0.4407
Slope position	1	0.47	0.4966	1.49	0.2254	0.78	0.3793	1.87	0.1742
Season x Fire	1	0.39	0.5332	0.06	0.8071	5.12	<b>0.0257</b>	3.81	<b>0.0534</b>
Season x Slope position	1	0.65	0.4221	1.34	0.2494	1.18	0.2803	1.51	0.2223
Fire x Slope position	1	0.00	0.9913	0.48	0.4885	0.14	0.7131	0.16	0.6869
Season x Fire x Slope position	1	0.09	0.7635	1.18	0.2801	0.02	0.8845	0.11	0.7425

Significant values are shown in bold.

There was a significant interaction effect of season x fire on NDF and CP ( $P < 0.05$ ), but not on CTs and TPs concentrations ( $P > 0.05$ ). These interaction effects (season x fire) on *S. plumosum* are presented for crude protein (Figure 5.1) and (Figure 5.2) for neutral detergent fibre.



**Figure 5. 1.** *Seriphium plumosum* L. mean crude protein (CP) concentrations during the dry and wet seasons in burned (fire) and unburned (no fire) areas at RHG. Bars extending beyond the bar graphs denote SE. Bars graphs followed by different letters are significantly different ( $P < 0.05$ ).



**Figure 5. 2.** *Seriphium plumosum* L. mean neutral detergent fibre (NDF) concentrations during the dry and wet seasons in burned (fire) and unburned (no fire) areas at RHG. Bars represent standard errors (SEM). Different letters on the error bars mean that  $P < 0.05$ .

#### 5.4. Discussion

*Seriphium plumosum* crude protein (CP) concentrations were 28 % higher during the wet season than during the dry season. In contrast, NDF concentration were 92% lower during the wet season. In general, dietary nutrients (crude protein) percentages are higher in plant species during the wet season, and the reverse is true for percent dietary holocellulose and lignin (NDF) concentrations (Coppock et al. 1986). This result suggests that *S. plumosum* during the wet season is actively growing and it is likely that resources are available. Other studies also found that concentrations of crude protein in woody plants during the early growth stages exceed that of the same plant with advancing maturity (Ganqa et al. 2005; Scogings et al. 2014). The findings on *S. plumosum* CP and NDF concentration during the wet season are consistent with the plant defence trade-off hypothesis which proposes that, depending on the environment, there are trade-offs in plants allocation to growth and to defence against herbivores (Close and McArthur, 2002). This result further suggests that during the wet season, resources for plant

growth are not limiting, thus leading to fast growing and less defended *S. plumosum* plants. This result is consistent with our hypothesis that, because of resource availability during the wet season, *S. plumosum* CP concentrations will increase.

*Seriphium plumosum* condensed tannin (CT) concentrations in the wet season were 56 % higher than during the dry season. In contrast, TPs concentrations were 76 % higher during the dry season than during the wet season. Generally, in the wet season, resources are abundant, which will decrease tannins concentrations following herbivory, because defoliation reduces C relative to N concentrations (Scogings and Mopipi, 2018), in response to maturity. Furthermore, carbon based secondary metabolites concentrations vary inversely with growth and nutrients because of the physiological trade-off between cellular growth and differentiation (Scogings et al. 2015). Woody plants may also respond to resource limitations by making choices of investing in one or two functions instead of all, or investing more in one kind of anti-herbivore defence relative to others (Coley, 1983). This result suggests that *S. plumosum* plant parts are defended from browsers during the wet season through increased CTs concentrations. Condensed tannin concentrations of approximately 3% may reduce intake and digestibility of nutrients, while moderate concentrations (1%) may improve digestive efficiency of crude protein (Frutos et al. 2004). *Seriphium plumosum* CTs concentrations during the wet (0.16 %) and dry (0.1 %) seasons found in this study are relatively lower to serve as feeding deterrents, unless over-ingested beyond the animal coping threshold. Furthermore, this result demonstrated the potential to control *S. plumosum* encroachment during wet seasons using browsers because concentrations of CTs may improve efficiency of CP digestion (Frutos et al. 2004).

We hypothesised that slope position will affect *S. plumosum* CTs and TPs concentrations, with both CTs and TPs increasing up the slope, while resources increase down the slope. However,

this hypothesis is not supported in this study. This is probably because of a weak slope gradient from the top to the bottom slopes, leading to insufficient water and soil nutrients being transported downslopes. Clearly, seasonal and topographic variations in N, P and carbon based secondary metabolites (CBSMs) in semi-arid savannas and grassland cannot be easily generalised because they also depend on species and annual rainfall variability (Scogings et al. 2015).

*Seriphium plumosum* crude protein concentrations were higher in previously burned area compared to unburned areas. Snyman (2015) found that crude protein concentrations of growing plant materials following burning is higher than of the dormant plant material in an unburned area. Fire creates burn patches during certain times of the year, which can be used strategically to make underutilized plant species such as *S. plumosum* more appealing to browsers. Fire increases plant nutrient availability, through accelerating the mineralization of organic matter (Giardina et al. 2000), increasing *S. plumosum* CP concentration. Although fire may contribute to increase *S. plumosum* CP concentrations, while contributing to control its encroachment, its efficacy in the absence of browsers is still questioned (Clark et al. 2020).

The relatively high neutral detergent fibre content during the dry season compared to the wet season in this study resulted from the advancing maturity of *S. plumosum* (Scogings et al. 2004; Waterman et al. 2007). Physical traits such as high fibre content render biting, chewing and digestibility costly to herbivores (Shipley and Yanish, 2001). Forages that contain 40% NDF or less are generally of higher digestibility than forages with 60% or more (Hoffman et al. 2001). Neutral detergent fibre concentrations between 55 - 60% may reduce intake of forages. However, NDF concentration levels of 57 % and 52 % during the dry and wet seasons, with or without fire may provide an opportunity to use *S. plumosum* with other feed ingredients as a

possible feed source. This in turn may contribute to control its encroachment. Generally, fire-browser interactions may contribute to improving *S. plumosum* forage quality, making them acceptable to browsers, and thereby contribute to controlling *S. plumosum* encroachment.

### **5.5. Management implications**

The study demonstrated that strategic use of fire may contribute to improve *S. plumosum* CP concentrations, especially in the wet season. This may result in improved preference and intake of *S. plumosum* by browsers, thus contributing to control its encroachment on semi-arid grassland communities. The presence of condensed tannins and total phenolics are inevitable in woody plant, including *S. plumosum*. However, improving browser nutrient requirement with supplemental feeding may improve their ability to cope with plant secondary metabolites in *S. plumosum*.

### **5.6. Acknowledgements**

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### **5.7. References**

Addisu, S. 2016. Effect of dietary tannin source feeds on ruminal fermentation and production of cattle; a review. *Journal of Animal and Feed Research*. 6: 45 – 56.

- Allred, B.W., Fuhlendorf, S.D., Engle, D.M., Elmore R.D., 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecol. and Evol.* 1, 132 – 144. <https://doi.org/10.1002/ece3.12>.
- Archer, S.R., Predick, K., 2014. An ecosystem services perspective on brush management: Research priorities for competing land-use objectives. *J. of Ecol.* 102, 1394 – 1407. <https://doi.org/10.1111/1365-2745.12314>.
- Barbehenn, R.V., Constabel, C.P., 2011. Tannins in plant – herbivore interactions. *Phytochem.* 72, 1551 – 1562. <https://doi.org/10.1016/j.phytochem.2011.01.040>.
- Barton, K.E., Koricheva., J. 2010. The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *Am Nat.* 175, 481 – 493. <https://doi.org/10.1086/650722>.
- Bayat, H., Shecklabadi, M., Moradhaseli, M., Ebrahimi, E., 2017. Effect of slope aspect, grazing, and sampling position on the soil penetration resistance curve. *Geod.* 303, 150 – 164. <http://dx.doi.org/10.1016/j.geoderma.2017.05.003>.
- Bond, W.J., Archibald, S., 2003. Confronting complexity: fire policy choices in South African savanna parks. *Intern. J. of Wildl. Fire.* 12, 381 – 389. <https://doi.org/10.1071/WF03024>.
- Britz, M.L., Ward, D., 2007. Dynamics of woody vegetation in the semi-arid savanna, with focus on woody plant encroachment. *Afri. J. of Rang. For. Sci.* 24, 131 – 140. <https://doi.org/10.2989/AJRFS.2007.24.3.3.296>.
- Clark, M.D., Wonkka, C.L., Kreuter, U.P., Rogers, W.E. 2020. Interactive effect of prescribed fire and livestock grazing on *Seriphium plumosum* in South African sour bushveld. *African Journal of Range and Forage Science.* 37, 278 – 285. <https://doi.org/10.2989/10220119.2020.1751287>.

- Close, D.C., McArthur, C., 2002. Rethinking the role of many plant phenolics-protection from phytodamage not herbivore? *Oikos*. 99, 166 -172. <https://doi.org/10.1034/j.1600-0706.2002.990117.x>.
- Coley, P.D., 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53, 209 – 234. <https://doi.org/10.2307/1942495>.
- Covelo, F., Gallardo, A., 2001. Temporal variation in total leaf phenolics concentration of *Quercus robur* in forest and harvested stands in northwestern Spain. *Can. J. of Bot.* 79, 1262 – 1269. <https://doi.org/10.1139/b01-109>.
- Eby, S.L., Anderson, T.M., Mayemba, E.P., Ritchie, M.E. 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology*. 83, 1196 –1205.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impact of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709 –722. <https://doi.org/10.1111/j.1461-0248.2011.01630.x>.
- Endara, M.J., Coley, P.D., 2011. The resource availability hypothesis revisited a meta-analysis. *Evol. Ecol. of Plant Def.* 25, 389 – 398. <https://doi.org/10.1111/j.1365-2435.2010.01803.x>.
- Frutos, P., Hervas, G., Giraldez, F.J. and Mantecon, A.R. 2004. An in vitro study on the ability of poly ethylene glycol to inhibit the effect of quebracho tannins and tannic acid on rumen fermentation in sheep, goats, cows and deer. *Austr. J. of Agric. Res.* 55, 1125-1132.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hilton, R., 2009. Pyric herbivory: Rewilding landscape through the recoupling fire and grazing. *Conserv. Biol.* 23, 588 – 598. <https://doi.org/10.1111/j.1523-1739.2008.01139.x>.

- Ganqa, N.M., Scogings, P.F., Raats, J.G., 2005. Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great fish river reserve, South Africa. *S. Afri. J. of Wildl. Res.* 35, 77 – 83. <https://hdl.handle.net/10520/EJC117203>.
- Giardina, C.P., Sanford, R.L., Dockersmith, I.C., Jaramillo, V.J., 2000. The effect of slash burning on ecosystem nutrients during the land preparation phase of shifting cultivation. *Plant and Soil*. 220, 247–260. <https://doi.org/10.1023/A:1004741125636>.
- Gross, G.G., 2008. From lignins to tannins: Forty years of enzyme studies on the biosynthesis of phenolic compounds. *Phytochem.* 69, 3018 – 3031. <https://doi.org/10.1016/j.phytochem.2007.04.031>.
- Hattas, D., Julkunen-Tiitto, R., 2012. The quantification of condensed tannins in African tree species. *Phytochem.* 5, 329 – 334. <https://doi.org/10.1016/j.phytol.2012.02.013>.
- Hoffman, P.C., Shaver, R.D., Combs, D.K., Undersander, D.J., Bauman, L.M., Seeger, T.K., 2001. Understanding digestibility of forages. *Focus on For.* 3, 1 – 3.
- House, J., Archer, S.R., Breshears, D.D., Scholes, R.J., Nceas, T.G.I.P., 2003. Conundrums in mixed woody-herbaceous plant systems. *J. of Biogeogr.* 30, 1763 – 1777. <https://doi.org/10.1046/j.1365-2699.2003.00873.x>.
- Hu, M., Liu, Y., Sun, Z., Zhang, K., Liu, Y., Miao, R., Wan, S. 2018. Fire rather than nitrogen addition affects understory plant communities in the short term in a coniferous- broadleaf mixed forest. *Ecology and Evolution*. 8, 8135 – 8148.
- Johnson, C.N., Prior, L.D., Archibald, S., Poulos, H.M., Barton, A.M., Williamson, G.J., Bowman D. M. J. S. 2018. Can trophic rewilding reduce the impact of fire in a more flammable world? *Philosophical Transactions B*. 373, <http://dx.doi.org/10.1098/rstb.2017.0443>.

- Joubert, D.F., Smit, G.N., Hoffman, M.T., 2012. The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. *J. of Arid Environ.* 87, 1 – 7. <https://doi.org/10.1016/j.jaridenv.2012.06.012>.
- Kraaij, T., Ward, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecol.* 186, 235 – 246. <https://doi.org/10.1007/s11258-006-9125-4>.
- Liu, J., Qiu, L., Ao, G., Zheng, B., Wei, X., Zhang, Y., Gao, H., Cheng, J. 2019. Effect of clipping on aboveground biomass and nutrients varies with slope position but not with slope aspect in hilly semi-arid restored grassland. *Journal of Ecological Engineering.* 134, 47 – 55. <https://doi.org/10.1016/j.ecoleng.2019.05.005>.
- Min, B.R., Pomroy, W.E., Hart, S.P., Sahlu, T., 2003. The effect of short-term consumption of a forage containing condensed tannins on gastro-intestinal nematode parasite infections in grazing wether goats. *S. Rum. Res.* 51, 279 – 283. [https://doi.org/10.1016/S0921-4488\(03\)00204-9](https://doi.org/10.1016/S0921-4488(03)00204-9).
- Moore, B.D., Andrew, R.L., Külheim, C., Foley, W.J., 2014. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. *New Phytol.* 201, 733 – 750. <https://doi.org/10.1111/nph.12526>. Epub 2013 Oct 1.
- Mucina, L., Rutherford, M.C., 2006. The Vegetation of Southern Africa, Lesotho and Swaziland,” *Strelitzia* 19, South African National Botanical Institute, Pretoria, South Africa.
- Oztas, T., Koc, A., Comakli, B., 2003. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. *J. Arid Environm.* 55, 93 – 100. [https://doi.org/10.1016/S0140-1963\(02\)00267-7](https://doi.org/10.1016/S0140-1963(02)00267-7).

- Porter, L.J., Foo, L.Y., Furneaux, R.H., 1985. Isolation of 3 naturally occurring O-beta-glucopyranosides of procyanidin polymers. *Phytochem.* 24, 567–570.  
[https://doi.org/10.1016/S0031-9422\(00\)80767-0](https://doi.org/10.1016/S0031-9422(00)80767-0).
- Price, M.L., Butler, L.R., 1977. Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain,” *J. Agric. Food Chem.*, vol. 25, pp 1268 – 1273.  
<https://doi.org/10.1021/jf60214a034>.
- Sankaran, M., Ratnam, J., Hanan, N.P., 2004. Tree-grass coexistence in savannas revisited – insight from an examination of assumptions and mechanisms invoked in existing models. *Ecol. Lett.* 7, 480 – 490. <https://doi.org/10.1111/j.1461-0248.2004.00596.x>.
- Schindler, J.R., Fulbright, T.E., Forbes, T. 2004. Shrub regrowth, antiherbivore defenses, and nutritional value following fire. *Range. Ecol. and Manag.* 5, 178–186.  
<https://doi.org/10.2111/1551-5028> (2004)057[0178:SRDAN]2.0CO;2.
- Scogings, P.F., Hattas, D., Skarpe, C., Hjalten, J., Dziba, L., Zobolo, A., Rooke, T. 2015. Seasonal variation in nutrients and secondary metabolites in semi-arid savannas depend on year and species. *J. of Arid Environ.* 114, 54 – 61. <https://doi.org/10.1016/j.jaridenv.2014.11.003>.
- Scogings, P.F., Hjalten, J., Skarpe, C., Hattas, D., Zobolo, A., Dziba, L., Rooke, T., 2014. Nutrients and secondary metabolite concentrations in a savanna are independently affected by large herbivores and shoot growth. *Plant. Ecol.* 215, 73 – 82.  
<https://doi.org/10.1007/s11258-013-0279-6>.
- Scogings, P.F., Hjalten, J., Skarpe, C., 2013. Does large herbivores removal affect secondary metabolites, nutrients and shoot length in woody species in semi-arid savannas? *J. of Arid Environ.* 88, 4 – 8. <https://doi.org/10.1016/j.jaridenv.2012.08.010>.
- Scogings, P.F., Mopipi, K., 2008. Effect of water, grass and N on responses of *Acacia karroo* seedlings to early wet season simulated browsing: Leaf N, fibre and tannin

- concentrations. J. of Arid Environ. 72, 1666 – 1674.  
<https://doi.org/10.1016/j.jaridenv.2008.03.008>.
- Seccombe-Hett, P., Turkington, R., 2018. Summer diet selection of snowshoe hares: a test of nutritional hypotheses. Oikos. 117, 1874 – 1884. <https://doi.org/10.1111/j.1600-0706.2008.16773.x>.
- Shipley LA and Yanish CR 2001. Structural anti-quality: The bones and gristle of rangeland forage. In: Launchbaugh K (ed.) Anti-quality Factors in Rangeland and Pastureland Forages. Bulletin no. 73 of the Idaho Forest, Wildlife and Range Experiment Station. University of Idaho, Moscow, USA. pp 13–17.
- Skidmore, A.K., Ferwerda, J.G., Mutanga, O., Van Wieren, S.E., Peel, M., Grant, R.C., Prins, H.H.T., Balcik, F.B., Venus, B., 2010. Forage quality of savannas – Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. Rem. Sen. of Envir. 114, 64 – 72. <https://doi.org/10.1016/j.rse.2009.08.010>.
- Snyman, H.A., 2009a. A physiological approach to the distribution and spread of *Seriphium plumosum*. Newslett. of the Grassl. Soc. of S. Afr. 9, 29 – 37.
- Snyman, H.A., 2009b. Germination potential of *Seriphium plumosum* (bankrupt bush, slangbos or vaalbos). Grassroots 9, 43 – 48.
- Snyman, H.A., 2010. Allelopathic potential, seed ecology and germination of the encroacher shrub *Seriphium plumosum*. Afr. J. of Range and For. Sci. 27, 29 – 37.  
<https://doi.org/10.2989/10220111003718482>.
- Snyman, H.A., 2011. Short-term response of the encroacher shrub *Seriphium plumosum* to fire. Afr. J. of Range and For. Sci. 28, 65 – 77.  
<https://doi.org/10.2989/10220119.2011.609266>.
- Snyman, H.A., 2012a. Control measures for the encroacher shrub *Seriphium plumosum*. S. Afr. J of Plant and Soil. 29, 157–163. <https://doi.org/10.1080/02571862.2012.745905>.

- Snyman, H.A., 2012b. Short term response of southern African semi-arid rangelands to fire-a review of impact on plants. *Arid Land Res. Manage.* 29, 237 – 254. <http://dx.doi.org/10.1080/15324982.2014.960625>.
- Snyman, H.A., 2015. Short-term response of Southern African semi-arid rangelands to fire: A review of impact of soils. *Arid Land Res. and Manage.* 29, 222 – 236. <https://doi.org/10.1080/15324982.2014.944244>.
- Somers, N., D’Haese, B., Bossuyt, B., Lens, L., Hoffmann, M., 2008. Food quality effects diet preference of rabbits: experimental evidence. *Belg. J. of Zool.* 138, 170 – 176.
- Sorensen, J.S., Heward, E., Dearing, M.D., 2005a. Plant secondary metabolites alter the feeding patterns of a mammalian herbivore (*Neotoma lepida*). *Oecol.* 146, 415– 422. <https://doi.org/10.1007/s00442-005-0236-8>.
- Sorensen, J.S., McLister, J.D., Dearing, M.D., 2005b. Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecol.* 86, 125 –139. <https://doi.org/10.1890/03-0627>.
- Speed, M.P., Fenton, A., Jones, M.G., Roxton, G.D., Brockhurst, M.A., 2015. Coevolution can explain defensive secondary metabolite diversity in plants. *New Phyt.* 208, 1251 – 1263. <https://doi.org/10.1111/nph.13560>.
- Stamp, N., 2003. Out of the quagmire of plant defense hypotheses. *Q. Rev Biol.* 78, 23 – 55. <https://www.ncbi.nlm.nih.gov/pubmed/12661508>.
- Tateno, R., Hishi, H., Takeda, H. 2004. Above and belowground biomass and net primary production in cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. *For. Ecol. and Manag.* 193, 297 – 306. <https://doi:10.1016/j.foreco.2003.11.011>.
- Twidwell, Dirac, William E. Rogers, Samuel D. Fuhlendorf, Carissa L. Wonkka, David M. Engle, John R. Weir, Urs P. Kreuter, Charles A. Taylor, Jr. (2013) The rising Great Plains

- fire campaign: citizenry response to woody plant encroachment. *Frontiers in Ecology and the Environment* 11:e64-e71. DOI: <https://doi.org/10.1890/130015>.
- Venter, Z.S., Cramer, M.D., Hawkins, J.H., 2018. Drivers of woody plant encroachment over Africa. *Nat. Comm.* 9, 2272. <https://doi:10.1038/s41467-018-04616-8>.
- Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? *Afri. J of Range and For. Sci.* 22, 101 – 105.  
<https://doi.org/10.2989/10220110509485867>.
- Waterman, R.C., Grings, E.E., Geary, T.W., Roberts, A.J., Alexander, L.J., MacNiel, M.D., 2007. Influence of seasonal forage quality on glucose kinetics of young beef cows. *J. of Anim. Sci.* 85, 2582 – 2595. <https://doi.org/10.2527/jas.2007-0023>.

## CHAPTER 6

### 6.1. Synthesis

There are many factors responsible for causing and/or promoting woody plant encroachment. Once these woody plants have encroached in rangeland communities, both negative and positive effects on ecosystem functioning are probable. Consequently, this limits the development of control or management measures, especially when the cost-benefits of their control relative to retaining them are unknown. The main aim of this study was to explore the causes and the consequences of *S. plumosum* L. encroachment in the semi-arid grassland communities of Gauteng Province.

This study focused on the ecology of *S. plumosum* L. to aid understand the environmental (abiotic and biotic) factors that contribute to cause and/or promote its encroachment in grassland communities. This is because research on the ecology of *S. plumosum* is lacking, yet important in the control of its encroachment (Snyman 2012). Furthermore, there is an increased research emphasis on multi-factorial experiments as an alternative way to study the causes of woody plant encroachment (Ward 2005; Kraaij and Ward 2006), but this has not been extensively conducted on *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng Province. Consequently, this limits the development of management strategies for reducing its rate and extent of encroachment.

The focus of chapter 2 was to understand the role of environmental factors on *S. plumosum* invasion susceptibility. This study showed that, decreased herbaceous basal cover, soil sand content and magnesium content increase the likelihood of *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng Province. This result suggested that, improving herbaceous basal cover and soil fertility, especially magnesium content would result in conditions that discourage *S. plumosum* encroachment. Chapter 3 focused on the role of

abiotic factors and grassland community on *S. plumosum* density and canopy size. As shown in the first experimental chapter, magnesium content is a key soil property. Where soil magnesium content was low in grassland communities, the density of *S. plumosum* was significantly higher. Furthermore, components of soil fertility (SOC, TN, P, K, and Ca) were relatively less concentrated in grassland communities where *S. plumosum* densities were higher. Consequently, the studies demonstrated that by reducing grass competition; particularly for space in well-drained nutrient poor soils may promote *S. plumosum* encroachment susceptibility. Generally, interactions of multiple factors cause woody plant encroachment (van Auken 2009; Eldridge et al. 2011) including encroachment by *S. plumosum* (Table 6.1).

Chapter 4 explored the effect of *S. plumosum* canopy cover, fire and soil depth on components of soil fertility. All the components of soil fertility measured showed a significant decrease with soil depth and increase with post-fire treatment. In this study however, the components of soil fertility were not significantly different between *S. plumosum* canopied areas and un-canopied areas. This finding demonstrates that the species functional traits (Scholes and Archer 1997) and encroachment stage (Archer et al. 2017) also influence the outcome of encroachment. This study showed that *S. plumosum* encroachment contributes to accelerate rather than reverse rangeland degradation, and fire alone is not a recommended management tool to control *S. plumosum* encroachment in grassland, because it may reduce grass competitive ability, thus improving the conditions for *S. plumosum* recruitment and encroachment.

Chapter 5 explored the interaction effects of season, fire and slope position on *S. plumosum* forage quality. This study demonstrated that, the wet season and post burned *S. plumosum* regrowth had the highest crude protein content. Furthermore, *S. plumosum* CTs and TPs concentrations were not affected by fire or slope position alone or in combination. *Seriphium plumosum* CTs and TPs concentrations were insufficient to act as feed deterrents or

anti-nutritional factors. This is because herbivore nutrient intake is limited by relatively low nutritional quality of plants and higher concentrations of plant secondary metabolites (Ulappa et al. 2014). Consequently, a combination of fire, browsers and supplemental feeding may contribute to controlling *S. plumosum* encroachment in the semi-arid grassland communities. The summary of the causes and consequences of *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng Province is presented below (Table 6.1).

**Table 6. 1.** Schematic representation of the summary of the causes and consequences of *Seriphium plumosum* L on the semi-arid grassland communities of Gauteng Province

Factors	Experiment	Results	Conclusion
Causes of <i>S. plumosum</i> encroachment	<b>Experiment 1:</b> Effect of environmental factors on <i>S. plumosum</i> encroachment susceptibility	Nutrient poor well-drained soils and poor basal cover	<ul style="list-style-type: none"> <li>Multiple interacting factors such as nutrient poor well-drained soils, fire suppression and overgrazing for a prolonged duration are responsible for <i>S. plumosum</i> encroachment in South African semi-arid grassland communities</li> <li><i>Seriphium plumosum</i> encroachment leads to rangeland degradation</li> <li><i>S. plumosum</i> encroachment may be successfully managed or controlled by integrating fire and browsers, while maintaining rangelands in good condition</li> </ul>
	<b>Experiment 2:</b> Effects of abiotic factors on <i>S. plumosum</i> density and canopy size	Nutrient poor well-drained soils	
Consequences of <i>S. plumosum</i> encroachment	<b>Experiment 3:</b> Effect of <i>S. plumosum</i> canopy cover, fire and soil depth on components of soil fertility	Fire improves soil fertility, but not in <i>S. plumosum</i> sub-canopy areas	
	<b>Experiment 4:</b> Effect of season, fire and slope position on <i>S. plumosum</i> forage quality	<i>Seriphium plumosum</i> CP content increases during the wet season in burned areas more than in unburned areas	

## 6.2. Management implications

The results in this study showed that overgrazed and/or burned areas with well-drained poor quality soils in the semi-arid grassland communities of Gauteng Province are most likely to be encroached by *S. plumosum*. Furthermore, its densities in grassland communities increase in well-drained nutrient poor soils. *Seriphium plumosum* encroachment contributes to accelerate rather than reverse rangeland degradation. This negative effect on rangeland communities justifies the need for its control in rangeland communities. The control measures chosen for *S. plumosum* encroachment must be economically and ecologically justifiable (Snyman 2012). There is a need for inexpensive and easy restoration and management interventions for encroaching and invasive plants species (Belnap et al. 2012). As such, the land users who wish to restore *S. plumosum* encroached grassland communities may explore ecological measures that integrate fire, soil fertilization and nutrients-supplemented browsers in managing its encroachment. This study has also shown that, grazing management strategies that maintain sufficient grass cover, while improving soil fertility may discourage *S. plumosum* encroachment susceptibility. This is because managing grazing rates is a better strategy than focusing on shrub removal (Eldridge et al. 2013). These integrated management strategies need ongoing monitoring to ensure long-term success (Nkosi et al. 2018).

The fact that marginal soils, withdrawn from cash-crop cultivation, are among the most actively encroached areas might be ascribed to the lower soil fertility (organic matter, N and C contents), forming a more favourable habitat for *S. plumosum* (Snyman 2012). Consequently, the study proposes maintaining or converting abundant cash-crop lands in to pasturelands to improve grass cover and probably soil fertility which will in turn disfavour *S. plumosum* encroachment. Long-term cultivation causes an increase in both total and available P in the soil, but it decreases after crop abandonment (Duguy et al. 2007), thus creating the conditions

likely to favour *S. plumosum* encroachment. These conditions can be avoided by crop rotation and continuous addition of limiting soil nutrients in the form of fertilizers.

### 6.3. Acceptance/ Rejection of the hypotheses

Generally, this study had rejected and accepted some of the hypotheses that we put forward;

- The interaction of abiotic and biotic factors were hypothesized to contribute to increase the likelihood of *S. plumosum* encroachment susceptibility in the semi-arid grassland communities of Gauteng Province. This hypothesis was consistent with our results in terms of basal cover, sand and magnesium, which increased the likelihood of *S. plumosum* encroachment in the semi-arid grassland communities of Gauteng Province
- *Seriphium plumosum* density and canopy size to be higher at the bottom slopes and different between rangeland communities. These hypotheses were consistent for *S. plumosum* density at Rand Highveld Grassland, but not consistent for Carletonville Dolomite Grassland.
- The topsoils to be relatively fertile under *S. plumosum* canopy cover during post-burning treatment. The results rejected this hypothesis, as this increased fertility under *S. plumosum* canopy was not observed in this study.
- *Seriphium plumosum* CP and TP to increase and decrease in the wet season post-burn and at bottom slopes. This hypothesis is consistent with the results from this study with regard to CP concentration during the wet season post-burn, but not on CP at the bottom slopes. This result also rejected the hypothesis that *S. plumosum* TP concentrations decreases during the wet season post-fire and at bottom slopes.

#### 6.4. Recommendations

The study recommend the following management interventions in the control of *S. plumosum* in the semi-arid grassland communities of Gauteng Province.

- The strategic management of rangelands in mostly bottoms slopes where *S. plumosum* increases in relative abundance in Gauteng semi-arid grassland communities.
- Strategic management of old-lands on relatively nutrient poor sandy soils is imperative for successful control of *S. plumosum* encroachment.
- The use of fire during the dry season and browsing herbivores during the wet season in the control of *S. plumosum* encroachment.
- Explore alternative ways of improving *S. plumosum* forage quality and possibilities of controlling its encroachment on rangelands using the utilization approach.

#### 6.5. Future research

It is shown in this study that multiple interacting factors are responsible for *S. plumosum* encroachment. Furthermore, that no single model of woody-herbaceous species interaction and co-existence can account for the variety of phenomena at all locations, or even the range of behaviour exhibited at one location in different seasons or stages of succession. Consequently, multiple factorial experiments might contribute insight into the development of ecological control measures for *S. plumosum* encroachment in the semi-arid grassland of Gauteng Province. The following ecological research are proposed in this study;

- Fire and browsers either alone or in combination has the potential to control woody plant encroachment. However, their role in the control of *S. plumosum* are less explored, with more research on how fire might contribute to increase its nutritive quality and potentially preference by browsing herbivores still required.
- The role of plant secondary metabolites on mammalian herbivores in controlled experiments are well studied, but few have tested their effects on herbivores in their

natural condition. As such, there is a need for more ecological research in the field to understand how seasonal variation in *S. plumosum* CBSMs and nutrients affect herbivore foraging behaviour and feed intake.

- There is a need for more research on how soil fertilization might influence *S. plumosum* forage quality and on the likelihood of its encroachment in the semi-arid grassland communities of Gauteng Province.
- The role of fire in the control of *S. plumosum* encroachment requires more research attention.
- More research attention on the use of remote sensing and GIS to quantify the extent and rate of *S. plumosum* encroachment in relation to environmental factors (e.g. rainfall and temperature) is needed.
- The role of grazing intensity in causing *S. plumosum* encroachment need more research attention, especially in the field. This is because grazing dampens the positive effect of shrub encroachment, especially on sandy soils

This insight may contribute to managing *S. plumosum* encroachment in Gauteng Province and other encroached semi-arid grassland communities in South Africa.

## 6.6. References

- Archer, S.R., Anderson, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., Woods, S.R., 2017. Woody plant encroachment: Causes and Consequences. In Briske DD, editor. Rangelands Systems. Springer Series on Environmental Management, pp 25 – 84.
- Belnap, J., Ludwig, J.A., Wilcox, B.P., Betancourt, J.L., Dean, W.R.J., Hoffmann, B.D., Milton, S.J. 2012. Introduced and invasive species in novel rangeland ecosystems: Friends or foes? Rangeland Ecology and Management. 65: 569 – 578.

- Brym, Z.T., Lake, J.K., Allen, D., Ostling A. 2011. Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. *Journal of Applied Ecology*. 45: 1098 –1106.
- Duguy, D., Rovira, P., Valleja, R. 2007. Land-use history and fire effects on soil fertility in eastern Spain. *European Journal of Soil Science*. 58: 83 – 91.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecological Letters*. 14: 709 – 722.
- Eldridge, D.J., Soliveres, S., Bowker, M.A., Val, J. 2013. Grazing dampens the positive effect of shrub encroachment on ecosystem functions in a semi-arid woodland. *Journal of Ecology*. 50: 1028 – 1038.
- Kraaij, T., Ward, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*. 186.
- Nkosi, S.E., Brown, L.R., Barrett, S.A. 2018. A baseline study for controlling the indigenous encroacher *Stoebe vulgaris* in natural grasslands of Southern Africa. *Agriculture, Ecosystems and Environments*. 265: 209 – 216.
- Snyman, H.A. 2012. Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *South African Journal of Botany*. 81: 34 – 39.
- Ulappa, A.C., Kelsey, R.G.K., Frye, G.G., Rachlow, J.L., Shipley, L.S., Bond, L., Pu, x., Forbey, J.S. 2014. Plant protein and secondary metabolites influence diet selection in a mammalian specialist herbivore. *Journal of Mammalogy*. 95: 834 – 842.
- van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grassland. *Journal of Environmental Management*. 90, 2931 -2942.
- Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*. 22: 101–105.