EVALUATING THE IMPACT OF PRESCRIBED BURNING AND HERBIVORE GRAZING ON SOIL NUTRIENTS AND CARBON DYNAMICS IN A SAVANNA GRASSLAND IN SATARA, KRUGER NATIONAL PARK

by

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DECLARATION

I, Ramabopa Koketso Mmanare, hereby declare that the work reported in this dissertation is my original and has not previously been submitted by anyone in the University of Limpopo or any other institution for the degree of Master of Science in Agriculture (Soil Science). It was conceptualized and carried out by me and thus, does not contain any other person's data, images, or graphs unless acknowledged accordingly. The dissertation does not contain any other persons' writing unless specifically mentioned that it was sourced from other studies. Where applicable, the relevant sources were cited accordingly in the dissertation and were fully referenced. The ideas of other researchers have been re-written and specifically acknowledged in cases where their information or content have been retained.

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Ramabopa KM (Miss)   Date

DEDICATION

I dedicate this research to the Almighty God, my provider, who has continuously guided me and provided me with the strength and wisdom to complete this study.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ABSTRACT

Savanna grasslands in South Africa are well adapted to fire and herbivory, yet these land management practices modify vegetative biomass and overtime affect forage productivity. Fire-herbivory interaction effects offer a more credible explanation for the occurrence of sporadic changes in savanna ecosystems and are crucial for maintaining tree-grass coexistence. Although, fire and herbivory have often been studied independently, they both act together in savanna ecosystems to influence soil quality leading to a depletion in soil nutrients and soil organic carbon (SOC). There is ongoing uncertainty regarding the underlying mechanisms controlling the decline in soil nutrients and little is known on the destabilization mechanisms involved in SOC depletion in grassland soils. The objectives of this study were (1) to quantify the effect of late burning and herbivore grazing on soil nutrients in the topsoil of a savanna grassland, (2) to determine the effect of late burning and herbivore grazing on soil aggregate stability and distribution of carbon (C) within micro-and-macro-aggregates in a savanna grassland. To achieve these goals, topsoil from Satara experimental sites in Kruger National Park (KNP), South Africa were examined where late burning plus grazing and fire-grazing exclusion (control) experiments had been conducted annually for 7 years. Within the 25-ha experimental plot, three 10 × 10 m sub-plots were laid out randomly and soil samples were collected in the 0-10 cm depth for laboratory analysis. Results revealed that late burning and herbivore grazing depleted SOC in loamy sand soils at the KNP site. The depletion of SOC associated with late burning and herbivore grazing were accompanied by a reduction in total C and nitrogen (N) by 26% and 18%, respectively. This led to a further decrease in soil aggregate stability and concomitant decrease in calcium (Ca) by 6%, effective cation exchange capacity (ECEC) by 3% and zinc (Zn) by 5%. The alteration of the soil structure and depletion of SOC and some nutrients was ascribed to the disruption in the physical and chemical nature of the soil associated with the disaggregating effects linked to fire and grazing disturbances. Collectively, the findings obtained in this study demonstrates that 7-years of frequent burning and herbivore grazing in savanna grasslands leads to in a decline in micro- and macronutrients, which overtime may reduce overall soil fertility.

Keywords: Late burning, herbivore grazing, soil quality, soil organic carbon, savanna grasslands

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

Globally, savanna grasslands cover approximately 20% of the land-surface, with the largest proportion found in Africa. Over one third of South Africa's land is covered by savanna grasslands, which makes approximately 46% of the landscape (Low and Rebelo, 1996; Osborne *et al*., 2018). Savanna ecosystems are characterized by the co-occurrence of two diverse plant forms, namely trees and grasses. Although the delineation of these life forms differs across savanna types, they generally consist of a community of intermittent cluster of trees and a continuous layer of herbaceous vegetation (Sankaran *et al*., 2004). Savannas are fire-driven ecosystems where fires can occur naturally through lightning or by anthropogenic actions, either unintentionally or deliberately (Bond and Keeley, 2005; Archibald *et al*., 2009). Fire is a fundamental part of these ecosystems (Bowman *et al*., 2009), playing a key role in restructuring the architecture of plants, species composition and overall vegetation structure (Bond, 2005; Archibald *et al*., 2019).

Prescribed burning and controlled grazing have been widely adopted as management practices to control the co-dominance of trees and grasses (Sankaran *et al*., 2005) in arid and semiarid savanna grasslands (Browning and Archer, 2011; Wang *et al*., 2019). An increasingly common land management practice in African savannas is prescribed burning, which is defined as the intentional or planned use of fire to assist in achieving a land management goal (Beale *et al*., 2018; Kranz and Whitman, 2019). Land managers primarily incorporate prescribed burns to eliminate fuel that generates a high intensity fire (Santín and Doerr, 2016). The total fuel consumption and overall removal of aboveground biomass, however, depends on the season (early or late) of burning (Bond, 2005).

Equally important, grazing is another management practice incorporated and occurs concurrently with fires to manage savanna ecosystems. A significant land use requirement that is essential to maintaining environmental quality, ecological sustainability, and providing ecosystem services is grazing management (Lin *et al*., 2010).

Blair *et al*. (2014), defined grazing as a form of herbivory in which herbaceous and forage plants (grasses and trees) are consumed by herbivores. Both prescribed burning and grazing act as ecosystem engineers and important modifiers of ecosystems, especially in savannas, influencing vegetation composition, annual aboveground net primary productivity and nutrient cycling (Archibald *et al*., 2005).

Previously, fire and herbivory have been decoupled by most researchers and treated as two separate disturbance factors especially in savannas. In defiance of this presumption, Fuhlendorf *et al*. (2009) suggested that these disturbance factors be perceived as a single ecological interaction as each depends on the other both spatially and temporally. This interaction is termed 'pyric-herbivory' which is the spatial and temporal interaction between fire and grazing, where positive and negative feedbacks generate a dynamic pattern of disturbance over the landscape (Fuhlendorf and Engle, 2001). The feedbacks of pyric-herbivory are important in maintaining ecosystem function through the alteration of the spatial heterogeneity of vegetation (Allred *et al*., 2011), soil characteristics (McNaughton *et al*., 2001) and nutrient cycling (Yarnell *et al*., 2007; Furey and Tilman, 2021).

1.2 Problem statement

In the Kruger National Park (KNP), prescribed burning was established in 1954 as one of the most widely used management practices available to conservation authorities to achieve their mission to "conserve, protect and manage biodiversity" (Van Wilgen *et al*., 2000; SANParks, 2018). In recent times, there has been increasing concern from the land managers at KNP on the impacts of prescribed burning and herbivore grazing on soil quality in savanna grasslands. As such, considerable scientific attention is now being paid to understand the variations in soil physical, biological, and chemical properties following frequent burning and grazing at varying intensities. With regard to this proposed study, it is envisaged that prescribed burning and grazing both directly and indirectly affect soil nutrient and C dynamics in savanna grasslands.

There are numerous mechanisms through which these disturbance factors can influence soil C and nutrient storage in savanna soils. Both fire and grazing modify the chemistry and quantity of plant loads through changes in plant biomass and composition (Abdalla *et al*., 2018; Whitman, *et al*., 2019; Pellegrini *et al*., 2020). Fire directly alters the balance and movement of the soil nutrients through volatilisation of C and N (Chen *et al*., 2010) resulting in their loss to the atmosphere (Van der Werf *et al*., 2010). Not only does fire volatilise C and N, but also changes the physical, chemical and biochemical structure of organic matter (González-Pérez *et al*., 2004), thus influencing its decomposability (Knicker, 2007). Grazing also directly reduces vegetation cover, thereby reducing soil organic matter and above- and belowground C (Wang *et al*., 2017). Reduced organic matter can then directly or indirectly affect other soil physical and biological properties, such as, water repellency, bulk density, aggregate stability, and microorganisms (Alcañiz *et al*., 2018). Soil aggregate stability has been shown to decrease due to compaction during animal trampling and the combustion of organic cements crucial for soil stabilisation. The collapse of aggregates weakens the soil structure leading to blockage of voids by the ash and scattered clay minerals. Soil dispersion and clogging of pores in turn leads to a decrease in soil porosity and permeability (Martin and Moody, 2001). This subsequently leads to an increase in soil water repellency or hydrophobicity, runoff and erosion (Certini, 2005). Ultimately, the deterioration of the above-mentioned soil properties by these degradation processes reduces soil quality and quantity, thereby, reducing ecosystem functioning (Alcañiz *et al*., 2018).

1.3 Rationale

Until now, studies conducted in savanna grasslands at KNP have looked at prescribed burning plus grazing effects on grass community composition and formation of grazing lawns (Pollard, 2016; Donaldson *et al*., 2017), but the impacts of these management practices on nutrient availability, organic matter levels and distribution of C within soil aggregates have not been established. Despite that, fire and grazing have generally been widely researched, few scientists have looked into the potential synergistic effects that these two factors may have on savanna ecosystems (Archibald *et al*., 2005; Fuhlendorf *et al*., 2009). Fire and herbivore are mutually inclusive factors and often act together to control species composition (Donaldson *et al*., 2017) and heterogeneity of vegetation (Allred *et al*., 2011) within savannas. As such, the dynamic co-occurrence of both grasses and woody plants in savannas has piqued scientists' interest (Higgins *et al*., 2000), and more research revealed that fire and herbivory are the most significant drivers that interact and strongly influence the dynamics of this relationship (Van Wilgen *et al*., 2003). It has been observed that fire influences grazing by altering foraging patterns whereas, herbivores affect fire by reducing the amount of fuel loads and the fire's ability to spread across a landscape (Archibald *et al*., 2005). Therefore, it is evident that fire and grazing both play a role in limiting the growth and spread of grazing lawns. However, their interaction effect is complex, and depends on the timing, intensity and frequency with which the disturbances occur. The experimental burn plots at KNP are quite convenient and practical for determining the effects of alternating burning and grazing frequencies on soil properties (Strydom *et al*., 2019). The interaction effect of fire and grazing is dependent upon various factors including the type of soil, vegetation type and landscape position which may vary over very small distances. These factors as well as the traditional regimes (intensity, periodicity, and seasonality) should be considered because they drive the feedbacks of fire and grazing (Alcañiz *et al*., 2018). In the existing literature, only few studies have investigated how these regimes influence soil properties (Scharenbroch *et al*., 2012). This is because the timing of the interventions and the actual intensity of disturbances can be quite difficult to determine in practice (Wang *et al*., 2019). Thus, it is imperative to investigate the combined effect of prescribed burning and grazing on soil properties at varying intensity, periodicity and seasonality. A better insight of the factors influencing C and nutrient dynamics in savanna grasslands is critical for their proper management.

1.4 Purpose of the study

1.4.1 Aim

The study aims to investigate the effects of late burning and herbivore grazing on soil nutrients and C dynamics in a savanna grassland at KNP.

1.4.2 Objectives

The objectives of the study were:

i. To quantify the effect of late burning and herbivore grazing on soil nutrients in the topsoil of a savanna grassland.

ii. To determine the effect of late burning and herbivore grazing on soil aggregate stability and distribution of C within micro-and-macro-aggregates in a savanna grassland.

1.4.3 Research questions

The study addressed the following research questions:

i. How does late burning and grazing influence soil nutrients in savanna grasslands?
ii. How does late burning and grazing influence the distribution of SOC within aggregate fractions in savanna grassland soils?

1.5 Mini-dissertation structure

The structure of this document follows that of a conventional masters' dissertation. It constitutes five chapters. The first chapter mainly describes the background of the study, a rationale for the research, as well as the aims and objectives. Chapter 2 reviews literature on prescribed burning and herbivore grazing as land management tools in savanna grasslands and their impact on soil physical and chemical properties. Chapter 3 and 4 are free standing research chapters including extensive introductions to their respective sub-titles of the research, methodologies, as well as separate results interpretation and discussions. Specifically, Chapter 3 focuses on the effect of prescribed burning and herbivore grazing on soil nutrients in the pedoderm layer of grassland soils. Meanwhile, Chapter 4 discusses the effect of prescribed burning and herbivore grazing on the distribution of SOC within whole soil and aggregate size fractions of the soil. These two chapters are written as stand-alone chapters for the purpose of publication. Lastly, Chapter 5 is an overarching conclusion, which summarizes the findings of the study and recommends further areas of research that can be explored in the future. Each individual chapter includes a list of referenced literature.

REFERENCES

Abdalla, M., Hastings, A., Chadwick, D.R., Jones, D.L., Evans, C.D., Jones, M.B., Rees, R.M. and Smith, P. 2018. Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. *Agriculture, Ecosystems & Environment*. 253: 62-81.

Alcañiz, M., Outeiro, L., Francos, M. and Úbeda, X. 2018. Effects of prescribed fires on soil properties: A review. *Science of the Total Environment*. 613-614: 944-957.

Allred, B., Fuhlendorf, S., Engle, D. and Elmore, D. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*. 1: 132-144.

Archibald, S., Bond, W.J. and Fairbanks, D.H.K. 2005. Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*. 15: 96-109.

Archibald, S., Hempson, G.P. and Lehmann, C. 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist*. 224: 1490-1503.

Archibald, S., Roy, D.P., Van Wilgen, B.W. and Scholes, R.J. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology*. 15: 613-630.

Beale, C.M., Courtney Mustaphi, C.J., Morrison, T.A., Archibald, S., Anderson, T M., Dobson, A.P., Donaldson, J.E., Hempson, C.P., Probert, J. and Parr, C.L. 2018. Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas. *Ecology Letters*. 21: 557-567.

Blair, J., Nippert, J. and Briggs, J. 2014. Grassland Ecology. Springer Science and Business Media: New York.

Bond, W.J. 2005. Large parts of the world are brown or black: a different view on the ‘Green World’ hypothesis. *Journal of Vegetation Science*. 16: 261-266.

Bond, W.J. and Keeley, J.E. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*. 20: 387-394.

Bowman, D.M., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D’Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P. and Johnston, F.H. 2009. Fire in the earth system. *Science*. 324: 481-484.

Browning, D.M. and Archer, S.R. 2011. Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecological Applications*. 21: 1629-1642.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia*. 143: 1-10.

Chen, Y., Randerson, J.T., Van der Werf, G.R., Morton, D.C., Mu, M. and Kasibhatla, P.S. 2010. Nitrogen deposition in tropical forests from savanna and deforestation fires. *Global Change Biology*.16: 2024-2038.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. and Parr, C.L. 2017. Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*. 55: 225-235.

Fuhlendorf, S. and Engle, D. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience*. 51: 625-632.

Fuhlendorf, S., Engle, D., Kerby, J. and Hamilton, R. 2009. Pyric-herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. *Conservation Biology*. 23: 588-598.

Furey, G.N. and Tilman, D. 2021. Plant biodiversity and the regeneration of soil fertility. *Proceedings of the National Academy of Sciences*. 118: 1-8.

González-Pérez, J.A., González-Vila, F.J., Almendros, G. and Knicker, H., 2004. The effect of fire on soil organic matter-a review. *Environment International*. 30: 855-870.

Higgins, S.I., Bond, W.J. and Trollope, W.S. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*. 88: 213-229.

Knicker, H. 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry*. 85: 91-118.

Kranz, C. and Whitman, T. 2019. Short communication: Surface charring from prescribed burning has minimal effects on soil bacterial community composition two weeks postfire in jack pine barrens. *Applied Soil Ecology*. 144: 134-138.

Lin, Y., Hong, M., Han, G.D., Zhao, M.L., Bai, Y.F. and Chang, S.X. 2010. Grazing intensity affected spatial patterns of vegetation and soil fertility in a desert steppe. *Agriculture, Ecosystems and Environment*. 138: 282-292.

Low, A.B. and Rebelo, A.G. 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism: Pretoria.

Martin, D.A. and Moody, J.A. 2001. Comparison of soil infiltration rates in burned and unburned mountainous watersheds. *Hydrological Processes*.15: 2893-2903.

McNaughton, S., Banyikwa, F. and McNaughton, M. 2001. Promotion of cycling of diet-enhancing nutrients by African grazers. *Science*. 278: 1798-1800.

Osborne, C.P., Charles-Dominique, T., Stevens, N., Bond, W.J., Midgley, G. and Lehmann, C.E.R. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*. 220: 10-24.

Pellegrini, A.F.A., Hobbie, S.E., Reich, P.B., Jumpponen, A., Jack Brookshire, E. N., Caprio, A.C., Coetsee, C. and Jackson, R.B. 2020. Repeated fire shifts carbon and nitrogen cycling by changing plant inputs and soil decomposition across ecosystems. *Ecological Monographs*. 0: 1-20.

Pollard, A.D., 2016. Grazer Response to Fire in an African Savanna: Exploring the Role of Fires in Grazing Lawn Formation (Doctoral dissertation, University of the Witwatersrand, Faculty of Science, School of Animal, Plant and Environmental Sciences).

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F. and Ardo, J. 2005. Determinants of woody cover in African savannas. *Nature*. 438: 846-849.

Sankaran, M., Ratnam, J. and Hanan, N.P. 2004. Tree-grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology letters*. 7: 480-490.

SANParks. 2018. Kruger National Park management plan: Purpose and vision. South African National Parks: Pretoria.

Santín, C. and Doerr, S.H. 2016. Fire effects on soils: the human dimension. *Philosophical Transactions of the Royal Society Biological Sciences*. 371: 150-171.

Scharenbroch, B.C., Nix, B., Jacobs, K.A. and Bowles, M.L. 2012. Two decades of low severity prescribed fire increases soil nutrient availability in Midwestern, USA oak (Quercus) forest. *Geoderma*. 183-184: 89-91.

Strydom, T., Riddell, E.S., Rowe, T., Govender, N., Lorentz, S.A., le Roux, P.A.L. and Wigley-Coetsee, C. 2019. The effect of experimental fires on soil hydrology and nutrients in an African savanna. *Geoderma*. 345: 114-122

Van der Werf, G.R., Randerson, J.T., Giglio, L., Collatz, G., Mu, M., Kasibhatla, P.S., Morton, D.C., DeFries, R., Jin, Y. and van Leeuwen, T.T. 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires. *Atmospheric Chemistry and Physics*. 10: 11707-11735.

Van Wilgen, B., Trollope, W., Biggs, H., Potgieter, A. and Brockett, B. 2003. Fire as a Driver of Ecosystem Variability. Island Press: Washington.

Van Wilgen, B.W., Biggs, H.C., O'Regan, S.P. and Marè, N. 2000. A fire history of the savanna ecosystems in Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Sciences*. 96: 167-178.

Wang, G., Li, J. and Ravi, S. 2019. A combined grazing and fire management may reverse woody shrub encroachment in desert grasslands. *Landscape Ecology*. 34: 2017-2031.

Wang, H., Liu, H., Wang, Y., Xu, W., Liu, A., Ma, Z., Mi, Z., Zhang, Z., Wang, S. and He, J.S. 2017. Warm-and cold-season grazing affect soil respiration differently in alpine grasslands. *Agriculture, Ecosystems & Environment*. 248: 136-143.

Whitman, T., Whitman, E., Woolet, J., Flannigan, M.D., Thompson, D.K. and Parisien, M. 2019. Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. *Soil Biology and Biochemistry*. 138: 107571.

Yarnell, R., Scott, D., Chimimba, C. and Metcalfe, D. 2007. Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia*. 154: 387-402.

CHAPTER 2

LITERATURE REVIEW

2.1 Prescribed burning as a land management tool in savanna grasslands

Prescribed burning is becoming widely recognised and incorporated as a management technique in arid and semi-arid savanna grasslands (Castellnou *et al*., 2010). It contributes largely to the nature of savanna grasslands and has the potential to manipulate their vegetation, particularly the structure and composition (Trollope and Trollope, 1996). This is due to its substantial influence on the nutrient cycling and ecological processes of a savanna ecosystem (Mapiye *et al*., 2008; Augustine *et al*., 2014). Wildlife managers in African savannas utilise this management tool to achieve various objectives (Goldhammer and de Ronde, 2004; Castellnou *et al*., 2010) and ecosystem services such as improving forage quality and removing unpalatable grass material, reducing woody encroachment, controlling invasive alien plants, reducing greenhouse gas emissions and protecting the surrounding infrastructure to promote safety (Waldrop and Goodrick, 2012; Alcañiz *et al*., 2018; Nieman *et al*., 2021). These specific goals among others can be achieved by the use of prescribed fires and will be discussed broadly.

2.1.1 Enhance forage quality by removing unpalatable grass material

Burning is a management technique that can be used to remove low-nutrient moribund grass as a way to improve forage quality for the benefit of grazers, encourage uniform grazing and reduce unpalatable grass material and bare ground patches (Bond and Archibald 2003; Van Wilgen *et al*., 2003). The ultimate goal is to achieve a balanced woody to grass ratio and improve the quality of feed for wildlife by encouraging herbivores to move to less desirable regions to avoid overuse and overexploitation of biomass (Trollope, 2007). In order to accomplish these goals, Trollope (2007) recommends that prescribed fires be conducted either in the early dry season to produce an even regrowth of green grass or in the early wet season to remove moribund grass that lingers after the dry season.

2.1.2 Reduce encroachment of woody species

In situations where there is a surge of undesirable woody plant species, wildlife managers can implement the use of relatively high intensity fires to restrict recruitment of trees and overabundance of encroaching woody species (Van Wilgen *et al*., 2014). However, the season of burning should be considered in such instances, since fires become intense in the late dry season resulting in increased mortality rates of very large trees (Govender *et al*., 2006; Smit *et al*., 2016). Therefore, early wet season fires are usually preferred as they can safely reverse encroachment of woody species, assuming that grass fuel loads are sufficient to support fire of a reasonably high intensity (Crowley *et al*., 2009).

2.1.3 Manage invasive alien plants

Alien plant species are increasingly encroaching on protected areas such as African savannas (Te Beest *et al*., 2012) and have become a huge problem (Foxcroft *et al*., 2013). Oftentimes, fires are involved in both their spread and management depending on the level of intensity (Dew *et al*., 2017). Te Beest *et al*. (2012) suggested that recurrent high intensity fires would be necessary to control invasive alien plants and reduce their seedling densities. Nieman *et al*. (2021) argued that a species-specific approach would be a prerequisite to managing alien invasions since alien plant responses to fire are species-specific.

2.1.4 Control greenhouse gas emissions

In recent years, the increasing emissions of greenhouse gases such as methane (CH_4) and nitrous oxide (N_2O) (Landry and Matthews, 2016) as a result of wildfires have become a global problem. It has thus been proposed that application of prescribed fires in the early dry season in savanna ecosystems can reduce these gas emissions (Van Der Werf *et al*., 2017). According to Lipsett-Moore *et al*. (2018), a transition from late to early dry season fires can reduce these gas emissions by approximately 37%.

2.1.5 Protection of infrastructure

The level of fire intensity and use of firebreaks in savannas should be considered to enhance the safety of humans, wildlife and the surrounding infrastructure. Low intensity fires in the early dry season are mostly preferred as they can be controlled easily compared to high intensity fires in the late dry season. As a result, land managers usually adapt to the tradition of applying prescribed fires in the early dry season to promote safety (Kamminga, 2001). Alternatively, the use of firebreaks before the onset of the fire season may be a better option to completely exclude fires from areas with a high human population or infrastructure density (Nieman, 2020).

Fundamentally, conservation authorities are urged to adhere to appropriate conservation measures and proper application when conducting prescribed fires (Augustine *et al*., 2014). Inappropriate application of fires can affect major ecosystem processes and pose a threat to ecosystem resources, forage quality and biodiversity. In order to minimise these harmful effects, the above-mentioned factors should be considered during the onset of prescribed fires (Trollope, 1999; Mapiye *et al*., 2008). The knowledge of fire regimes (intensity, frequency, season and type of fire) is also important when scheduling prescribed fires to avoid any harmful effects to the ecosystem. Savanna grasslands are dynamic ecosystems that require planning of prescribed fires beforehand and should be integrated with proper grazing management techniques to attain ecosystem productivity (Mapiye *et al*., 2008).

2.2 Fire regimes and their significance in savanna grasslands

Prescribed burning is recognised as an effective means for controlling undesirable plant species and a useful tool for wildlife management in savanna ecosystems (Nieman *et al*., 2021). It is extensively utilised by conservation authorities as a management technique to achieve several objectives in savanna grasslands (Goldhammer and de Ronde, 2004). However, it is important that conservation managers adhere to safety when scheduling prescribed burns. The inability to control fires, inappropriate application and inappropriate fire regimes can pose a threat to the ecosystem. The significance of fire regimes in conservation areas and their relative role in managing ecosystems has been overlooked. According to Trollope and Trollope (2010), fire regime refers to the patterns of fire seasonality, intensity, frequency and type in a particular ecosystem. Fire regimes play a fundamental role in shaping the ecosystem and affect its productivity and availability of resources. The spatial and temporal variability within a particular ecosystem determines the fire regime over a specific period. Therefore, understanding changes in the fire regime and factors that can alter these fire regimes is crucial for better planning of safe prescribed burns and better management of ecosystem resources (Morgan *et al*., 2001).

2.2.1 Season of burning

The season of burning is one of the critical components of the fire regime which contributes largely to the level of fuel consumption and fire characteristics in savanna ecosystems (de Groot and Wein, 2004; Hamman *et al*., 2008). The two main types of burning seasons include early and late burning which differ greatly in terms of intensity and the level of fuel loading. According to Roberts *et al*. (2018), early season burns are low intensity fires primarily characterised by high fuel moisture, low fuel loads and a high degree of patchiness whereas, late season burns are medium to high intensity fires that result in high total fuel consumption and low levels of patchiness. In African savannas, early burning is normally carried out in April/May season whereas late burning is typically conducted in September/October after fuel moisture has dropped and weather variables have moderated but before the onset of late season storms (Donaldson *et al*., 2017).

The suitable time of the year to apply prescribed fires in African savannas will depend on the rainfall pattern of the region, the fuel moisture and soil moisture (Trollope, 1989). Majority of studies in African savannas recommended that when burning to remove moribund, fires should preferably be applied after the first rainfall of approximately 15-20 mm, at the start of the growing season when the grass is still dormant and the fire hazard is low. Conversely, burning should be used to suppress encroaching vegetation before the first rains when the grass is extremely dry to ensure a high intensity fire (Trollope and Trollope, 1996; Trollope and Trollope, 2010).

2.2.2 Fire intensity

The level of fire intensity plays a huge role in the maintenance and conservation of African savanna ecosystems and should be considered amongst important factors when planning prescribed fires. Despite the fact that fire intensity is a crucial component of the fire regime, it is rarely included in fire records (Trollope and Trollope, 2010). According to Bond and Van Wilgen (1996), fire intensity refers to the rate of heat release per unit time per unit length of fire front and it is mostly measured in kilojoules per second per metre ($kJ\ s^{-1}\ m^{-1}$). Certain factors such as season, fuel properties, topography and wind among other weather conditions determine the level of intensity of fire. Based on a study by Trollope (1999), fire intensities normally range between 100-4000 kJ s^{-1} m^{-1} in savannas. However, Govender *et al*. (2006), reported higher ranges of about 11000-17 500 kJ s^{-1} m^{-1}. Research on fire behaviour in African savannas has indicated that fire intensity can be classified into six groups as shown in Table 1.

Table 1: Fire intensity classes.

Fire intensity (kJ s^{-1} m^{-1})	**Description**
<500	Very cool
501 to 1000	Cool
1001 to 2000	Moderately hot
2001 to 3000	Hot
>3000	Extremely hot

Source: Trollope and Trollope (2010)

A cool fire of 1000 KJ s^{-1} m^{-1} is recommended by Trollope and Trollope (2010) to remove low-nutrient moribund grass material. This can be achieved when the air temperature is below 20 ºC, and the relative humidity is above 50%. In contrast, a hot fire of >2000 kJ s^{-1} m^{-1} is required when burning to control unwanted encroaching plant species to ensure a great top kill of stems and branches of bush species up to a height of 3 m. A wind speed of <20 km/h is required for both cases (Trollope and Trollope, 2010). It is important that land managers select ignition patterns prior to prescribed burns to control the level of intensity of fire (Trollope *et al*., 2002).

2.2.3 Frequency of burning

Mapiye *et al*. (2008), defined fire frequency as a period of time (i.e., interval) between burns. Factors such as the availability of fuel, environmental and climatic conditions of a specific area determine the frequency of burning (Bigalke and Willan, 1984). According to Trollope and Trollope (2010), the burning frequency will depend on the rate at which the phytomass of grass material accumulates and it is recommended that the excess grass litter should not exceed 4000 kg/ha when burning to remove moribund vegetation. Therefore, the burning frequency will be based on the accumulation rate of excess grass litter. On the other hand, the amount of rainfall an area receives also determines the frequency of burning in that particular area. Generally, in high rainfall areas (i.e., moist savanna grasslands) receiving rainfall > 700 mm per annum, the recommended burning frequency should be every 2 to 4 years whereas, in lower rainfall areas or semiarid savannas the frequency should be much lower (5-8 years) (Van Wilgen *et al*., 1997).

2.2.4 Type of fire

Fire type is another critical component of fire regime that plays a fundamental role in shaping the structure of the savanna grasslands. According to Gill (1975), there are different types of fires which can be distinguished as follows: (1) fires that burn in organic layers of the soil referred to as ground fires; (2) those burning in the canopies of trees, i.e., crown fires, and (3) surface fires which spread along the ground and burn only surface litter or plant material. These distinct fire types behave differently and have varied effects on the savanna grasslands' vegetation. The most frequent types of fires in the savanna grasslands, as opposed to crown fires and ground fires, are surface fires that burn as either head or back fires (Bond and Van Wilgen, 1996).

The effect of the type of fire on plants is of utmost importance because it determines the vertical level at which heat energy is released and the level of fuel consumption thereof (Trollope, 1978). Most authors (Bond and Van Wilgen, 1996; Trollope *et al*., 2002; Mapiye *et al*., 2008) recommend the application of surface fires in savannas because they spread slowly, cause the least damage to the grass sward and do not produce high intensity fires that can cause maximum damage to woody vegetation. Crown fires are more likely to inflict harm to trees because they typically burn with a much higher intensity, and spread more quickly. These fires are characterised by a lot of smoke production, tend to be difficult to suppress by normal firefighting techniques and usually result in 100% tree mortality (Trollope, 1999).

Owing to the importance of fire regimes in the management of savanna ecosystems, managers should attempt to maintain some aspects of the fire regime within specified limits by adjusting the frequency, intensity, season, and fire types. Although implementing and maintaining any chosen fire regime may be challenging, this will help them attain their desired outcomes during fire management (Nieman *et al*., 2021).

2.3 Fire intensity impacts on grassland productivity and soil nutrients

Fire intensity is a key component of the fire regime and has important effects on the vegetation and soil nutrient dynamics of savanna ecosystems (Govender *et al*., 2006). Although there are numerous elements at play and their interconnections make understanding the relationship between fire, vegetation, and soil nutrients difficult, fire intensity is typically the most important element influencing post-fire nutrient dynamics. (Fisher and Binkley 2000). Managers of African savannas determine fire intensity using relationships between season of fire, fuel loads, heat yields of fuel and the rates of fire spread (Govender *et al*., 2006).

Fire intensity may also vary according to the weather patterns of an area and is expected to increase as the climate changes (Hamman *et al*., 2007). Therefore, the level of fire intensity is a combination of fuel and climatic conditions of a savanna ecosystem (Neary *et al*., 1999). Fire intensity will most likely influence post-fire soil nutrient dynamics depending on the level of intensity (i.e., low, medium or high). High intensity fires often lead to a decline in soil nutrient pools as compared to low intensity fires and can have many other post-fire impacts that reduce grassland productivity (Wan *et al*., 2001). Low intensity prescribed fires, however, have been shown to yield inconclusive results and lead to a variable response of soil nutrients.

The key pathways and mechanisms that generally contribute to nutrient losses during and immediately post fires are combustion, volatilisation, mineralisation, ash convection, erosion, runoff and leaching as shown in Figure 1 (Neary *et al*., 1999). Organic soil layers are rich in nutrients, and the amount of these layers consumed depends on the intensity of fires. Intense fires can consume nearly all or entire aboveground biomass, reduce soil organic matter and volatilise nutrients (Certini, 2005). Nutrient-rich ashes remaining after prescribed burning can be moved over a burned region by surface wind transport or convection in a smoke column. These mechanisms should at most be considered after high intensity fires because they contribute to a negligible change of atmosphere-related nutrient losses after low-intensity fires. While ash losses in convective smoke columns can surpass 11% in higher intensity fires, they typically range from 1-4% of the mass of the burned fuel in low intensity fires (Raison *et al*., 1985).

Numerous mechanisms that influence soil nutrient pools and dynamics are affected by fire intensity both directly and indirectly (Neary *et al*., 1999). Fire temperature directly determines the types and quantities of nutrients that will be volatilised. For example, N starts to vaporise from organic matter at only 200 ºC, while other soil nutrients require exceptionally high temperatures (750 ºC) for volatilisation to take place (Neary *et al*., 1999). As an indirect consequence, the physical transportation of nutrients away from the location site is linked to fire intensity. High intensity fires can alter the physical attributes of the soil making it more prone to nutrient loss via erosion (McColl and Grigal, 1977). Due to the comparatively small mass transfer of soil and ash in wind from the majority of burned sites, nutrient losses in wind-borne ash following fires are predicted to be low. Large woody debris and other surface-based organic materials that are combusted, lead to the greatest nutrient losses through volatilisation and have a considerable impact on biogeochemical cycles (Neary *et al*., 1999).

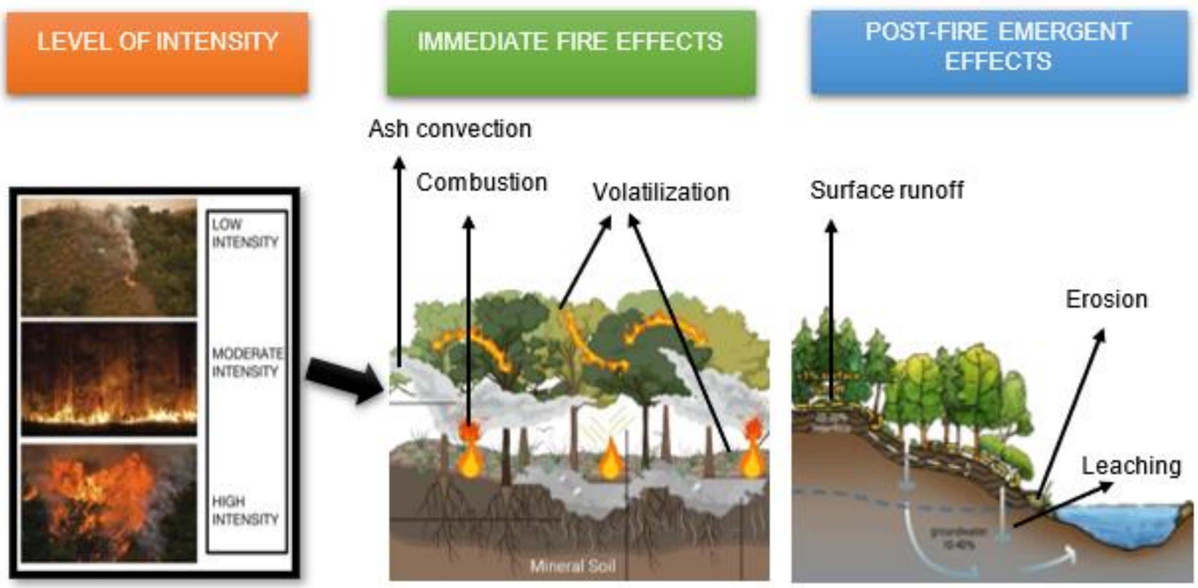

Figure 1: Key pathways and mechanisms contributing to nutrient losses during and immediately post-fire.

Source: DellaSalla (2018); Flores *et al*. (2020); Datta (2021)

2.4 Impact of fire-herbivory interactions on the structure and nutrients in savannas

2.4.1 Mechanisms driving tree-grass co-existence in savannas

Several explanations on the co-existence of trees and grasses in savanna ecosystems have been derived thus far. These explanations arose from an attempt to answer the savanna question: '*What is special about the savanna environment that allows trees and grasses to coexist, as opposed to the general pattern in other areas of the world where either one or the other is dominant*?' which has attracted the interest of many scientists (Scholes and Archer, 1997; Van Langevelde *et al*., 2003; Sankaran *et al*., 2004; D'Odorico *et al*., 2006; Accatino *et al*., 2010) among others. The co-occurrence of trees and grasses is central to understanding the savanna ecology (Govender *et al*., 2006).

In a savanna ecosystem, the co-dominance of trees and grasses is determined by the fire and herbivory interaction effects. These interaction effects are dependent upon positive feedbacks between fuel load (grass biomass) and fire intensity which operates at various spatial and temporal scales to maintain balance within savannas (Scholes and Archer, 1997). When grazing, browsing, and fire intensity levels fluctuate, the balance between grasses and trees becomes altered (Van Langevelde *et al*., 2003). The connection between fire intensity and the growth of grasses and trees, as mediated by either browsing or grazing is depicted in Figure 2.

As observed from the figure, it is clearly evident that increasing grazing levels result in a reduction of grass biomass (fuel load) which results in less intense fires that cause less damage to trees and, as a consequence, an increase in woody vegetation. (Figure 2A). On the other hand, browsers reduce woody vegetation (i.e., by either killing or reducing the size of trees) and may improve the effect of fire on trees, thus, encouraging grass development. As a result, the increase in fuel load promotes highly intense fires and a significant decrease in biomass (Figure 2B). Eventually, the co-existence of grasses and is maintained within the ecosystem.

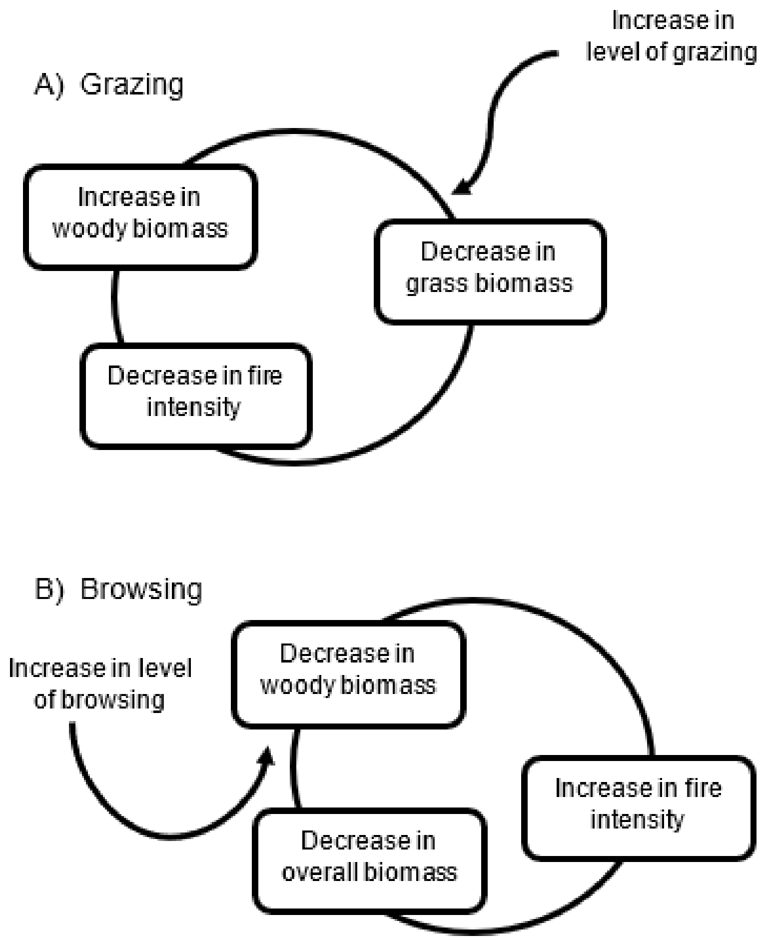

Figure 2: Positive feedback mechanism between grass biomass (fuel load) and fire intensity, triggered by (A) grazing and (B) browsing.
Source: Van Langevelde *et al*. (2003)

Although the importance of the interactions between fire, grazing and browsing on savanna dynamics has long been acknowledged (Norton-Griffiths, 1979; Scholes and Archer, 1997; Van de Vijver, 1999; Higgins *et al*., 2000), further research into the effects on the balance between trees and grasses is continued. Ecologists continue to debate the validity of these factors (fire and herbivory) in an effort to answer the 'savanna question' (Scholes and Archer, 1997; Higgins *et al*., 2000; Jeltsch *et al*., 2000).

Fire and herbivory are critical tools in shaping the savanna structure (Van Langevelde *et al*., 2003) but have been insufficient to generate long-term tree-grass co-existence in savannas and this has led to ecologists seeking additional mechanisms contributing to this co-existence (Jeltsch *et al*., 2000). According to Sankaran *et al*. (2004), proposed mechanisms for the persistence of both trees and grasses in savannas fall into two categories: those that emphasise the principal role of competitive interactions in promoting co-existence (i.e., competition-based models) and those that focus on the differential sensitivity to disturbances (i.e., demographic-bottleneck models).

In competition-based models, fire and grazing are referred to as 'modifiers', while water and nutrients are the 'primary determinants' that are limiting resources. (Stott, 1991). Grasses and trees co-dominate in savannas due to their varied capacities for acquiring and dividing scarce resources (Van Langevelde *et al*., 2003). There are four different yet related types of competition-based models namely: the root niche separation model, the phenological niche separation model, the balanced competition model and the hydrologically driven competition-colonisation model (Sankaran *et al*., 2004). However, only those within the equilibrium paradigm (e.g., root niche separation, phenological niche separation, balanced competition) will be explained in detail.

Walter (1971), proposed the root niche separation model, a typical equilibrium savanna model. It is predicated on the idea that water is the main resource and that trees and grasses have variable access to it depending on where their roots profiles are located. Although grasses are better competitors for water in the top horizons, trees are able to persist in the system because they have exclusive access to deeper water (Walter, 1971). Another proposed mechanism that may help to promote equilibrium types of tree-grass coexistence in savannas is niche separation by phenology (Scholes and Archer, 1997; House *et al*., 2003). In this model, the phenology of a savanna is influenced by the high variability in seasonal rainfall which is a major environmental driver of an ecosystem (Lehmann *et al*., 2011; Whitecross *et al*., 2016). Savanna trees have the capacity to retain nutrients and water, allowing them to reach full leaf expansion either before the rains begin or a few weeks afterwards (Scholes and Archer, 1997). Early and late in the growing season, trees frequently have exclusive access to resources. Grasses achieve their peak leaf area later in the growing season. In order to survive, grasses would then need to outcompete trees for resources when their growth cycles coincide. These implications for patterns of change in tree-grass ratios are not immediately visible because the outcome is not only dependent on the total rainfall but also on the length and predictability of the growing season (Sankaran *et al*., 2004). Lastly, in the case of the balance competition model, the superior competitor restricts its abundance to allow the weaker competitor to expand. Therefore, the superior competitor's intra-specific competition is more intense than the inter-specific competition (Amarasekare, 2003).

On the other hand, demographic-bottleneck models contend that trees and grasses continue to grow in savannas as a result of climate unpredictability and/or disturbances like fire and grazing that prevent successful tree seedling germination, establishment, and/or transition to mature size classes (Jeltsch *et al*., 2000; Higgins *et al*., 2000). Demographic-bottleneck models' basic tenet is that different stages of trees' life histories are affected differently by climate variability and perturbations. Most notably, these models' main focus is on the immediate consequences of these disturbances on tree germination, mortality, and demographic transition (Scholes and Archer, 1997). In general, models differ in terms of basic assumptions depending on who the better competitor is. Therefore, the structure of a savanna grassland is shaped by the effects of multiple interacting factors such as climatic variability, resource competition, herbivory and fire. Sankaran *et al*. (2004) emphasise the need to simultaneously consider both disturbances and competition for resources in order to capture their relative importance in shaping savannas.

2.4.2 Interactive effects of fire and herbivore grazing on soil nutrients

As part of the interactive factors shaping the structure of savanna ecosystems (Van Langevelde *et al*., 2003; Sankaran *et al*., 2004; Archibald *et al*., 2005), fire and herbivory are the most crucial drivers affecting soil nutrients. The fire-herbivory interaction effects on soil nutrients is multifaceted and may either be positive, negative or neutral (Kral *et al*., 2017; Thoresen *et al*., 2021; Vermeire *et al*., 2021). Fire and herbivory alter soil nutrients by affecting soil microorganisms and microbial activity through several direct and indirect mechanisms. By reducing litter inputs through browsing, increasing soil bulk density through trampling, and returning nutrients to the soil surface in a form suitable for plant and microbe uptake through urine and faeces deposits, herbivory has a direct impact on microorganisms and their activity (Bardgett and Wardle, 2003; Wardle *et al*., 2004; Harrison and Bardgett, 2008). Fire directly influences microbial populations through a temporary increase in soil temperature, volatilisation of minerals and inputs of C and ash (Neary *et al*., 1999). By modifying plant community composition, fire and herbivory both have an indirect impact on the soil microbial communities. As a result, the allocation of resources and the total biomass production vary (Neary *et al*., 1999; Bardgett and Wardle, 2003). Fire and herbivory reduce resources (i.e., soil organic matter, leaf litter, detritus, vegetation) through combustion, compaction and erosion processes (Cumming and Cumming, 2003; Pressler *et al*., 2019). Consequently, these alterations lead to reductions in microbial abundance, biomass and nutrient loading (Thoresen *et al*., 2021).

2.5 Effect of prescribed burning and herbivore grazing on soil C and N

Prescribed burning and herbivore grazing are often practiced together in many of the world's grasslands (Hobbs *et al*., 1991) and have been widely adopted as management interventions in arid and semiarid grasslands. Both have an influence on C and N pools by affecting their spatial distribution and facilitating their addition and losses (Hobbs *et al*., 1991). Prescribed burning can change soil C and N storage by altering the quantity and chemistry of plant inputs through changes in plant biomass and composition (Pellegrini *et al*., 2020). Herbivore grazing also contributes to these alterations by removing aboveground biomass, thereby affecting plant C inputs (Roques *et al*., 2001).

A study conducted by Pellegrini *et al*. (2020) across four main subtropical areas, reported that unburned plots had 48% higher soil C concentrations than repeatedly burned plots under sandy, well drained soils in the 0-5 cm depth layer. Changes in soil N concentrations followed similar trends to C concentrations whereby unburned plots had 69% higher total N concentrations than repeatedly burned plots. Furthermore, a study carried out by Gebregergs *et al*. (2019) in a semi-arid grassland, reported that total C and N decreased in silty soils. Compared to a 10-year grazing exclosure, total C and N decreased by 32% and 60%, respectively in the 0-10 cm soil depth layer due to open grazing. A study conducted by Brye (2006) in a humid-subtropical grassland, reported a

33% increase in total C and 15% increase in total N due to burning under silty loam soils in the 0-10 cm depth layer.

Pellegrini *et al*. (2014) argued that these significant reductions in the levels of C and N in the soil can be attributed to the removal of aboveground biomass due to fire and herbivore trampling leading to soil compaction and consequently reduced plant growth. Soil compaction induced by herbivore trampling may lead to reduced pore spaces, which limit gas exchange, microbial activity and root growth (Savadogo *et al*., 2007). In addition, the depletion of soil C and N can also be attributed to C loss as CO_2 into the atmosphere and volatilization of N at temperatures around 200°C during frequent burning (Muqaddas *et al*., 2015).

Conversely, the increase in C pools found in the abovementioned studies can be attributed to the incorporation of partially burned slash fragments into the soil or incomplete combustion of the organic matter due to the low temperatures reached in prescribed burning (Scharenbroch *et al*., 2012). Johnson and Curtis (2001) argued that the transformation of fresh residue into more recalcitrant forms may lead to an increase in C content in the soil. On the other hand, increases in total N may be due to low temperatures that facilitate the incorporation of ashes rich in N into soils and the subsequent decomposition of plant residues, which may release substantial amounts of N (Alcañiz *et al*., 2016).

2.6 Effect of prescribed burning on soil pH and exchangeable cations

Prescribed burning plays a significant role by altering soil pH and the amount and distribution of nutrients through the disruption of the nutrient cycle in the soil (McNabb and Cromack, 1990). A study conducted by Úbeda *et al*. (2005) in a Mediterranean grassland, reported a 3% increase in soil pH due to prescribed burning in the 0-5 cm soil layer of sandy loam soils. Similarly, a study carried out by Sherman *et al*. (2005) in a restored continental and humid-subtropical grassland reported an increase in soil pH as a result of prescribed burning under loamy textured soils in the 15-20 cm soil layer. Soil pH increased slightly by 6%, with 5.65 in burned soil and 5.39 in unburned soil. This rise in pH levels in the soil may be due to hydroxyl (OH^-) losses, the consumption of organic acids during complete oxidation of soil organic matter and the release of cations by ashes (Certini, 2005; Fisher and Binkley, 2000).

Prescribed burning reduces soil nutrient content by altering its spatial variability and distribution resulting in a variable response of exchangeable base cations (Brye *et al*., 2002). For instance, a study by Brye (2006) in a humid-subtropical grassland reported a decrease in exchangeable cations as a result of prescribed burns in the 0-10 cm soil layer in silty loam soils. Exchangeable calcium (Ca), magnesium (Mg) and potassium (K) decreased by 37%, 28% and 13%, respectively. The reduction in exchangeable cations was linked to gaseous losses by volatilization during combustion (Christensen, 1977) and the physical removal of nutrient-containing ash by wind (Brye *et al*., 2002). In contrast, work by Shakesby *et al*. (2015) in a Mediterranean shrubland, reported an increase in exchangeable cations as a result of prescribed burning in the uppermost 0-2 cm layer of loamy sand soils. Exchangeable Ca, Mg and K increased by 49%, 30% and 9%, respectively. This increase in exchangeable base cations was associated with the deposition of urine and dung by the grazing wildlife. Dung and urine have been reported to be potential sources of Ca, Mg and K (López-Mársico *et al*., 2015).

2.7 Effect of prescribed burning on soil physical properties

Prescribed burning clearly constitutes a disturbance on the environment and influences soil physical properties such as soil aggregation, bulk density, moisture content and soil water repellency (Hubbert *et al*., 2006; Alcañiz *et al*., 2018). Soil aggregation is usually severely affected by high intensity fires, while low intensity prescribed burning has often been thought to have negligible or neutral effects (Urbanek, 2013). As reported in many studies (Mataix-Solera *et al*., 2011), the response of soil aggregates to prescribed fires can be extremely varied. Research reveals a negligibly small effect of prescribed burning on the soil quality (Covington and Sackett, 1984; Stoof *et al*., 2012) and mechanisms of aggregate disruption during prescribed burning may explain the contradictory results (Albalasmeh *et al*., 2012).

In a study of slash and burn of agricultural systems in Nigeria, Are *et al*. (2009) reported a 44% decrease in mean weight diameter (MWD) at 0-10 cm depths and linked it to the combustion of soil organic matter (SOM) as a consequence of high severity fires (Mataix-

Solera *et al*., 2002). SOM serves as a principal binding agent in soils and its loss favours a strong disaggregation and a reduction in aggregate stability (Varela *et al*., 2010). In contrast, a study conducted by Thomaz *et al*. (2014) has reported no change in MWD after burning whereas, Thomaz (2017) reported a 10% increase in aggregate stability due to fires of medium to high severity in comparison to unburned soils. A possible explanation for this enhancement may be that the peak temperature did not last long enough to reduce SOM. Additionally, the topsoil was probably rich in larger aggregates (>2000-µm), which may have had a protective effect on SOM because much of it was located inside of aggregates isolated from the high surface temperatures (Thomaz, 2017).

Soil bulk density (BD) is a valuable soil parameter that reflects the soil's ability to function and serves as a good indicator of soil quality (Boerner *et al*., 2009). A study conducted by Hubbert *et al*. (2006) in a Mediterranean shrubland under loamy textured soils reported a 26% increase in BD as a result of prescribed burning in the 0-5 cm soil layer. In contrast, a study by Chief *et al*. (2012) in a semi-arid wooded shrubland under loamy textured soils, reported a 15% decrease in BD due to prescribed burning in the 0-2 cm soil layer. Kennard and Gholz (2001), mentioned that the destruction of soil aggregates and the loss of SOM due to burning contributes to the increase in soil BD. On the other hand, the decrease in BD may be attributed to increased belowground organic matter inputs as root biomass (Brye, 2006).

Moreover, a study conducted by Granged *et al*. (2011) in a Mediterranean heathland reported an increase in sand content and decreases in silt and clay content as a result of prescribed burning in the 0-2 cm soil layer of sandy loam soils. The sand content slightly increased by 26%, with decreases in silt and clay content by 15% and 45%, respectively. Giovannini and Lucchesi (1997), noted that high temperatures during fires lead to the aggregation of finer clay particles into larger silt and sand-sized particles, thereby increasing the average particle size. DeBano *et al*. (2005), argued that the most sensitive fraction to temperature effects is clay, hence the significant decrease. Additionally, the increase in the sand fraction may be attributed to the aluminium oxides and hydroxides released during clay decomposition, which may act as cementing agents in the formation of sand-sized particles (Terefe *et al*., 2008).

Soil moisture content is amongst the factors that influence the degree of post-fire water repellency (Huffman *et al*., 2001). However, prescribed fire can enhance, reduce or even induce water repellency in some shrub communities (Doerr and Shakesby, 2009). A study carried out by DeBano *et al.* (1979) in a Mediterranean chaparral brushland, reported an 80% decrease in moisture content post-fire, at a soil depth of 0-1 cm beneath the chaparral vegetation. Similarly, Granged *et al.* (2011), reported an 86% decrease in moisture content due to prescribed burning under loamy textured soils in the 0-5 cm soil layer. These significant reductions in moisture content can be ascribed to water evaporation in the near soil surface during fire and evapotranspiration, which may account for some of the moisture reduction at depth (Huffman *et al*., 2001).

Furthermore, a study by Vadilonga *et al.* (2008) in a semi-arid shrubland, reported an 87% increase in water repellency because of prescribed burning in the 0-25 cm soil layer of silty loam soils. Contrarily, a study conducted by Pierson *et al*. (2008) in a sagebrush ecosystem, reported a 60% decrease in water repellency due to prescribed burning in the 0-30 cm layer of sandy loam soils. DeBano *et al*. (1998), stated that the volatilization of organics that moved downward along a temperature gradient and re-condensed on mineral soil particles contribute to the increase in water repellency. On the other hand, the decrease in water repellency is because of the high temperatures during prescribed burning enough to destroy the water repellency of the soil (Granged *et al*., 2011).

REFERENCES

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D. and Scholes, R.J. 2010. Tree–grass co-existence in savanna: Interactions of rain and fire. *Journal of Theoretical Biology*. 267: 235-242.

Albalasmeh, A.A., Berli, M., Shafer, D.S. and Ghezzehei, T.A. 2012. Degradation of moist soil aggregates by rapid temperature rise under low intensity fire. *Plant and Soil*. 362: 335-344.

Alcañiz, M., Outeiro, L., Francos, M. and Úbeda, X. 2018. Effects of prescribed fires on soil properties: A review. *Science of the Total Environment*. 613-614: 944-957.

Alcañiz, M., Outeiro, L., Francos, M., Farguell, J. and Úbeda, X. 2016. Long-term dynamics of soil chemical properties after a prescribed fire in a Mediterranean forest. *Science of the Total Environment*. 572: 1329-1335.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*. 6: 1109-1122.

Archibald, S., Bond, W.J., Stock, W.D. and Fairbanks, D.H.K. 2005. Shaping the landscape: fire grazer interactions in an African savanna. *Ecological Applications*. 15: 96-109.

Are, K.S., Oluwatosin, G.A., Adeyolanu, O.D. and Oke, A.O. 2009. Slash and burn effect on soil quality of an alfisol: Soil physical properties. *Soil and Tillage Research*. 103: 4-10.

Augustine, D., Brewer, P., Blumenthal, D. and Derner, J. 2014. Prescribed fire, soil organic nitrogen dynamics and plant responses in a semiarid grassland. *Journal of Arid Environments*. 104: 59-66.

Bardgett, R.D. and Wardle, D.A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*. 84: 2258-2268.

Bigalke, R. C. and Willan, K., 1984. Effects of fire regime on fauna composition and dynamics. Ecological effects of fire in South African ecosystems: New York.

Boerner, R.E., Huang, J. and Hart, S.C. 2009. Impacts of Fire and Fire Surrogate treatments on forest soil properties: a meta-analytical approach. *Ecological Applications*. 19: 338-358.

Bond, W.J. and Archibald, S. 2003. Confronting complexity: Fire policy choices in South African savanna parks. *International Journal of Wildland Fire*. 12: 381-389.

Bond, W.J. and Van Wilgen, B.W. 1996. Fire and Plants. Chapman and Hall: London.

Brye, K.R. 2006. Soil physiochemical changes following 12 years of annual burning in a humid–subtropical tallgrass prairie: a hypothesis. *Acta Oecologica*. 30: 407-413.

Brye, K.R., Norman, J.M. and Gower, S.T. 2002. The fate of nutrients following three and six-year burn intervals in a restored tallgrass prairie in Wisconsin. *The American Midland Naturalist Journal.* 148: 28-42.

Castellnou, M., Kraus, D., Miralles, M., 2010. Prescribed Burning and Supression Fire Techniques. European Forest Institute: Europe.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia*. 143: 1-10.

Chief, K., Young, M.H. and Shafer, D.S. 2012. Changes in soil structure and hydraulic properties in a wooded- shrubland ecosystem following a prescribed fire. *Soil Science Society of America Journal.* 76: 1965-1977.

Christensen, N.L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. *Oecologia.* 31: 27-44.

Covington, W.W. and Sackett, S.S. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science*. 30: 183-192.

Crowley, G., Garnett, S. and Shephard, S. 2009. Impact of storm-burning on Melaleuca viridiflora invasion of grasslands and grassy woodlands on Cape York Peninsula, Australia. *Austral Ecology*. 34: 196-209.

Cumming, D.H. and Cumming, G.S. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia*. 134: 560-568.

D'Odorico, P., Laio, F. and Ridolfi, L. 2006. A probabilistic analysis of fire-induced tree–grass coexistence in savannas. *The American Naturalist*. 16: 79-87.

Datta, R. 2021. To extinguish or not to extinguish: The role of forest fire in nature and soil resilience. *Journal of King Saud University – Science*. 33: 1-7.

de Groot, W.J. and Wein, R.W. 2004. Effects of fire severity and season of burn on *Betula glandulosa* growth dynamics. *International Journal of Wildland Fire*. 13: 287-295.

DeBano, L.F., Eberlein, G.E. and Dunn, P.H. 1979. Effects of burning on chaparral soils. *Soil Science Society of America Journal.* 43: 504-509.

DeBano, L.F., Neary, D. and Ffolliot, P. 2005. Soil physical properties. Department of Agriculture, Forest Service: Washington, DC.

DellaSalla, D.A. 2018. Emergence of a New Climate and Human-Caused Wildfire Era for Western USA Forests. *Reference Module in Earth Systems and Environmental Sciences*.

Dew, L.A., Rozen-Rechels, D., Le Roux, E., Cromsigt, J.P.G.M. and Te Beest, M. 2017. Evaluating the efficacy of invasive plant control in response to ecological factors. *South African Journal of Botany*. 109: 203-213.

Doerr, S.H. and Shakesby, R.A. 2009. Soil water repellency: A key factor in post-fire erosion. Science Publishers: United States.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. and Parr, C.L. 2017. Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*. 1-11.

Fisher, R.F. and Binkley, D. 2000. 'Ecology and management of forest soils.' John Wiley: New York.

Flores, B.M., Staal, A., Jakovac, C.C., Hirota, M., Holmgren, M. and Oliveira, R.S. 2020. Soil erosion as a resilience drain in disturbed tropical forests. *Plant and Soil*. 450: 11-25.

Foxcroft, L.C., Pyšek, P., Richardson, D.M. and Genovesi, P. 2013. Plant invasions in protected areas: Patterns, problems and challenges. Springer Science & Business Media: Berlin.

Gebregergs, T., Tessema, Z.K., Solomon, N. and Birhane, E. 2019. Carbon sequestration and soil restoration potential of grazing lands under exclosure management in a semi-arid environment of northern Ethiopia. Department of Land Resources Management and Environmental Protection: Ethiopia.

Gill, A.M. 1975. Fire and the Australian flora: A review. *Australian Forestry*. 38: 4-25.

Giovannini, G. and Lucchesi, S. 1997. Modifications induced in soil physicochemical parameters by experimental fires at different intensities. *Soil Science*. 162: 479-486.

Goldhammer, J. and de Ronde C. 2004. Wildland fire management handbook for sub-Sahara Africa. AfriFireNet: Germany.

Govender, N., Trollope, W.S.W. and Van Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*. 43: 748-758.

Granged, A.J.P., Zavala, L.M., Jordán, A. and Bárcenas-Moreno, G. 2011. Post-fire evolution of soil properties and vegetation cover in a Mediterranean heathland after experimental burning: a 3-year study. *Geoderma.* 164: 85-94.

Hamman, S.T., Burke, I.C. and Knapp, E.E. 2008. Soil nutrients and microbial activity after early and late season prescribed burns in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*. 256: 367-374.

Hamman, S.T., Burke, I.C. and Stromberger, M.E. 2007. Relationships between microbial community structure and soil environmental conditions in a recently burned system. *Soil Biology and Biochemistry*. 39: 1703-1711.

Harrison, K.A. and Bardgett, R.D. 2008. Impacts of grazing and browsing by large herbivores on soils and soil biological properties. *The Ecology of Browsing and Grazing*. 0: 201-216.

Higgins, S., Bond, W.J. and Trollope, W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*. 88: 213-229.

Hobbs, N.T., Schimel, D.S., Owensby, C.E. and Ojima, D.S. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology*. 72: 1374-1382.

House, J., Archer, S., Breshears, D.D., Scholes, R.J. and NCEAS Tree-Grass Interaction Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*. 30: 1763-1777.

Hubbert, K.P., Preisler, H.K., Wohlgemuth, P.M., Graham, R.C. and Narog, M.G. 2006. Prescribed burning effects on soil physical properties and soil water repellency in a steep chaparral watershed, California, USA. *Geoderma*. 130: 284-298.

Huffman, E.L., MacDonald, L.H. and Stednick, J.D. 2001. Strength and persistence of fire-induces soil hydrophobicity under ponderosa and lodgepole pine. *Hydrological Processes.* 15: 2877-2892.

Jeltsch, F., Weber, G. and Grimm, V. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree–grass coexistence. *Plant Ecology*. 161: 161-171.

Johnson, D.W. and Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. *Forest Ecology and Management*. 140: 227-238.

Kamminga, E. 2001. Impact of the integrated forest fire management program on rural livelihoods in East Caprivi region. Namibia Finland Forestry Program, Directorate of Forestry, Ministry of Environment and Tourism: Namibia.

Kennard, D.K. and Gholz, H.L. 2001. Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. *Plant and Soil.* 234: 119-129.

Kral, K.C., Limb, R.F., Harmon, J.P. and Hovick, T.J. 2017. Arthropods and fire: previous research shaping future conservation. *Rangeland Ecology & Management*. 70: 589-598.

Landry, J.S. and Matthews, H.D. 2016. Non-deforestation fire vs. fossil fuel combustion: The source of CO2 emissions affects the global carbon cycle and climate responses. *Biogeosciences*. 13: 2137-2149.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A. and Bond, W.J. 2011. Deciphering the distribution of the savanna biome. *New Phytologist*. 191: 197-209.

Lipsett-Moore, G.J., Wolff, N.H. and Game, E.T. 2018. Emissions mitigation opportunities for savanna countries from early dry season fire management. *Nature Communications*. 9: 1-8.

López-Mársico, L., Altesor, A., Oyarzabal, M., Baldassini, P. and Paruelo, J.M. 2015. Grazing increases below-ground biomass and net primary production in a temperate grassland. *Plant and Soil*. 392: 155-162.

Mapiye, C., Mwale, M., Chikumba, N. and Chimonyo, M. 2008. Fire as a rangeland management tool in the savannas of Southern Africa: a review. *Tropical and Subtropical Agroecosystems*. 8: 115-124.

Mataix-Solera, J., Cerdà, A., Arcenegui, V., Jordán, A. and Zavala, L.M. 2011. Fire effects on soil aggregation: a review. *Earth-Science Reviews*. 109: 44-60.

Mataix-Solera, J., Gomez, I., Navarro-Pedreno, J., Guerrero, C. and Moral, R. 2002. Soil organic matter and aggregates affected by wildfire in a Pinus halepensis forest in a Mediterranean environment. *International Journal of Wildland Fire*. 11: 107-114.

McColl, J.G. and Grigal, D.F. 1977. Nutrient Changes Following a Forest Wildfire in Minnesota: Effects in Watersheds with Differing Soils. *Oikos*. 28: 105-112.

McNabb, D.H. and Cromack, Jr. K., 1990. Effects of prescribed fire on nutrients and soil productivity. Oregon State University Press: USA.

Morgan, P., Hardy, C.C., Swetnam, T.W., Rollins, M.G. and Long, D.G. 2001. Mapping fire regimes across time and space: Understanding coarse and fine-scale fire patterns. *International Journal of Wildland Fire*. 10: 329-342.

Muqaddas, B., Zhou, X., Lewis, T., Wild, C. and Chen, C. 2015. Long-term frequent prescribed fire decreases surface soil carbon and nitrogen pools in a wet sclerophyll forest of Southeast Queensland, Australia. *Science of the Total Environment*. 536: 39-47.

Neary, D.G., Klopatek, C.C., DeBano, L.F. and Folliott, P.F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management*. 122: 51-71.

Nieman, W.A., 2020. Integrated fire management plan: Majete Wildlife Reserve, Malawi. Technical report African Parks Limited: Johannesburg.

Nieman, W.A., Van Wilgen, B.W. and Leslie, A.J. 2021. A review of fire management practices in African savanna-protected areas. *Koedoe*. 63: 1655.

Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. University of Chicago Press: United States.

Pellegrini, A.F.A., Hobbie, S.E., Reich, P.B., Jumpponen, A., Jack Brookshire, E. N., Caprio, A.C., Coetsee, C. and Jackson, R.B. 2020. Repeated fire shifts carbon and nitrogen cycling by changing plant inputs and soil decomposition across ecosystems. *Ecological Monographs*. 90: 1409.

Pellegrini, A.F.A., Hoffmann, W.A. and Franco, A.C. 2014. Carbon accumulation and nitrogen pool recovery during transitions from savanna to forest in central Brazil. *Ecology*. 95: 342-352.

Pierson, F.B., Robichaud, P.R., Moffet, C.A., Spaeth, K.E., Williams, C.J., Hardegree, S.P. and Clark, P.E. 2008. Soil water repellency and infiltration in coarse-textured soils of burned and unburned sagebrush ecosystems. *Catena.* 74: 98-108.

Pressler, Y., Moore, J.C. and Cotrufo, M.F. 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos*. 128: 309-327.

Raison, R.J., Khanna, P.K. and Woods, P.V. 1985. Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian subalpine eucalypt forests. *Canadian Journal of Forest Research*. 15: 657-664.

Roberts, G., Wooster, M.J., Xu, W. and He, J. 2018. Fire Activity and Fuel Consumption Dynamics in Sub-Saharan Africa. *Remote Sensing*. 10: 1591.

Roques, K.G., O'connor, T.G. and Watkinson, A.R. 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.

Sankaran, M., Ratnam, J. and Hanan, N.P. 2004.Tree–grass coexistence in savannas revisited insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*. 7: 480-490.

Savadogo, P., Sawadogo, L. and 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.

Scharenbroch, B.C., Nix, B., Jacobs, K.A. and Bowles, M.L. 2012. Two decades of low-severity prescribed fire increases soil nutrient availability in Midwestern, USA oak (Quercus) forest. *Geoderma*. 183-184: 89-91.

Scholes, R.J. and Archer, S. 1997. Tree–grass interaction in savannas. *Annual Review of Ecology, Evolution, and Systematics*. 28: 517-544.

Shakesby, R.A., Bento, C.P.M., Ferreira, C.S.S., Ferreira, A.J.D., Stoof, C.R., Urbanek, E. and Walsh, R.P.D. 2015. Impacts of prescribed fire on soil loss and soil quality:

An assessment based on an experimentally burned catchment in central Portugal. *Catena.* 128: 278-293.

Sherman, L.A., Brye, K.R., Gill, D.E. and Koenig, K.A. 2005. Soil chemistry as affected by first-time prescribed burning of a grassland restoration on a coastal plain Ultisol. *Soil Science*. 170: 913-927.

Smit, I.P.J., Asner, G.P., Govender, N., Vaughn, N.R. and Van Wilgen, B.W. 2016. An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. *Journal of Applied Ecology*. 53: 1623-1633.

Stoof, C.R., Vervoort, R.W., Iwema, J., van den Elsen, E., Ferreira, A.J.D. and Ritsema, C.J. 2012. Hydrological response of a small catchment burned by experimental fire. *Hydrology and Earth System Sciences*. 16: 267-285.

Stott, P. 1991. Recent trends in the ecology and management of the world's savanna formations. *Progress in Physical Geography*. 15: 18-28.

Te Beest, M., Cromsigt, J.P.G.M., Ngobese, J. and Olff, H. 2012. Managing invasions at the cost of native habitat? An experimental test of the impact of fire on the invasion of Chromolaena odorata in a South African savanna. *Biological Invasions*. 14: 607-618.

Terefe, T., Mariscal-Sancho, I., Peregrina, F. and Espejo, R. 2008. Influence of heating on various properties of six Mediterranean soils. *Geoderma*. 143: 273-280.

Thomaz, L.E. 2017. Fire changes the larger aggregate size classes in slash-and-burn agricultural systems. *Soil &Tillage Research*. 165: 210-217.

Thomaz, L.E., Antoneli, V. and Doerr, S.H. 2014. Effects of fire on the physicochemical properties of soil in a slash-and-burn agriculture. *Catena*. 122: 209-215.

Thoresen, J., Vermeire, M.L., Venter, Z., Wolfaard, G., Krumins, J.A., Cramer, M. and Hawkins, H.J. 2021. Fire and herbivory shape soil arthropod communities through habitat heterogeneity and nutrient cycling in savannas. *Global Ecology and Conservation*. 25: 1413.

Trollope, L.A. and Trollope, L.A. 2010. Fire effects and management in African grasslands and savannas. *Range and Animal Sciences and Resources Management*. 2: 121-145.

Trollope, W.S.W. 1978. Fire behaviour - a preliminary study. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*. 13: 123-128.

Trollope, W.S.W. 1989. Veld burning as a management practice in livestock production. Department of Agriculture and Water Supply, Eastern Cape Region: South Africa.

Trollope, W.S.W. 1999. Veld burning. In: N.M., Tainton (ed). Veld and pasture management in South Africa. Shutter and Shooter: Pietermaritzburg.

Trollope, W.S.W. 2007. Fire – A key factor in the ecology and management of African grasslands and savannas. Tall Timbers Research Station: Florida.

Trollope, W.S.W. and Trollope, L.A. 1996. Fire in African savanna and other grazing ecosystems. Paper presented at the seminar on “Forest Fire and Global Change” held in Shushenkoye in the Russian Federation from the 4th-10th August 1996, 1-27.

Trollope, W.S.W., Trollope, L.A. and Harnett, D.C. 2002. Fire behaviour a key factor in the fire ecology of African grasslands and savannas. Millpress: Rotterdam.

Úbeda, X., Lorca, M., Outeiro, L., Bernia, S. and Castellnou, M. 2005. Effects of prescribed fire on soil quality in Mediterranean grassland. *International Journal of Wildland Fire*. 14: 379-384.

Urbanek, E. 2013. Why are aggregates destroyed in low intensity fire? *Plant and Soil*. 362: 33-36.

Vadilonga, T., Úbeda, X., Germann, P.F. and Lorca, M. 2008. Effects of prescribed burnings on soil hydrological parameters. *Hydrological Processes*. 22: 4249-4256.

Van de Vijver, C. A. D. M. 1999. Fire and life in Tarangire: Effects of burning and herbivory on an East African savanna system. Wageningen University: The Netherlands.

Van Der Werf, G.R., Randerson, J.T., Giglio, L., Van Leeuwen, T.T., Chen, Y., Rogers, B.M., Mu, M., van Marle, M.J.E., Morton, D.C., Collatz, G.J., Yokelson, R.J. and Kasibhatla, P.S. 2017. Global fire emissions estimates during 1997–2016. *Earth System Science Data*. 9: 697-720.

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., Bond, W.J., Prins, H.H.T. and Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*. 84: 337-350.

Van Wilgen, B.W., Andrea, M.O., Goldammer, J.G. and Lindeysay, J.A. 1997. Fire in Southern African savannas: ecological and atmospheric perspectives. Witwatersrand University Press: Johannesburg.

Van Wilgen, B.W., Govender, N., Smit, I.P.J. and Macfadyen, S. 2014. The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area. *Journal of Environmental Management*. 132: 358-368.

Van Wilgen, B.W., Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F. and Brockett, B.H. 2003. Fire as a driver of ecosystem variability. Island Press: Washington, DC.

Varela, M.E., Benito, E. and Keizer, J.J. 2010 Effects of wildfire and laboratory heating on soil aggregate stability of pine forests in Galicia: the role of lithology, soil organic matter content and water repellency. *Catena*. 83: 127-134.

Vermeire, M.L., Thoresen, J., Lennard, K., Vikram, S., Kirkman, K., Swemmer, A.M., Te Beest, M., Siebert, F., Gordijn, P., Venter, Z., Brunel, C., Wolfaard, G., Krumins, J.A., Cramer, M.D. and Hawkins, H.J. 2021. Fire and herbivory drive fungal and bacterial communities through distinct above- and belowground mechanisms. *Science of the Total Environment*. 785: 147189.

Waldrop, T.A. and Goodrick, S.L. 2012. Introduction to prescribed fires in Southern ecosystems. Department of Agriculture Forest Service, Southern Research Station: United States.

Walter, H. 1971. Ecology of Tropical and Subtropical Vegetation. Oliver and Boyd, Edinburgh: United Kingdom.

Wan, S., Hui, D. and Luo, Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications*. 11: 1349-1365.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. and Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. *Science*. 304: 1629-1633.

Whitecross, M.A., Archibald, S. and Witkowski, E.T.F. 2016. No two are the same: assessing variability in broad-leaved savanna tree phenology, with watering, from

2012 to 2014 at Nylsvley, South Africa. *South African Journal of Botany*. 105: 123-132.

CHAPTER 3

CHANGES IN SOIL CARBON AND NUTRIENTS FOLLOWING 7 YEARS OF FREQUENT BURNING AND HERBIVORE GRAZING IN A SAVANNA GRASSLAND

Abstract

Fire-herbivory feedback mechanisms driving soil nutrient dynamics in savannas remain poorly understood, yet soil nutrient availability influences the patterns of grassland productivity and tree species distribution. This study examined the effects of late burning and herbivore grazing on soil nutrients and carbon (C) dynamics in a savanna grassland at the Kruger National Park (KNP), South Africa. After 7 years of frequent burning and herbivore grazing, the average mean weight diameter decreased from 0.85 mm to 0.80 mm, revealing a low aggregate stability in the grassland soil. Aggregate stability is a key soil physical property that affects soil nutrients and C dynamics. Owing to the low aggregate stability at our site, there was a corresponding decrease in soil C and nitrogen (N) concentrations by 26% and 18%, respectively. This further explains the low levels of exchangeable calcium (Ca), magnesium (Mg) and potassium (K). As a result, the low levels of exchangeable base cations led to a minimal decrease (3%) in effective cation exchange capacity (ECEC). The slight decrease in exchangeable base cations was mirrored by an increase (32%) in exchangeable acidity in the burnt+grazed plots. Soil phosphorus (P) also increased by 16% probably due to ash addition which is a major contributor of P in the soil. Importantly, micronutrients: manganese (Mn) and copper (Cu) increased by 41% and 30%, respectively in the burnt+grazed plots because of increased soil acidity which enhances the solubility of these microelements. Altogether, the results reveal the variable response of soil C and nutrients to fire-herbivory interactions in a savanna grassland.

Keywords: Frequent burning, herbivore grazing, savanna grassland, soil nutrient, carbon

3.1 Introduction

Grassland soils serve as important reservoirs for C and N and are subject to ongoing alterations due to repeated burning and wildlife grazing (Sitters *et al*., 2020). Frequent burning and herbivore grazing affect plant C inputs and nutrients that are vital for productivity of savanna grasslands as they contribute to the maintenance of tree-grass coexistence (Wang *et al*., 2019; Pellegrini *et al*., 2020). Both these management practices control C storage and nutrient cycling in savanna ecosystems by altering the quantity and chemistry of plant inputs through changes in plant biomass and composition as well as via alteration of soil organic matter (SOM) decomposition (Bond-Lamberty *et al*., 2007). In addition to altering plant inputs and nutrient cycling in the soil, fire and herbivory can shift the rates of SOM decomposition by controlling the activities of soil microorganisms through several mechanisms (Wang *et al*., 2012; Vermeire *et al*., 2021). Fire and herbivory deplete resources such as leaf litter, detritus, and vegetation through combustion, compaction, and erosion (Pressler *et al*., 2019). This, in turn, reduces microbial biomass, abundance and nutrient loading. As a consequence, there is a shift in soil organic C storage affecting the availability of other crucial nutrients such as exchangeable base cations (Ca, Mg and K) and micronutrients (Zn, Mn, and Cu), which play a significant role in the functioning of savanna ecosystems (Santín *et al*., 2008; Pellegrini *et al*., 2018).

Knowledge of the mechanisms driving changes in C and soil nutrients is important for an in-depth understanding of the impact of frequent burning and herbivore grazing in savanna grasslands. Few studies have assessed the effects of frequent burning and herbivory grazing on soil C and nutrient dynamics in these ecosystems (Nghalipo *et al*., 2018). Therefore, this study was carried out with an objective to quantify the effect of late burning and herbivore grazing on soil nutrients in the topsoil of savanna grassland.

3.2 Materials and Methods

3.2.1 Description of the study area

The study site is located at the Kruger National Park (KNP, 24°23’35.17” S, 31°46’41.13” E), which is amongst the biggest game parks found in Africa and spreads over an area of about 19,485 km^2. It is situated between Mopani and Ehlanzeni districts in the eastern parts of Mpumalanga and Limpopo Provinces, South Africa as shown in Figure 3. The climate of the area is sub-tropical, and it is characterised by hot-wet summers and cool-dry winters with an average annual precipitation of 502 mm. The average temperature at the site ranges between 10°C and 27°C and the altitude ranges from 200 to 840 m above sea level (Foxcroft *et al*., 2008). The vegetation type is referred to as *Sclerocarya birrea-Acacia nigrescens* tree savanna (Gertenbach, 1983). The dominant grass species in the area include: *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, *Urochloa mosambicensis* and *Themeda triandra* (Knapp *et al*., 2012; van Oudtshoorn, 2012). These grasses mainly grow well during the summer season (i.e., between November and April) and tend to be dormant during the winter season (i.e., between May and October) (Venter *et al*., 2003).

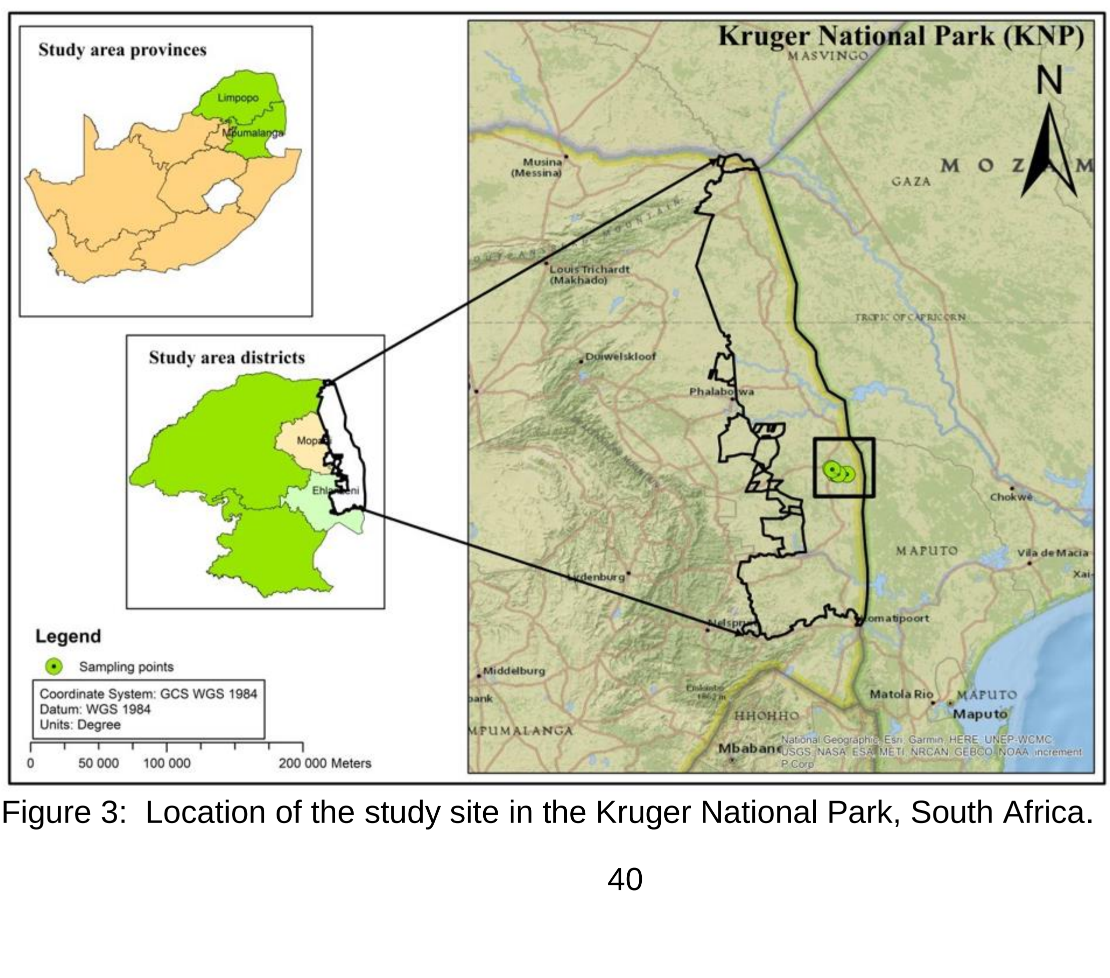

Figure 3: Location of the study site in the Kruger National Park, South Africa.

3.2.2 Experimental layout and soil sampling

This study characterised changes in soil C and nutrients in a landscape level burn-experiment at KNP established to investigate how fire-herbivory interactions drive the formation of savanna grazing lawns (Donaldson *et al*., 2017). The burn-experiment comprised ten 500 × 500 m (25-ha) plots whereby, starting in 2013, five plots were frequently burnt and grazed by wildlife leaving five plots unburnt and ungrazed (control). Three 10 × 10 m sub-plots were then randomly laid out in each 25-ha plot for soil sampling. After 7 years of frequent (late) burning and herbivore grazing, we collected five samples at 0-10 cm soil depth in each sub-plot using a 7-cm diameter punch corer following a radial basis sampling strategy. The soil cores were pooled to give one composite bulk sample per sub-plot. The collected samples were extruded into polyethene sampling bags, sealed and stored in crates. Thereafter, the soil samples were taken to the University of Limpopo Soil Science laboratory and transferred into aluminium trays for air-drying at room temperature (25°C). Post air drying, a 2 mm sieve was used to sieve the soil samples as preparation for soil chemical and physical analyses.

3.2.3 Soil chemical and physical analyses

Total soil C and N concentrations were analysed using a LECO CNS-2000 analyser by automated Dumas dry matter combustion (LECO Corporation, St. Joseph, MI). Exchangeable base cations: Ca, Mg and exchangeable acidity were first determined by extraction in 1 M KCl, while P and K were determined by extraction in Ambic 2-extract containing 0.25 M NH_4HCO_3, with detection by atomic absorption spectrometry (using an air-acetylene flame) on a 5 mL aliquot of the filtrate after dilution with 20 mL deionised water. Micronutrients: Mn, Cu and Zn were then extracted and determined by atomic absorption on the remaining undiluted filtrate (Manson and Roberts, 2000). Soil pH was measured using a Hanna Edge meter following the electrometric method by Rhoades (1982). It was determined by adding a 25 cm^3 KCl solution. Effective cation exchange capacity (ECEC) was calculated as the sum of extractable Mg, Ca, K and exchangeable acidity. Mean weight diameter (MWD) was determined using the wet sieving method by Elliott (1986) and explained in detail in Chapter 4, section 4.2.3. Particle size distribution was determined using the hydrometer method (Bouyoucos, 1962).

3.2.4 Statistical analysis

The dataset of measured soil properties was explored and analysed using the protocol described by Zuur *et al*. (2010). Basic statistics of the soil property data including minimum, maximum, median, average, standard error, standard deviation, and coefficient of variation were computed in Microsoft Excel following Webster (2001). Bar graphs including mean error bars were plotted using Sigma Plot software version 14.0 (Systat Software Inc., California, USA) to visually assess the changes in soil nutrients across burnt+grazed grassland soils in comparison to the control. An unpaired T-test was run using GraphPad Prism 9.0 (GraphPad Software, California, USA) to compare the means of the soil nutrients and carbon content between the burnt+grazed and unburnt grassland soils. Pearson's correlation coefficient (r) was used to test the strength of the correlation between the soil nutrients (Total C and N, Ca, Mg, K, Mn, Cu, Zn) and related inherent properties such as clay content, soil aggregate stability and soil pH. A correlation heat map was generated using GraphPad Prism 9.0 to visualize the strength of relationships between soil nutrients and related soil properties.

3.3 Results

3.3.1 General site characteristics of the savanna grassland

The soils at the sampled savanna grassland site are underlain by a basalt geology and are characterised by a dark reddish-brown colour (5YR 3/2). The textural class of the soil is a loamy sand with the average sand content ranging between 76% and 78%, silt content ranging between 7% and 9% and a similar clay content of 15% in the burnt+grazed plots and control plots. The surface soil A horizon (0-10 cm) of both the control and burnt+grazed plots was found to be moderately acidic (pH of 5.46 and 5.25, respectively). On average, the mean weight diameter (MWD), which is a proxy indicator for aggregate stability ranged between 0.80 mm and 0.85 mm in the burnt+grazed plots and control plots, respectively (Table 2). The area/site is regarded to as a *Sclerocarya birrea-Acacia nigrescens* savanna dominated by the grass species highlighted in Table 2.

Table 2: Descriptive site characteristics of the surface soil (0-10 cm) in the control and burnt+grazed grassland soils at the Satara land system of the Kruger National Park, South Africa. Values are means ± standard errors.

	Treatment	
Variable	**Control**	**Burnt+grazed**
Altitude (m above sea level)	216-265	229-264
Soil depth (cm)	0-10	0-10
Parent material	Basalt	Basalt
Dry soil colour	5YR 3/2	5YR 2.5/2
Soil pH (KCl)	5.46 ± 0.15	5.25 ± 0.05
Sand (%)	78.00 ± 2.71	76.00 ± 3.06
Silt (%)	7.33 ± 1.94	9.33 ± 2.67
Clay (%)	14.67 ± 1.33	14.67 ± 0.82
Textural class	Loamy sand	Loamy sand
Mean weight diameter (MWD)	0.85 ± 0.08	0.80 ± 0.03
Dominant species	Trees: *Sclerocarya birrea-Acacia nigrescens* Grasses: *Bothriochloa radicans, Digitaria eriantha, Panicum coloratum, Themeda triandra* and *Urochloa mosambicensis* Animals: Impala, Rhinoceros, Wildebeest, Zebra	

3.3.2 Impact of frequent burning and grazing on total C, N and C: N ratio

Our T-test analysis (Appendix 1) revealed that there was no significant difference at P< 0.05 between the means of total C, N and C/N ratio following frequent burning and herbivore grazing. However, these land management practices led to a decline in some of these nutrients. As observed on Figure 4 (a-c), total C, total N and C/N ratio in the 25-ha plot decreased after frequent burning and herbivore grazing. Total C content decreased from 30.12 g kg^{-1} in the control plots to 22.44 g kg^{-1} in the burnt+grazed plots. Similarly, total N content decreased from 1.60 g kg^{-1} in the control to 1.32 g kg^{-1} in the burnt+grazed plots. On average, frequent late burning and herbivore grazing decreased total C and N content by 26% and 18%, respectively. Soil C/N ratio, decreased from 19 in the control to 18 in the burnt+grazed plots.

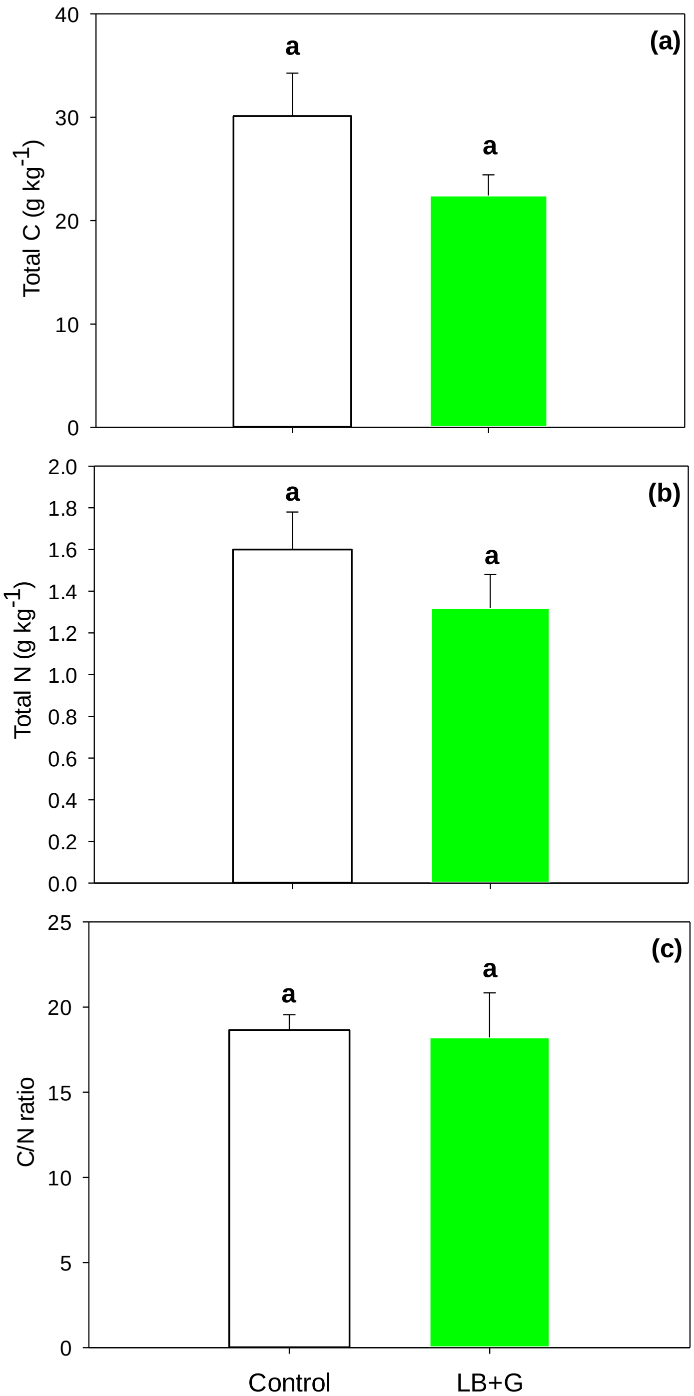

Figure 4: Bar graphs showing changes in soil carbon (C), nitrogen (N) and carbon to nitrogen (C:N) ratio (a-c), at 0-10 cm soil depth after 7 years of late burning and herbivore

grazing (green bars) compared to the control (white bars) in a savanna grassland at Kruger National Park, South Africa. Means and standard errors are shown for n = 5 per treatment plot.

3.3.3 Effect of frequent burning and grazing on soil P and exchangeable cations

In the 25-ha grassland plots subjected to frequent burning and herbivore grazing, soil phosphorus (P) [Figure 5 (a)] increased by 16% from 29.20 mg kg^{-1} in the control to 33.80 mg kg^{-1} in the burnt+grazed plots. Exchangeable acidity [Figure 5 (e)] was greater under the burnt+grazed plots compared to the control with an increase of 32% from 0.04 cmol kg^{-1} to 0.06 cmol kg^{-1}. Exchangeable Mg [Figure 5 (c)] and K [Figure 5 (d)] were also higher in the burnt+grazed plots compared to the control (8% and 4%, respectively). Exchangeable Mg increased from 809.2 mg kg^{-1} to 874.8 mg kg^{-1} whereas, exchangeable K increased from 530.6 mg kg-1 to 549.6 mg kg^{-1}. In contrast, exchangeable Ca [Figure 5 (b)] was lower in the burnt+grazed plots (3926.6 mg kg^{-1}) compared to the control (4196.2 mg kg^{-1}) which corresponds to a 6% decrease. However, ECEC [Figure 5 (f)] decreased by 3% from 29.00 cmol kg^{-1} in the control to 28.26 cmol kg^{-1} in the burnt+grazed plots. Although, the T-test analysis (Appendix 1) revealed that there was no significant difference ($P< 0.05$) in the means of the above soil nutrients, the changes brought about by frequent burning and herbivore grazing were considered.

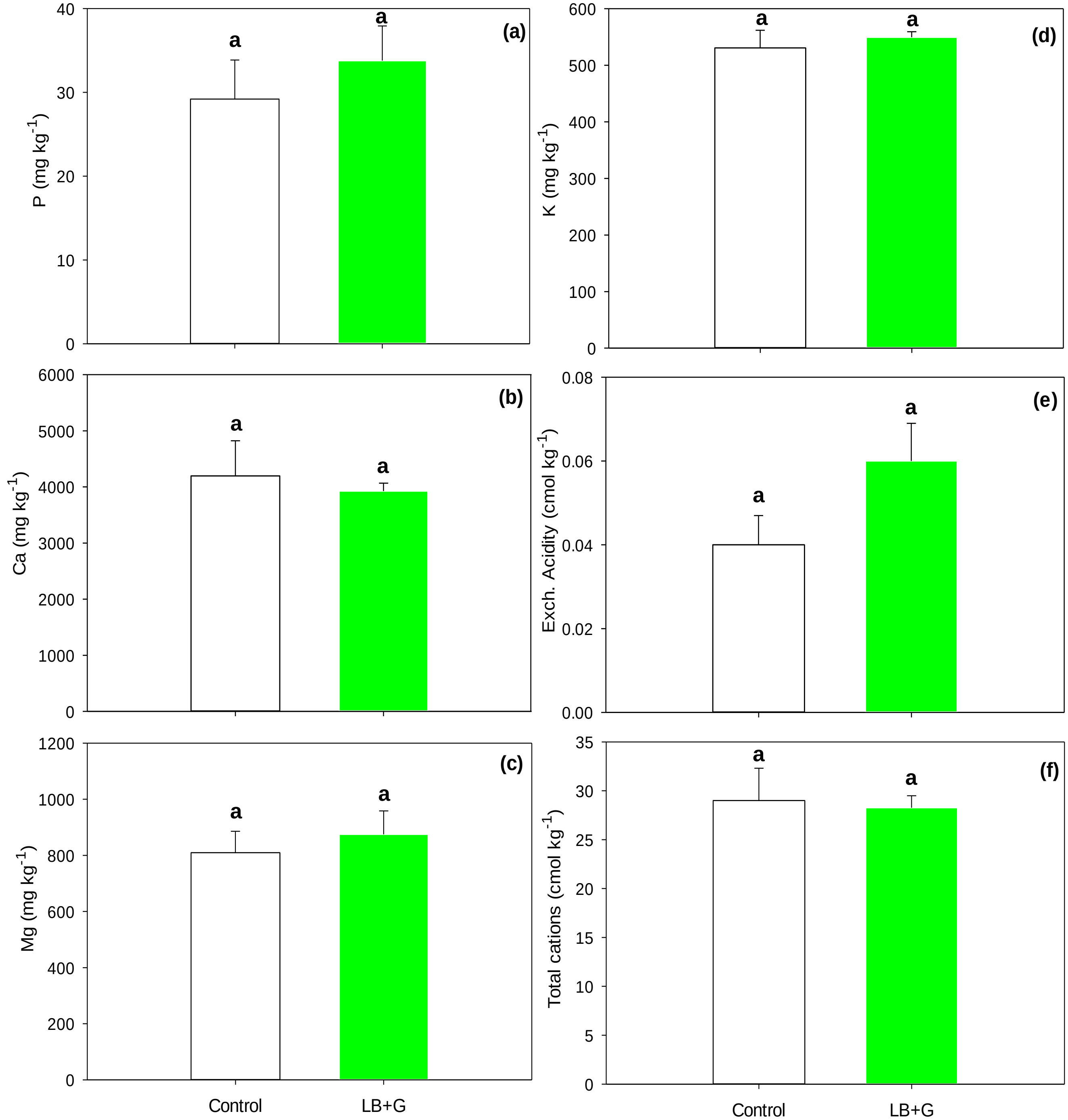

Figure 5: Bar graphs showing changes in soil phosphorus (P), exchangeable acidity, exchangeable base cations and effective cation exchange capacity (a-f) at 0-10 cm soil depth after 7 years of late burning and herbivore grazing (green bars) compared to the control (white bars) in a savanna grassland at Kruger National Park, South Africa. Means and standard errors are shown for n = 5 per treatment plot.

3.3.4 Effect of frequent burning and grazing on micronutrients

Under the frequently burnt and grazed 25-ha grassland, there was an increase in Mn [Figure 6 (b)] and Cu [Figure 6 (c)] in the burnt+grazed plots in relation to the control (41% and 30% respectively). Manganese increased from 8.40 mg kg^{-1} to 11.80 mg kg^{-1} while copper increased from 10.02 mg kg^{-1} to 13.06 mg kg^{-1}. On the other hand, there was a 5% decrease in Zn [Figure 6 (a)] from 1.94 mg kg^{-1} in the control to 1.84 mg kg^{-1} in the burnt+grazed plots. As observed from the T-test analysis (Appendix 1), there were no significant differences between the means of the micronutrients. However, the changes brought by frequent burning and herbivore grazing have an influence on the savanna grassland soils.

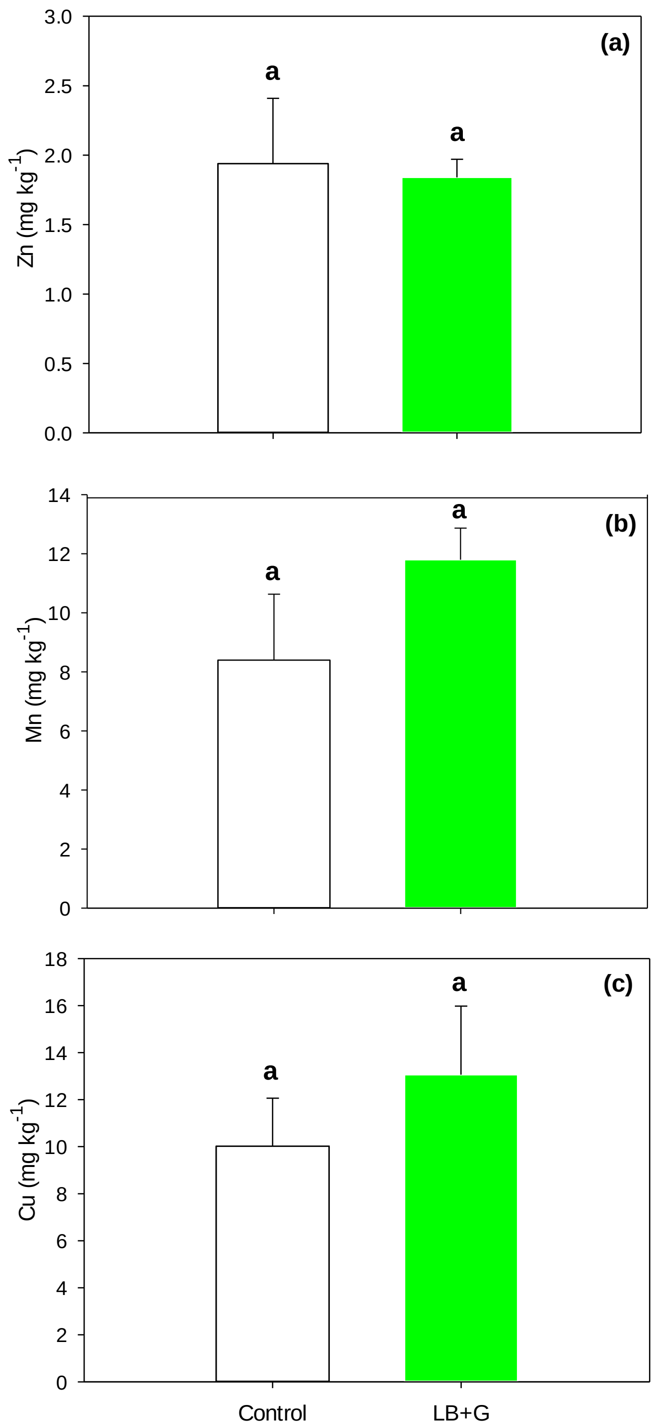

Figure 6: Bar graphs showing changes in soil micronutrients: manganese (Mn), copper (Cu) and zinc (Zn) (a-c), at 0-10 cm soil depth after 7 years of late burning and herbivore grazing (green bars) compared to the control (white bars) in a savanna grassland at Kruger National Park, South Africa. Means and standard errors are shown for n = 5 per treatment plot.

3.3.5 Correlation between soil properties determined in the control and burnt+grazed savanna grasslands

Our correlation analysis revealed that in the control [Figure 7(a)], total C was positively correlated to zinc (r= 0.70; P <0.05) and negatively correlated to mean weight diameter (MWD) (r= -0.96) and exchangeable acidity (r= -0.72). Total N was significantly positively correlated to total C (r=0.92) but negatively correlated to MWD (r=-0.87) and exchangeable acidity (r=-0.75). Exchangeable acidity (Exch.Ac) was negatively correlated to calcium (Ca) (r= -0.76). Effective cation exchange capacity (ECEC) was also negatively correlated to Ca (r= -0.98), phosphorus (P) (r= -0.70) and exchangeable acidity (r= -0.64). Soil pH was strongly negatively correlated to P (r= -0.90) and potassium (K) (r= -0.72) while positively correlated to Ca (r=0.64) and ECEC (r=0.67). Moreover, zinc (Zn) was positively correlated to P (r=0.82) and negatively correlated to pH (r= -0.77). Manganese (Mn) was positively correlated to P (r=0.78) and K (r=0.71) whereas negatively correlated with magnesium (Mg) (r= -0.88) and pH (r= -0.67). Copper (Cu) was negatively correlated with Ca (r= -0.98), ECEC (r= -0.95) and pH (r= -0.72) while positively correlated to P (r=0.64) and exchangeable acidity (r= 0.75). Lastly, MWD was positively correlated to exchangeable acidity (r= 0.72) and negatively correlated to ECEC (r= -0.68) and Ca (r= -0.68).

The correlation analysis also indicated positive and negative correlations in the burnt+grazed savanna grassland [Figure 7(b)], between total C and Mg (r= 0.64; P <0.05), Ca (r= 0.77), ECEC (r= 0.80), Mn (r= 0.95), P (r= -0.73) and Cu (r= -0.79). Meanwhile, total N was positively correlated to P (r= 0.72), Cu (r= 0.84) and clay content (r= 0.83) but negatively correlated to Mg (r= -0.80), Mn (r= -0.64), MWD (r= -0.63) and total C (r= -0.64). Calcium was positively correlated to K (r= 0.85) and negatively correlated to P (r= -0.66). Furthermore, ECEC was negatively correlated with P (r= -0.90) while positively correlated with Ca (r= 0.89), Mg (r= 0.87) and K (r= 0.60). Soil pH was negatively correlated with Exch.Ac (r= -0.70). It was also revealed that Zn was negatively correlated with pH (r= -0.87) and K (r= -0.79), while Mn was also negatively correlated with pH (r= -0.75). Copper was positively correlated to P (r= 0.97) and negatively correlated to Mg (r= -0.91), ECEC (r= -0.82) and Mn (r= -0.76). Finally, MWD was positively correlated to Mg (r= 0.63).

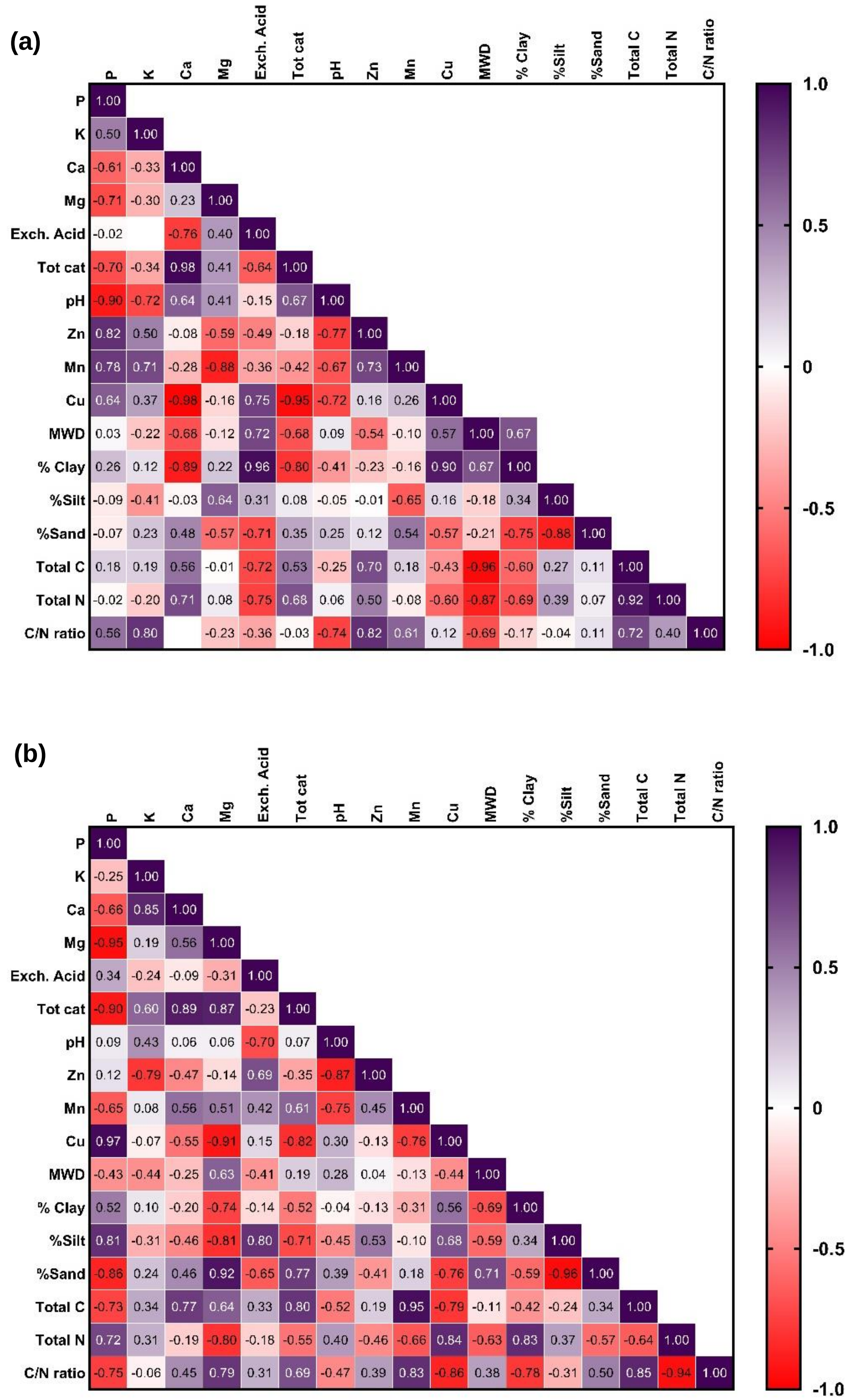

Figure 7: Correlation matrix showing Pearson's correlation coefficients between selected soil properties across the control (a) and burnt+grazed (b) grassland soils.

P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; Exch.Acid, exchangeable acidity; Tot cat, total cations/ effective cation exchange capacity; pH; Zn, zinc; Mn, manganese; Cu, copper; MWD, mean weight diameter; %Clay, clay content; %Silt, silt content; %Sand, sand content; Total C, total carbon content; Total N, total nitrogen content; C/N ratio, carbon to nitrogen ratio

3.4 Discussion

3.4.1 Fire-herbivory feedback mechanisms driving soil C and N depletion

The results obtained in this study revealed that frequent burning and herbivore grazing decreased soil C and N. Specifically, total C and N were 26% and 18% lower in the burnt+grazed plots compared to the control. The depletion of C and N in the burnt+grazed plots were caused by the combustion of organic matter and its losses through volatilization during repeated burning and the removal of tree and grass biomass by herbivore grazing (Fynn *et al*., 2003; Pellegrini *et al*., 2014). According to Rumpel *et al*. (2006), changes in SOM quantity and quality as a result of frequent burning and grazing depends not only on the removal of aboveground biomass, losses by combustion and volatilization, but also on post-fire inherent soil properties.

Several mechanisms that may be linked to inherent soil properties further explain the depletion of C and N concentrations in the burnt+grazed grassland soils. First, the average soil pH at our site was 5.25 after frequent burning and grazing, which is categorized as being moderately acidic. Soil pH is broadly recognised as a dominant factor that influences numerous soil biological, chemical, and physical properties and processes such as soil nutrient bioavailability, vegetation community structure and soil microbial activities (i.e., microbial turnover of OM) (Kemmitt *et al*., 2006; Neina, 2019). Under acidic soils, the activities of the soil micro-organisms are generally reduced, and this has the potential to inhibit biological N fixation and nitrification processes which constitute to the depletion of C and N (Bolan *et al*., 2003, Zebarth *et al*., 2015). Secondly, the soils are characterised by coarse texture with up to 87% of sand and clay content of <15%. As such, there is lack of physical protection of organic matter by the clay particles which accounts for greater loss of soil C and N (Feller and Beare, 1997). This is further explained by the positive correlation between total N and clay content (r= 0.83) as observed on Figure 7 (b). Lastly, the MWD at the site was 0.80 mm, which is classified as being unstable (Appendix 2) by Le Bissonnais (1996) suggesting that there is disaggregation of soil particles due to repeated burning and grazing. Fire destroys the proportion of soil aggregates by combustion of organic matter (Mataix-Solera *et al*., 2002) and herbivores graze and trample the soil thus affecting the organization of aggregates leading to a decrease in aggregate stability (Milgo, 2015). Soil disaggregation caused by livestock trampling and the exposure of SOM as aggregates are destroyed during combustion leads to the rapid loss of C and N via soil erosion (González-Pérez *et al*., 2004). Certainly, the negative relationship between total C and MWD (r= -0.63) [Figure 7(b)] supports this.

3.4.2 Potential mechanisms driving the shifts in soil P and exchangeable cations following fire-herbivory interactions

Our results further showed that frequent burning and herbivore grazing leads to an increase in soil P and a variable response in exchangeable cations. Soil P increased by 15% in burnt+grazed plots compared to the control. Exchangeable Ca decreased by 6% while exchangeable acidity, exchangeable Mg and K increased by 32%, 8% and 4%, respectively. Total cations (ECEC) decreased slightly by 3% under the burnt+grazed plots compared to the control.

A number of reasons are likely to explain the different responses of these soil chemical properties to frequent burning and herbivore grazing. The increase in soil P content is ascribed to mineralization of organic forms of this element and incorporation of ash into the soil (Fonseca *et al*., 2017). According to Ekinci (2006) and Pereira *et al*. (2012), ash is a major contributor to P increase in the topsoil after prescribed fires. The solubility of P increases markedly due to the combined effects of soil heating and ash addition into the soil (Raison *et al*. 1993; Guinto *et al*., 2001).

Furthermore, soil acidity is a potential mechanism driving the low levels of exchangeable base cations and an increase in exchangeable acidic cation (Al^{3+}) at our site. Berthrong *et al*. (2009) reported that under acidic soils, exchangeable base cations such as Ca, Mg and K are weakly bound to the soil. This is probably due to a decrease in cation exchange capacity (CEC) owing to the depletion of soil C at our site caused by fire and grazing. When CEC is lowered, the capacity of soils to store cations is reduced, suggesting that new inputs of cations in the soil might not always increase them (Jobbagy and Jackson,

2003) given our sandy acidic soils. This is further justified by the unstable soil aggregates (Appendix 2) at our site caused by frequent burning and grazing which may have reduced the retention of the base cations. Rheinheimer *et al*. (2003) showed that slight increases in Mg and K may also be related to the release of oxides from the ashes after burning while Raison *et al*. (1985) explains that the decrease in Ca may be due to leaching and erosion. Nonetheless, the increase in exchangeable acidity is most probably driven by the acidic soils at our site. Increased soil acidity leads to an increase in Al^{3+} ions in the soil which explains the remarkable shift in exchangeable acidity (Kemmitt *et al*., 2006). Taken together, the low levels of the exchangeable base cations in the soil subsequently decreased the overall ECEC (total cations).

3.4.3 Fire-herbivory interactions effect on soil micronutrients

The results of the study further revealed that there was an increase in Mn and Cu and a slight decrease in Zn following frequent burning and grazing. Manganese and copper increased by 41% and 30%, respectively in the burnt+grazed plots compared to the control. Zinc decreased by 5% in the burnt+grazed plots compared to the control. The great upsurge in micronutrients in the burnt+grazed grassland soils may be due to a number of reasons. The low pH at our site is probably driving this increase in Mn and Cu in the soil. Previous research studies have shown that soil acidification enhances the solubility and mobilization of these microelements in the soil (Bolan *et al*., 2003; Neina, 2019). Furthermore, Rau *et al*. (2008) has shown that the deposition of ash into the soil surface after frequent burning incorporates Mn and Cu into the soil. Stankov Jovanovic *et al*. (2011) added that the accrual of these microelements in the soil is caused by the enrichment of Cu and Mn oxides emanating from the ash material. These oxides are both toxic to soil and plants and their toxicity is highly favoured under acidic soils (Watmough *et al*., 2007). Research has shown that Cu oxides affect the soil by reducing their degree of nitrification, denitrification, and respiration. They tend to inhibit the production of vital nitrates and their effect become severe mostly in coarse-textured soils (Fischer *et al*., 2021). Additionally, Mn toxicity causes biochemical disorders such as oxidative stress and a decrease in biomass and photosynthetic activity (Millaleo *et al*., 2010). As a result, the reduction in plant biomass and shifts in plant communities driven by the bioavailability of Mn and Cu may in turn affect the quantity and composition of C inputs into the soil (Li *et al*., 2021). On the other hand, the decrease in Zn is attributable to its loss to the atmosphere via volatilization and ash convection by prescribed fires. Zinc is highly mobile in the soil and can be easily redistributed within a burned area either by convection or surface wind transport (Neary *et al*., 1999).

3.5 Conclusion

The findings from this study revealed that the management of tree-grass co-existence in savanna grasslands via frequent burning and herbivore grazing alters C and nutrient cycling. Specifically, this study showed that 7-years of frequent burning combined with grazing by wildlife at KNP led to a decline in soil C and N concentrations, a variable response in exchangeable base cations (Ca, Mg, K) and an increase in soil P, exchangeable acidity and micronutrients (Mn, Cu). This is because continuous burning and wildlife grazing modifies plant C inputs and this affects the storage of SOM. Reduced SOM in turn, affects the storage of other soil nutrients critical for the productivity of grasses and distribution of tree species in savanna grasslands.

REFERENCES

Berthrong, S.T. Jobbágy, E.G. and Jackson, R.B. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon and nitrogen with aforestation. *Ecological Applications*. 19: 2228-2241.

Bolan, N.S., Adriano, D.C. and Curtin, D. 2003. Soil acidification and liming interactions with nutrient and heavy metal transformation and bioavailability. *Advances in Agronomy*. 78: 5-272.

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E. and Gower, S.T. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature*. 450: 89-92.

Bouyoucos, G.J. 1962. Hydrometer Method improved for making particle size analysis of soils. *Agronomical Journal*. 54: 464-465.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. and Parr, C.L. 2017. Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*. 55: 225-235.

Elliott, E.T. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *Soil Science Society of America Journal*. 50: 627-633.

Ekinci, H. 2006. Effect of forest fire on some physical, chemical and biological properties of soil in Çanakkale, Turkey. *International Journal of Agriculture and Biology*. 8: 102-106.

Feller, C. and Beare, M.H. 1997. Physical control of soil organic matter dynamics in the tropics. *Geoderma*. 79: 69-116.

Fischer, J., Evlanova, A., Philippe, A. and Filser, J. 2021. Soil properties can evoke toxicity of copper oxide nanoparticles towards springtails at low concentrations. *Environmental Pollution*. 270: 116084.

Fonseca, F., de Figueiredo, T., Nogueira, C. and Queirós, A. 2017. Effect of prescribed fire on soil properties and soil erosion in a Mediterranean mountain area. *Geoderma*. 307: 172-180.

Foxcroft, L.C., Richardson, D.M. and Wilson, J.R. 2008. “Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa". *Environmental Management*. 41:32-51.

Fynn, R.W.S., Haynes, R.J. and O'Connor, T.G. 2003. Burning causes long-term changes in soil organic matter content of a South African grassland. *Soil Biology and Biochemistry*. 35: 677-687.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*. 26: 9-121.

González-Pérez, J.A., González-Vila, F.J., Almendros, G. and Knicker, H. 2004. The effect of fire on soil organic matter—a review. *Environment International*. 30: 855-870.

Guinto, D.F., Xu, Z.H., House, A.P.N. and Saffigna, P.G. 2001. Soil chemical properties and forest floor nutrients under repeated prescribed burning in eucalypt forests of south-east Queensland, Australia. *New Zealand Journal of Forestry Science*. 31: 170-187.

Jobbágy, E.G. and Jackson, R.B. 2003. Patterns and mechanisms of soil acidification in the conversion of grasslands to forests. *Biogeochemistry*. 64: 205-229.

Kemmitt, S.J., Wright, D., Goulding, K.W. and Jones, D.L. 2006. pH regulation of carbon and nitrogen dynamics in two agricultural soils. *Soil Biology and Biochemistry*. 38: 898-911.

Knapp, A.K., Hoover, D.L., Blair, J.M., Buis, G., Burkepile, D.E., Chamberlain, A. and Zinn, A. 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. *Journal of Plant Ecology*. 5: 357-365.

Le Bissonnais, Y. 1996. Aggregate stability and assessment of soil erodibility: I. Theory and methodology. *European Journal of Soil Science*. 47: 425-437.

Li, H., Santos, F., Butler, K. and Herndon, E. 2021. A critical review on the multiple roles of manganese in stabilizing and destabilizing soil organic matter. *Environmental science & technology*. 55: 12136-12152.

Manson A.D and Roberts V.G. 2000. Analytical methods used by the soil fertility and analytical services section. KwaZulu-Natal Department of Agriculture and Environmental Affairs. Government paper: KwaZulu-Natal.

Mataix-Solera, J., Gomez, I., Navarro-Pedreno, J., Guerrero, C. and Moral, R. 2002. Soil organic matter and aggregates affected by wildfire in a Pinus halepensis forest in a Mediterranean environment. *International Journal of Wildland Fire*. 11: 107-114.

Millaleo, R., Reyes-Díaz, M., Ivanov, A.G., Mora, M.L. and Alberdi, M. 2010. Manganese as essential and toxic element for plants: transport, accumulation and resistance mechanisms. *Journal of Soil Science and Plant Nutrition*. 10: 470-481.

Mligo, C. 2015. The impact of livestock grazing on soil characteristics in Mount Kilimanjaro, Tanzania. *Journal of Geoscience and Environment Protection*. 3: 24-37.

Neary, D.G., Klopatek, C.C., DeBano, L.F. and Folliott, P.F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management*. 122: 51-71.

Neina, D. 2019. The role of soil pH in plant nutrition and soil remediation. *Applied and Environmental Soil Science*. 2019: 1-7.

Nghalipo, E., Joubert, D., Throop, H. and Groengroeft, A. 2018. The effect of fire history on soil nutrients and soil organic carbon in a semi-arid savanna woodland, central Namibia. *African Journal of Range & Forage Science*. 36: 9-16.

Pellegrini, A.F., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzik, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R., Randerson, J.T. and Jackson, R.B. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature*. 553: 194-198.

Pellegrini, A.F., Hoffmann, W.A. and Franco, A.C. 2014. Carbon accumulation and nitrogen pool recovery during transitions from savanna to forest in central Brazil. *Ecology*. 95: 342-352.

Pellegrini, A.F.A., Hobbie, S.E., Reich, P.B., Jumpponen, A., Jack Brookshire, E. N., Caprio, A.C., Coetsee, C. and Jackson, R.B. 2020. Repeated fire shifts carbon and nitrogen cycling by changing plant inputs and soil decomposition across ecosystems. *Ecological Monographs*. 0:1-20.

Pereira, P., Úbeda, X. and Martin, D. 2012. Fire severity on ash chemical composition and wàter-extractable elements. *Geoderma*. 191: 105-114.

Pressler, Y., Moore, J.C. and Cotrufo, M.F. 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos*. 128: 309-327.

Raison, R.J., Khanna, P.K. and Woods P.V. 1985. Transfer of elements to the atmosphere during low-intensity prescribed fires in 3 Australian subalpine eucalypt forests. *Canadian Journal of Forest Research*. 15: 657-664.

Raison, R.J., O'connell, A.M., Khanna, P.K. and Keith, H. 1993. Effects of repeated fires on nitrogen and phosphorus budgets and cycling processes in forest ecosystems. Commission of the European Communities: Brussels.

Rau, B.M., Chambers, J.C., Blank, R.R. and Johnson, D.W. 2008. Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. *Rangeland Ecology & Management*. 61: 169-181.

Rheinheimer, D.D.S., Santos, J.C.P., Fernandes, V.B.B., Mafra, Á.L. and Almeida, J.A. 2003. Changes in the chemical attributes of soil under native field submitted to burning. *Rural Science*. 33: 49-55.

Rhoades, J.D. 1982. In Methods of Soil Analysis, Part 2. Second Edition (A.L. Page, R.H. Miller and D.R. Keeney, Eds.). American Society of Agronomy: United States.

Rumpel, C., Chaplot, V., Planchon, O., Bernadou, J., Valentin, C. and Mariotti, A. 2006. Preferential erosion of black carbon on steep slopes with slash and burn agriculture. *Catena*. 65: 30-40.

Santín, C., Knicker, H., Fernández, S., Menéndez-Duarte, R. and Álvarez, M.Á. 2008. Wildfires influence on soil organic matter in an Atlantic mountainous region (NW of Spain). *Catena*. 74: 286-295.

Sitters, J., Wubs, E.J., Bakker, E.S., Crowther, T.W., Adler, P.B., Bagchi, S., Bakker, J.D., Biederman, L., Borer, E.T., Cleland, E.E., Eisenhauer, N., Firn, J., Gherardi, L., Hagenah, N., Hautier, Y., Hobbie, S.E., Knops, J.M.H., MacDougall, A.S., McCulley, R.L., Moore, J.L., Mortensen, B., Peri, P.L., Prober, S.M., Riggs, C., Risch, A.C., Schütz, M., Seabloom, E.W., Siebert, J., Stevens, C.J. and (Ciska) Veen, G.F. 2020. Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Global Change Biology*. 26: 2060-2071.

Stankov Jovanovic, V.P., Ilic, M.D., Markovic, M.S., Mitic, V.D., Nikolic Mandic, S.D. and Stojanovic, G.S. 2011. Wildfire impact on copper, zinc, lead and cadmium distribution in soil and relation with abundance in selected plants of Lamiaceae family from Vidlic Mountain (Serbia). *Chemosphere*. 84: 1584-1591.

van Oudtshoorn, F. 2012. Guide to grasses of Southern Africa. Briza Publications: Pretoria.

Venter, F.J., Scholes, R.J. and Eckhardt, H.C. 2003. The abiotic template and its associated vegetation pattern. Island Press: Washington, DC.

Vermeire, M.L., Thoresen, J., Lennard, K., Vikram, S., Kirkman, K., Swemmer, A.M., Te Beest, M., Siebert, F., Gordijn, P., Venter, Z., Brunel, C., Wolfaard, G., Krumins, J.A., Cramer, M.D. and Hawkins, H.J. 2021. Fire and herbivory drive fungal and bacterial communities through distinct above-and belowground mechanisms. *Science of the Total Environment*. 785: 147189.

Wang, G., Li, J. and Ravi, S. 2019. A combined grazing and fire management may reverse woody shrub encroachment in desert grasslands. *Landscape Ecology*. 34: 2017-2031.

Wang, Q., Zhong, M. and Wang, S. 2012. A meta-analysis on the response of microbial biomass, dissolved organic matter, respiration, and N mineralization in mineral soil to fire in forest ecosystems. *Forest Ecology and Management*. 271: 91-97.

Watmough, S.A., Eimers, M.C. and Dillon, P.J. 2007. Manganese cycling in central Ontario forests: response to soil acidification. *Applied Geochemistry*. 22: 1241-1247.

Webster, R. 2001. Statistics to support soil research and their presentation. *European Journal of Soil Science*. 52: 331-340.

Zebarth, B.J., Forge, T.A., Goyer, C. and Brin, L.D. 2015. Effect of soil acidification on nitrification in soil. *Canadian Journal of Soil Science*. 95: 359-363.

Zuur, A.F., Leno, E. and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology Evolution*. 1: 3-14.

CHAPTER 4

DISTRIBUTION OF SOIL ORGANIC CARBON IN AGGREGATES AFTER 7 YEARS OF FREQUENT BURNING AND HERBIVORE GRAZING IN A SAVANNA GRASSLAND

Abstract

Fire-herbivory interactions leads to a considerable loss of soil organic carbon (SOC) content in savanna grasslands. However, the underlying mechanisms driving the loss of SOC following fire and herbivory are poorly understood, thereby limiting the implementation of effective management strategies to enhance SOC storage. To address this knowledge gap, the study quantified the distribution of SOC in bulk soil and within aggregate fractions. Physical fractionation of soils sampled from the pedoderm layer (0-10 cm) was conducted for the control and burnt+grazed grassland sites to determine the distribution of SOC within macroaggregates and microaggregates. Soil aggregates were separated into four classes using a wet-sieving procedure, namely large macroaggregates (>2000 µm), small macroaggregates (212-2000 µm), microaggregates (50-212 µm) and silt+clay (<50 µm). Following fire and herbivory, SOC was lower in all aggregate fractions when compared to the control, with the greatest SOC reduction in the large macroaggregates by 40% and the smallest decline in the silt+clay fraction of the soil. The huge reduction of SOC within the large macroaggregates is attributable to the breakdown of macroaggregate stabilizing agents induced by fire-herbivory interactions and the sensitivity of large aggregates to these soil disturbances. Conversely, the lower levels of SOC in the clay-and-silt sized particles of the savanna grassland soil is because they are characterised by a high surface activity, which chemically stabilises SOC and form building blocks for aggregates, thereby inducing physical protection of SOC by occlusion in aggregates.

Keywords: Fire, herbivory, soil organic carbon, aggregate fractions, savanna grasslands

4.1 Introduction

Frequent burning and herbivore grazing are interrelated and their co-existence has a synergistic effect on SOC dynamics. Both management strategies function concurrently leading to a reduction in SOC by removing aboveground biomass and leaf litter inputs through combustion and grazing pressure (Savadogo *et al*. 2007, Chen *et al*., 2017). This in turn leads to a change in the biological, physical and chemical properties of the soil, owing to the disaggregation of soil aggregates induced by fire and herbivore grazing. The structural disaggregation of the soil has a major influence on numerous biological, chemical and physical processes in the soil (Tisdall and Oades, 1982). It impedes microbial activity by restricting root growth as well as the movement of air and water in and through the soil as a result of compaction (Reichert *et al*., 2016). As such, the activities of soil biota and soil organic matter (SOM) inputs are reduced leading to an overall decrease in forage production. Destabilization of soil aggregates further affects the protection of SOC and can lead to drastic losses of SOC through erosion. Physical protection of SOC within aggregates is an important mechanism for C storage (Jastrow, 1996; Six *et al*., 2002).

In savanna ecosystems, the soil structure is exposed to deterioration during fire and overgrazing (Greenwood and McKenzie, 2001). As a result, SOC is prone to loss as the aggregates are weakened and unstable to physically hold SOC for longer periods. This disintegration of aggregates serves as a driver for SOC depletion within aggregate fractions (Wiesmeier *et al*., 2012). Few studies have quantified the effect of frequent burning and herbivore grazing on the distribution of SOC within different sized aggregates in grassland soils (Liao *et al*., 2006). The physicochemical inhibition of SOM decomposition via surface interactions with mineral soil particles and within soil microaggregates over decadal–millennial timeframes is broadly recognized as a key mechanism for enhancing SOC persistence (Lugato *et al*., 2021). More research on the mechanisms governing organic matter destabilization is required to better understand how fire and grazing affects SOC losses. It is imperative to measure and monitor SOC in savannas because improved SOC levels have been linked to decreased vulnerability to soil loss and improved soil quality (Lal *et al*., 2020).

4.2 Methodology

4.2.1 Site Description

The experimental site is the Satara land system, a savanna grassland amongst the four major land systems found at KNP (Figure 8). It is characterized by the co-occurrence of a moderately developed shrub layer and open tree savannas (Gertenbach, 1983; Rutherford *et al*., 2006). The site has been subjected to prescribed fires and herbivore grazing for the past 7 years and tends to have palatable grasses throughout the year with high levels of herbivory (Van Wilgen *et al*., 2000). The area consists of two main vegetation types, namely Tshokwane-Hlane Basalt Lowveld, which is the dominant vegetation type within the study site, and Delagoa Lowveld which occurs southwest of Satara (Rutherford *et al*., 2006). The landscape consists of fairly flat plains (Venter *et al*., 2003) with well-defined drainage channels and relatively nutrient-rich, basalt-derived soils. The soils vary from black, brown or red clayey and are, on average, no more than 1m in depth (Rutherford *et al*., 2006). Gertenbach (1983) describes the soil pattern as being ‘relatively homogeneous’. See Chapter 3 section 3.2.1 for further description.

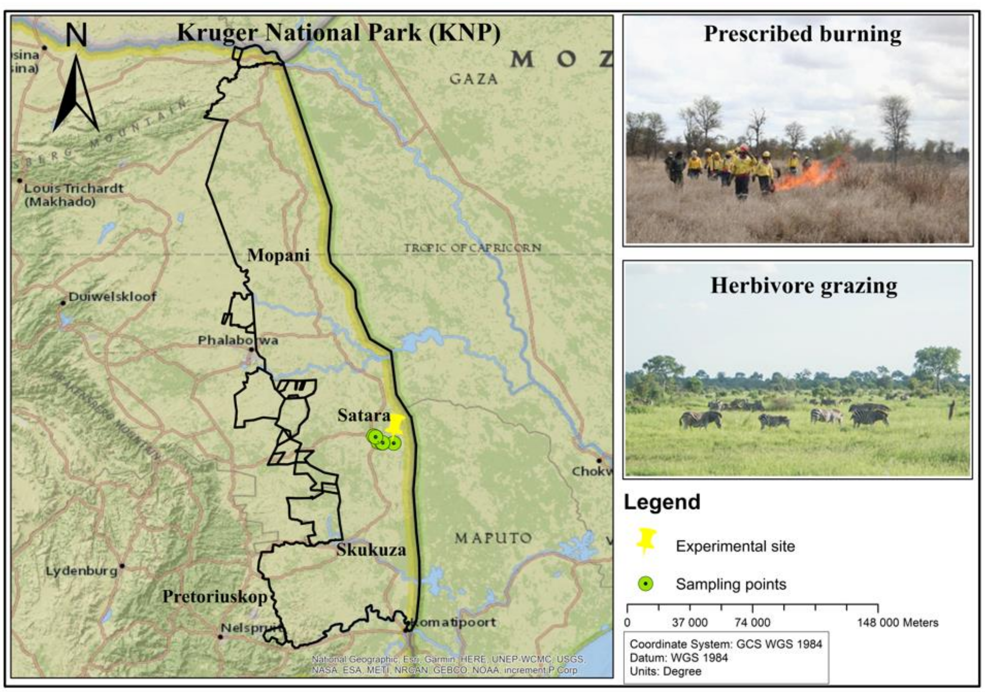

Figure 8: Map of the experimental site showing location of the Satara land system in Kruger National Park.

4.2.2 Research Design and field sampling strategy

The study was conducted on long-term experimental burn plots following the layout described in Chapter 3 section 3.2.2. Experienced teams from 'Working on Fire' applied all the experimental burns while any unplanned fires in the area were suppressed by field rangers. Prior to soil sampling, a soil survey was conducted across the selected plots to assess site variability. To limit site variability, we ensured that the control and burn treatment plots were adjacent to each other, lied along the same topographic landscape position, and had the same soil type and similar parent material. The same sampling strategy outlined in Chapter 3 section 3.2.3 was followed and the collected soil samples were transported to the University of Limpopo Soil Science laboratory for air-drying. The samples were further analysed for organic carbon from whole and fractionated soils.

4.2.3 Laboratory analyses

The physical fractionation of aggregates was performed after air drying the samples in the laboratory. Post air-drying, the bulk soil was sieved, and soil aggregates between 3 mm and 5 mm were separated and collected. Air-dried soil aggregates were separated through a series of three sieves to set apart four aggregate size fractions using the method described by Elliott (1986). The wet sieving method was followed to separate each sample into four aggregate sizes namely: large macroaggregates (>2000-µm), small macroaggregates (212-2000-µm), microaggregates (50-212-µm) and silt plus clay (<50-µm). An 80g of the soil sample was spread on the 2000-µm sieve and then submerged in deionized water for 5 minutes, which resulted in slaking of the soil. The soil was then sieved to separate water-stable aggregates by moving the sieve in an up-and-down motion with 50 repetitions over a period of 2 minutes. The material remaining on the 2000-µm sieve was backwashed into the beaker for drying. Soil and water that passed through the 2000-µm sieve was subjected to a smaller sized sieve whereby the sieving procedure was repeated and done for all the sieve sizes. Aggregates that were separated were oven dried at 105˚C, weighed and stored at room temperature for analyses (Figure 9). Mean weight diameter (MWD), a measure of soil aggregate stability was calculated using the following equation:

$$MWD = (2 \times LM) + (1.106 \times sM) + (0.131 \times m) + (0.025 \times (s+c))$$

Where: LM represents the percentage of large macroaggregates, sM the percentage of small macroaggregates, m the percentage of microaggregates, and (s + c) the percentage of unaggregated silt and clay in each soil sample (Blaser *et al*., 2017).

Furthermore, all the aggregate fractions were dried and SOC content of each aggregate fraction and whole soil was determined using the Walkley-Black method (Walkley and Black, 1934).

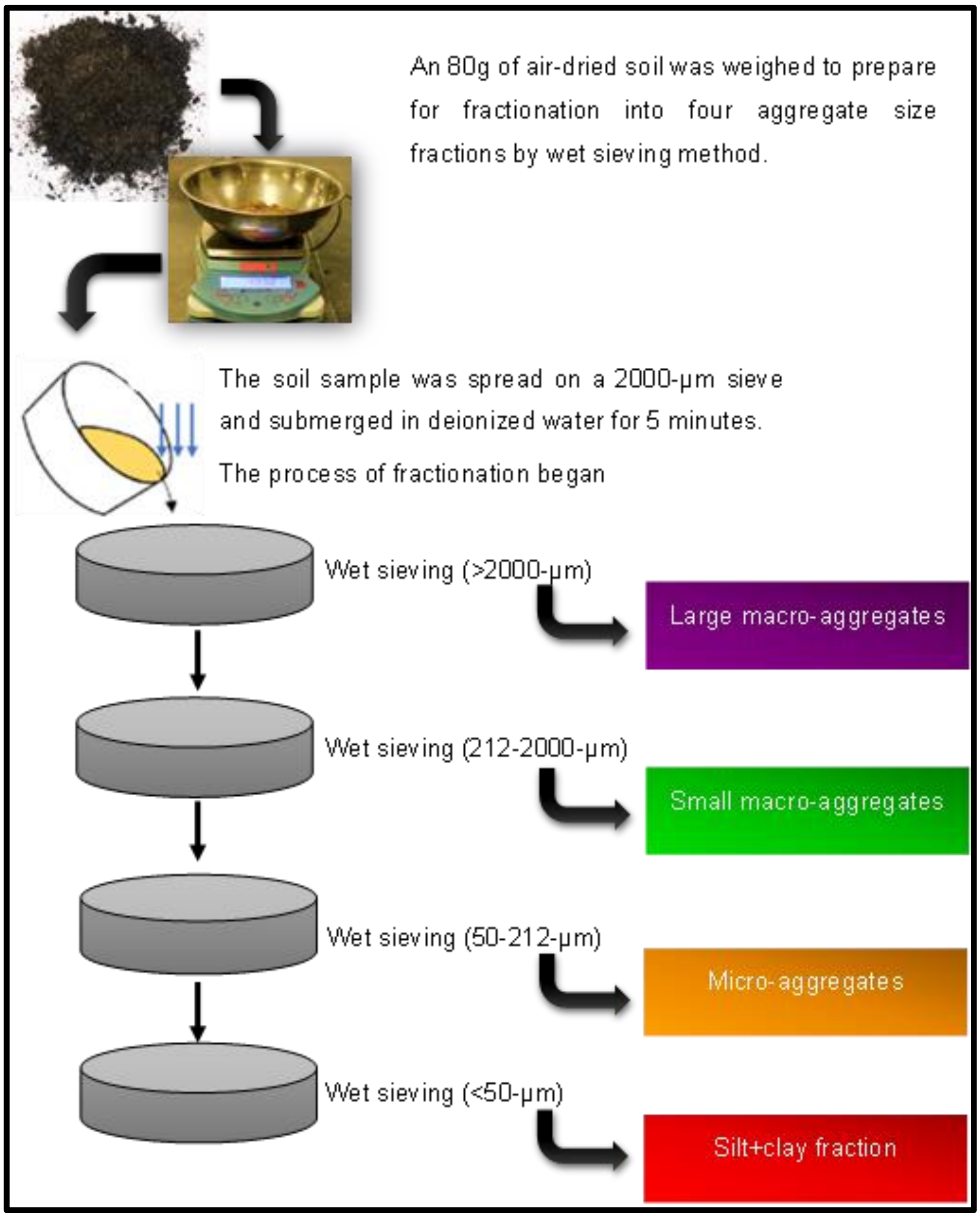

Figure 9: A flow diagram showing the process of physical fractionation of soil aggregates.

4.2.4 Statistical analysis

The dataset of measured soil properties was explored and analysed using the protocol described by Zuur *et al*. (2010). Basic statistics of the soil property data including minimum, maximum, median, average, standard error, standard deviation, and coefficient of variation were computed in Microsoft Excel following Webster (2001). Bar graphs including mean error bars were plotted using Sigma Plot 14.0 (Systat Software Inc., California, USA), to visually compare the distribution of SOC in whole soil and within aggregate fractions across the control and burnt+grazed grassland soils. A two-way analysis of variance (ANOVA) was run using GenStat 18th edition to test the effect of frequent burning and herbivore grazing on the distribution of SOC within aggregate fractions. Significant mean differences ($P < 0.05$) between the aggregate fractions were separated using Tukey's HSD test using GenStat 18th edition. A correlation heatmap was generated using Graph pad Prism 9.0 (GraphPad Software, California, USA) to determine the strength of the relationship between SOC and other soil properties.

4.3 Results

4.3.1 Effect of frequent burning and grazing on SOC content and MWD in bulk soil

In the 25ha grassland subjected to frequent burning and herbivore grazing, SOC content in bulk soil decreased by 31% from 24.22 g kg^{-1} in the control to 16.81 g kg^{-1} in the burnt+grazed plots [Figure 10 (a)]. Mean weight diameter (MWD) decreased from 0.85 mm in the control to 0.80 mm in the burnt+grazed plots, corresponding to a 6% decrease [Figure 10 (b)].

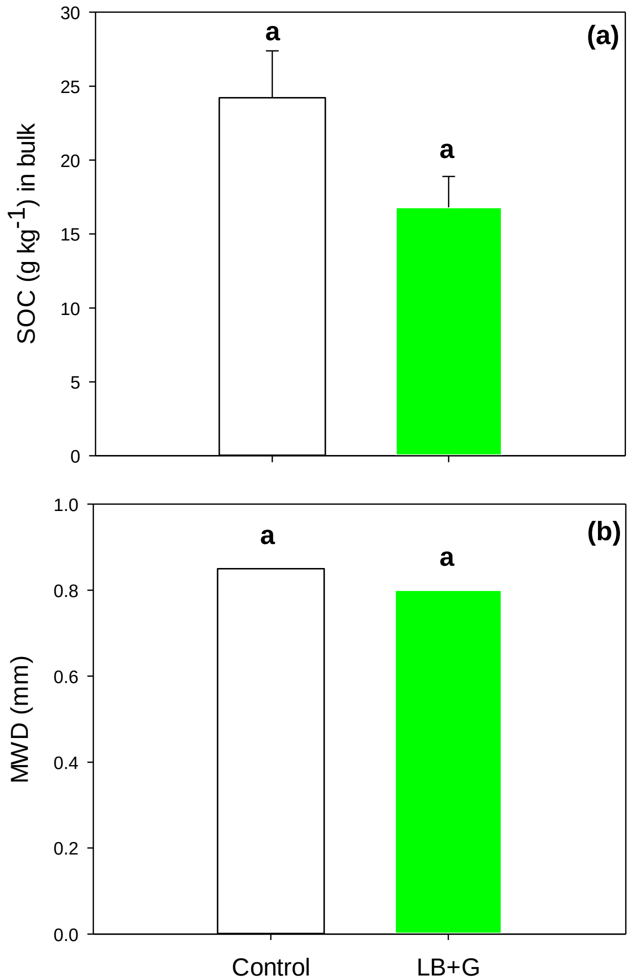

Figure 10: Bar graphs showing soil organic carbon (SOC) content and mean weight diameter (MWD) in bulk soil (a-b), at 0-10 cm soil depth after 7 years of late burning and herbivore grazing (green bars) compared to the control (white bars) in a savanna grassland at Kruger National Park, South Africa. Values are means (n=5) and error bars represent standard errors.

4.3.2 Influence of frequent burning and herbivore grazing on the relationship between SOC content and aggregate stability

In the 25-ha grassland subjected to frequent burning and herbivore grazing, there was a weak positive correlation between MWD and SOC content in the burnt+grazed plot, where R2= 0.0273 and y= 0.0023x + 0.7607. Conversely, there was a strong negative relationship between MWD and SOC content in the control, where R2= 0.9205 and y= -0.0246x + 1.4468 (Figure 11).

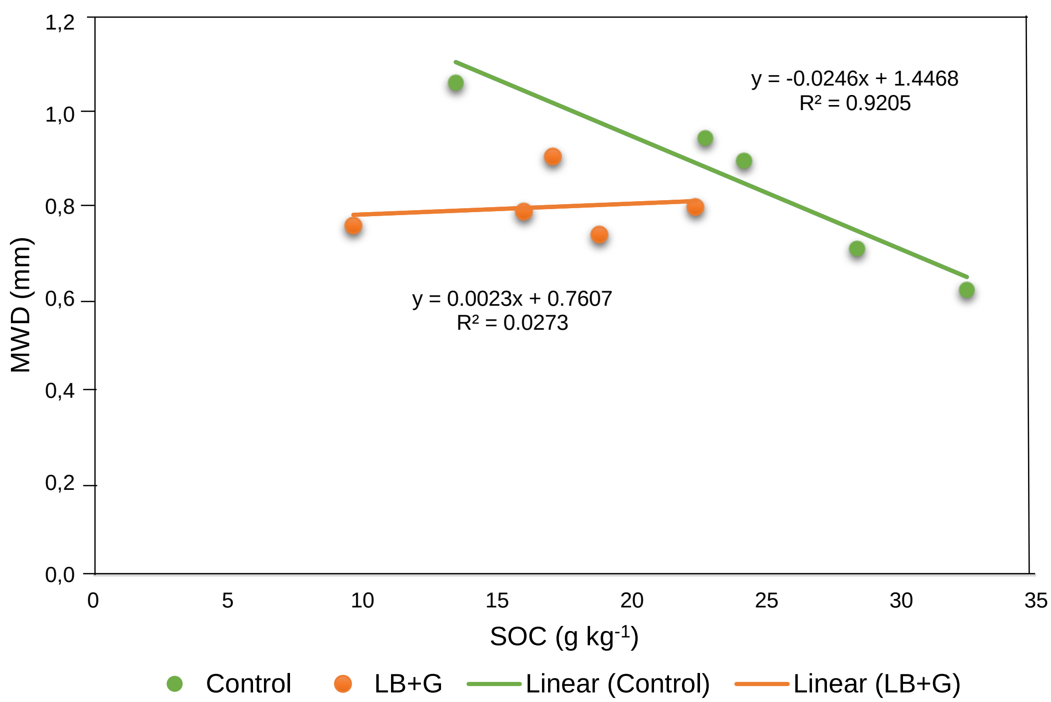

Figure 11: Relationship between mean weight diameter (MWD) and SOC content after 7 years of late burning and herbivore grazing (LB+G) compared to the control in a savanna grassland at Kruger National Park, South Africa.

4.3.3 Effect of frequent burning and grazing on the distribution of SOC within soil aggregate fractions

Our analysis of variance (ANOVA) revealed that there was a significant difference ($P<0.05$) in the concentration of SOC within soil aggregate fractions under the burnt+grazed grassland soil compared to the control (Appendix 4). The concentration of SOC in all aggregate fractions was lower under the burnt+grazed grassland soil compared to the control. In the large macroaggregates (>2000-µm), SOC content decreased from 7.20 g kg^{-1} to 4.32 g kg^{-1} which corresponds to a 40% change, followed by a change of 29% and 24% from 19.11 g kg^{-1} to 13.55 g kg^{-1} and 20.47 g kg^{-1} to 15.54 g kg^{-1} in the microaggregates (50-212-µm) and small macroaggregates (212-2000-µm) respectively. Lastly, the silt plus clay fraction (<50-µm) had a minimal change of 3% from 24.80 g kg^{-1} to 23.99 g kg^{-1} [Figure 12].

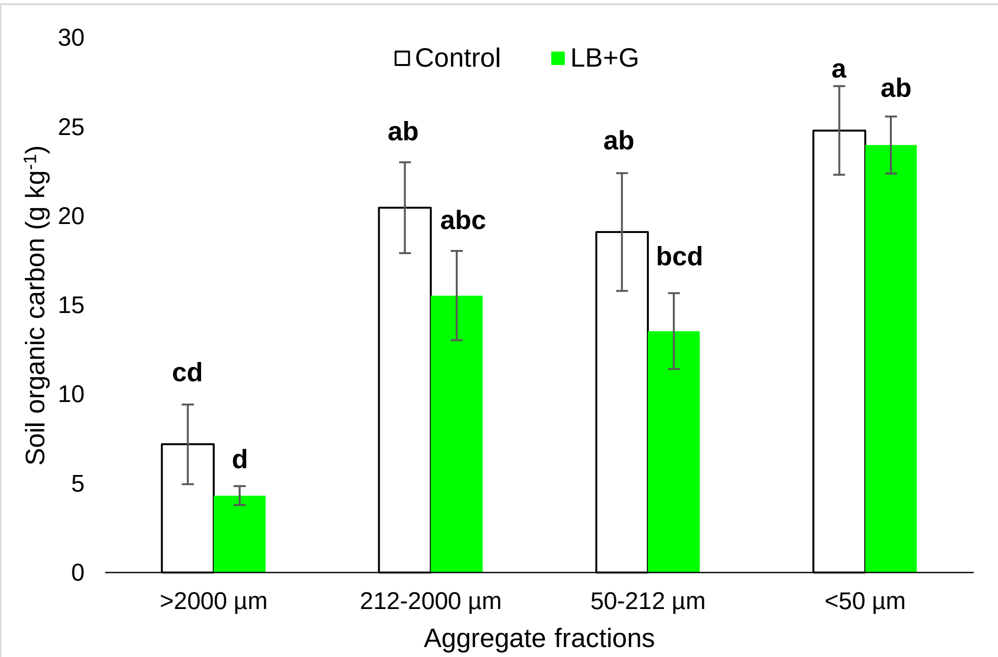

Figure 12: Bar graphs showing the distribution of soil organic carbon (SOC) content within aggregate fractions at 0-10 cm soil depth after 7 years of late burning and herbivore grazing (green bars) compared to the control (white bars) in a savanna grassland at Kruger National Park, South Africa. Values are means (n=5) and error bars represent standard errors. Different letters indicate significant differences at P< 0.05 among the aggregate fractions.

4.3.4 Correlation coefficients (r) between soil properties and SOC determined in the control and burnt+grazed savanna grasslands

The correlation analysis between SOC and selected soil properties showed that in the control [Figure 13 (a)], SOC in bulk soil and within all aggregate fractions was positively correlated to Ca (r=0.54-0.85; P<0.05) and ECEC (r=0.55-0.82). Additionally, SOC in bulk soil and within all aggregate fractions except in large macroaggregates was negatively correlated with Exch.Ac (r=-0.57-(-0.84); P<0.05); MWD (r=-0.90-(-0.97); P<0.05) and clay content (r=-0.52-(-0.84); P<0.05). SOC in bulk and all aggregate fractions also correlated with Cu (r=-0.40-(-0.076); P<0.05).

Our correlation analysis further revealed that under the burnt+grazed savanna grassland [Figure 13 (b)], SOC in whole soil positively correlated with Ca (r=0.80; P<0.05), Mg (r=0.86), ECEC (r=0.94) and Mn (r=0.83) while negatively correlated with P (r= -0.94) and Cu (r= -0.93). It was also revealed that SOC within the large macroaggregates was positively correlated to Ca (r=0.67), Exch.Ac (r=0.57) and Mn (r=0.84) while negatively correlated to pH (r= -0.64) and MWD (r=-0.61). Moreover, SOC within small macroaggregates was positively correlated with the following soil properties: Ca (r=0.72), Mg (r=0.76), ECEC (r=0.83), Mn (r=0.85) and negatively correlated with P (r= -0.81), Cu (r= -0.75) and %Clay= (r= -0.64). Similarly, SOC in microaggregates also positively correlated to Ca (r=0.75), Mg (r=0.91), ECEC (r=0.93) and Mn (r=0.80) while negatively correlated to P (r= -0.93), Cu (r= -0.94) and %Clay (r= -0.64). Lastly, silt+clay associated SOC showed positive correlations with Ca (r=0.73), Mg (r=0.91), ECEC (r=0.93) and negative correlations with P (r= -0.81), Cu (r=-0.75) and %Clay (r= -0.79).

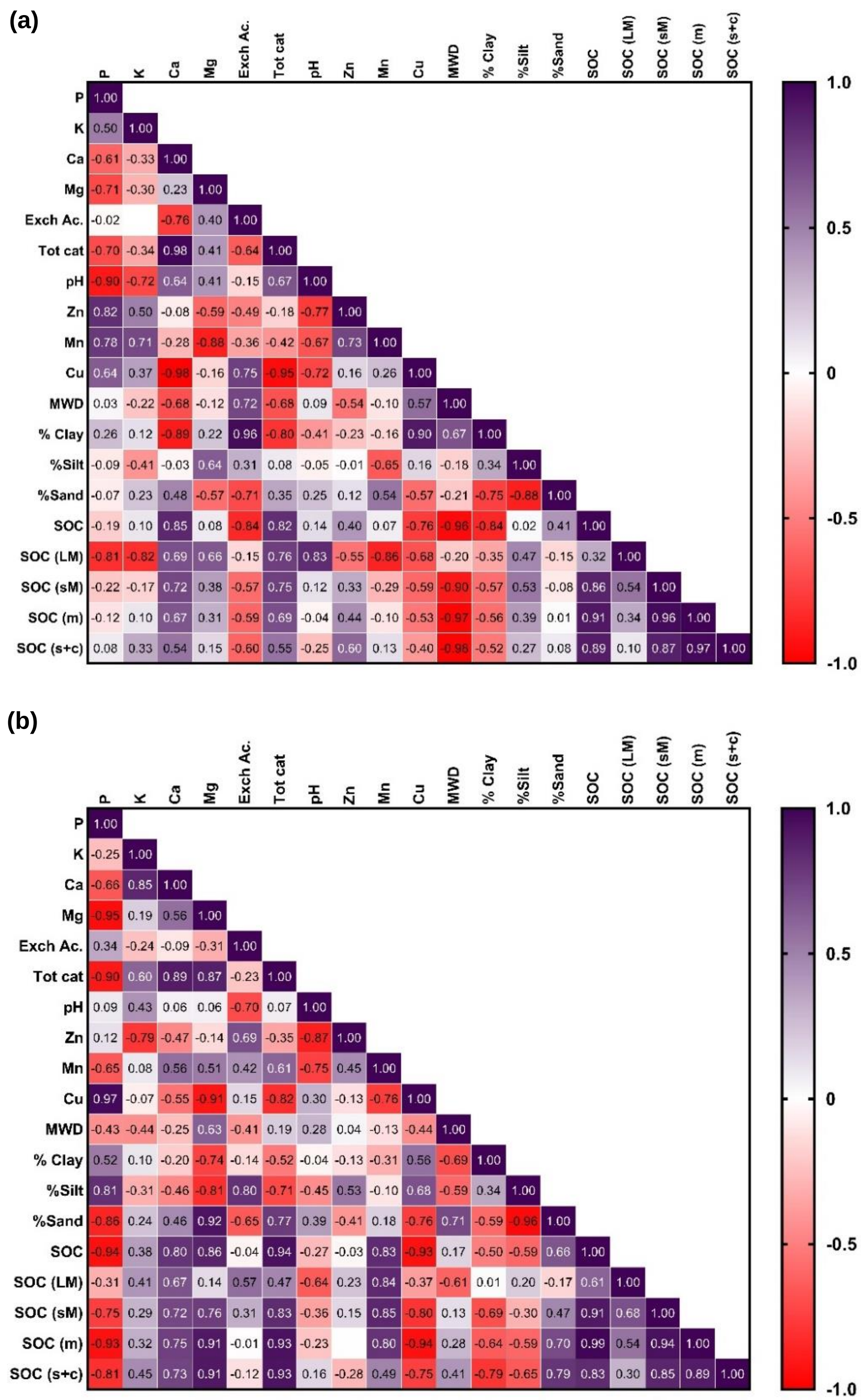

Figure 13: Correlation matrix showing Pearson's correlation coefficients between soil properties and SOC content across the control (a) and burnt+grazed (b) grassland soils.

P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; Exch.Acid, exchangeable acidity; Tot cat, total cations/ effective cation exchange capacity; pH; Zn, zinc; Mn, manganese; Cu, copper; MWD, mean weight diameter; %Clay, clay content; %Silt, silt content; %Sand, sand content; SOC, SOC in bulk soil; SOC(LM), SOC in large macroaggregates; SOC(sM), SOC in small macroaggregates; SOC(m), SOC in microagggregates; SOC(s+c), SOC in silt plus clay fraction

4.4 Discussion

4.4.1 Fire-herbivory interactions effect on SOC in bulk soil and aggregate stability

The findings of this study, conducted in a subtropical climate, revealed that bulk soil SOC was lower in the topsoil of a savanna grassland site after frequent burning and grazing. The concentration of SOC in the topsoil decreased from 24.22 g kg^{-1} in the control to 16.81 g kg^{-1} in the burnt+grazed plots, which corresponds to a 31% decline. Understanding factors that control SOC is as important as quantifying it (Mayer *et al*., 2019). Several factors interact to determine SOM and control soil C pools in the topsoil (Mills and Fey, 2004). The primary factors driving SOC concentrations are prescribed burning and herbivore grazing which simultaneously reduce organic matter inputs through the removal of aboveground biomass (Savadogo *et al*., 2007; Aynekulu *et al*., 2021). Frequent burning induces combustive losses of leaf litter and grasses leading to a decrease in organic matter inputs and the stability of aggregates (Savadogo *et al*., 2007). By removing aboveground biomass and leaf litter, repeated burning exposes the soil surface to raindrop impact leading to the dispersion of clay particles and a further breakdown of aggregates (Moyo *et al*., 1998). Subsequently, leading to a decrease in aggregate stability which may be attributed to the blockage of surface pores and crusting as a result of mechanical energy input from raindrops and the present losses of organic matter (Hillel, 1998). The ash particles produced during burning aggravate blocked surface pores preventing any further inputs of organic matter in the soil, consequently Faleading to a reduction in the SOC (Mills and Fey, 2004).

Furthermore, herbivore grazing partly contributed to the low SOC levels at our site through increased biomass removal and trampling pressure (Rietkerk *et al*., 2000). Grazers reduce the fuel load mainly by consumption and trampling (Mwendera *et al*., 1997), thereby weakening the soil structure by breaking up soil aggregates (Chen and Weil, 2011). Pugging breaks up aggregates and causes damage to large soil pores which increases bulk density, resulting in compaction. Compaction then reduces water infiltration, root growth and plant development thereby limiting inputs of organic materials into the soil (Hiernaux *et al*., 1999; Chen *et al*., 2017). As a result, a lack of balance in organic material negatively affected by both compaction and grazing then decreases SOC overtime.

Additionally, structural destabilization brought about by fire and grazing constitutes another factor contributing to SOC depletion. Such a disturbance leads to a disruption of aggregates which are important for the physical protection of organic matter through a variety of interactions (Tisdall and Oades 1982; Baldock and Skjemstad, 2000). The disaggregation that occurs as a consequence, results in SOC losses either through potential erosion of organic matter or through associated atmospheric CO_2 emissions as SOC becomes more vulnerable (Dlamini *et al*., 2014). This is further explained by the observed decrease in MWD under the burnt+grazed grassland soils [Figure 10 (b)].

4.4.2 Relationship between MWD and SOC content following frequent burning and herbivore grazing

The results of this study showed that there is a strong negative relationship between MWD and SOC in the control, which implies that as MWD decreases there is an increase in SOC concentration. These findings seem to contradict most literature which shows that as aggregate stability decreases, it is also expected that SOC decreases due to lack of physical protection of organic matter (Zinn *et al*., 2005). Nevertheless, this was the case under the burnt+grazed plots where a positive relationship is observed between SOC and MWD (Figure 11). This suggests that in surface soils, SOC content is strongly driven by aggregation. Therefore, it is observed in our case that fire and grazing leads to a decrease in aggregate stability which in turn reduces SOC content. This is explained by the reduction in organic material and litter inputs accompanied by fire and grazing interactions, which overtime reduces aggregation (Savadogo *et al*., 2007).

4.4.3 Fire-herbivory feedback mechanisms driving the distribution of SOC content within aggregate fractions

The concentration of SOC within all aggregate fractions was greatly reduced under the burnt+grazed plots compared to the control of the savanna grassland site investigated.

After frequent burning and herbivore grazing, large macroaggregates showed the greatest reduction in SOC by 40%. There was also a decline in the microaggregate associated SOC by 29%, followed by 24% of the small macroaggregate associated SOC and a 3% slight drop of the silt+clay associated SOC. The varying distribution of SOC amongst the aggregate fractions was further revealed by our analysis of variance (ANOVA) showing a significant effect at $P<0.05$ as a result of frequent burning and herbivore grazing. The depletion of SOC within aggregate fractions as a consequence of frequent burning and herbivore grazing may be due to a number of reasons. The reduction of SOC within the large macroaggregates and the silt+clay fraction is mainly due to combustion during burning and trampling by herbivores (Garcia-Oliva *et al*., 1999; Rietkerk *et al*., 2000). However, the substantial loss within the large macroaggregates is due to their vulnerability to soil disturbance because their transient and temporary binding agents, such as roots and mycelia, are sensitive to disturbance (Tisdall, 1994; Wang *et al*., 2016). Fire and grazing disrupt macroaggregate stabilization mechanisms and as a result exposes the labile and less highly processed SOM to loss (Elliot, 1986). Thus, an explanation for the huge depletion of large macroaggregate associated SOC. The slight reduction of the silt+clay associated SOC is probably as a result of a larger specific surface associated with this fraction, which can provide abundant adsorption sites for C and better physical protection of SOC (Reis *et al*., 2014).

Furthermore, several mechanisms contribute to the considerable amount of SOC reduction within large macroaggregates (Garcia-Oliva *et al*., 1999). This reduction brought on by the weakened biological stabilizing mechanisms associated with fire-herbivory interactions may be explained by three processes. Firstly, large macroaggregate associated SOC may have been preferentially removed by soil erosion (Lal, 1987), following the deterioration of macroaggregate stability. Secondly, the macroaggregates were most likely broken down by the physical action of raindrop impact which accelerates disaggregation (Moyo *et al*., 1998; Kinell, 2001). The third process is the disintegration of aggregates via slaking (Oades, 1993), which is particularly important in seasonally dry ecosystems. Slaking is most prevalent in regions such as our study site, where bouts of rainfall take place after soils have dried out (Haynes and Swift, 1990).

Additionally, other potential mechanisms of SOC depletion within large macro-aggregates and silt+clay fraction lies within the changes in the physical and chemical nature of the soil brought about by fire and grazing (Garcia-Oliva *et al*., 1999; Savadogo *et al*., 2007). The low aggregate stability induced by fire-herbivory interactions may explain the notable depletion in large macroaggregate associated SOC. Our correlation analysis showed that there was indeed a strong negative correlation between MWD and SOC in the large macro-aggregates ($r = -0.61$, $P<0.05$). The acidic soils at our site also contributed to this depletion through alleviation of acid-related retardation of microbial growth and organic matter degradation, leading to losses in large macroaggregate associated SOC through microbial decomposition (Malik *et al*., 2018). This is further proven by the strong negative correlation between pH and large macroaggregate SOC ($r = -0.64$).

Moreover, SOC within the silt+clay fraction showed a strong positive correlation with ECEC ($r=0.93$, $P<0.05$) and a strong negative correlation with P ($r = -0.81$). The low ECEC can be explained by lower litter inputs and reduced nutrient release caused by fire and grazing. This further reduced the soils' ability to retain cations due to reduced SOC content. Thus, explains the slight decline in silt+clay associated SOC. The high accumulation in P can be explained by the acidic soils at our site which increased P availability and its adsorption on the surface of the clay (Shen and Zhang, 2011; Jiang *et al*., 2015). Therefore, the increase in soil P is a driver for the decrease in silt+clay associated SOC which is proven by the strong negative correlation between them. The correlation matrix also revealed that in this study there was a strong positive correlation [Figure 13 (b)] between SOC within the silt+clay fraction and polyvalent cations, exchangeable bases Ca ($r=0.73$) and Mg ($r=0.91$). Under normal circumstances, polyvalent cations tend to hold more tightly onto the exchange sites of clay as compared to monovalent cations (Jiang *et al*., 2015). However, because of the generally low levels of the polyvalent cations, there is a slight drop in silt+clay associated SOC which is further explained by the strong positive correlation between them.

4.5 Conclusion

This study assessed the combined effect of frequent burning and herbivore grazing on the distribution of SOC within whole soil and aggregate fractions in the topsoil of a savanna grassland. The results revealed that frequent burning and grazing radically reduces SOC content in the surface layer with over 90% decrease in the large macroaggregates and a slight decline in the silt+clay fraction. This is because fire and grazing disrupt macroaggregate stabilization mechanisms and the feedback effect is further accelerated by the vulnerability of large macroaggregates to soil disturbance. The small decline in silt+clay associated SOC on the other hand, is due to greater surface area and their ability to provide better physical protection of SOC. In other words, SOC physically stabilized within the silt+clay fraction is protected for long and not easily susceptible to loss. Therefore, the protection of SOC is proportional to the decreasing size and increasing density of the soil fractions.

REFERENCES

Aynekulu, E., Sileshi, G.W., Rosenstock, T.S., van Noordwijk, M., Tsegaye, D., Koala, J., Sawadogo, L., Milne, E., de Leeuw, J. and Shepherd, K. 2021. No changes in soil organic carbon and nitrogen following long-term prescribed burning and livestock exclusion in the Sudan-savanna woodlands of Burkina Faso. *Basic and Applied Ecology*. 56: 165-175.

Baldock, J.A. and Skjemstad, J.O. 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry*. 31: 697-710.

Blaser, W.J., Oppong, J., Yeboah, E. and Six, J. 2017. Shade trees have limited benefits for soil fertility in cocoa agroforests. *Agriculture, Ecosystem and Environment*. 243: 83-91.

Chen, G. and Weil, R.R. 2011. Root growth and yield of maize as affected by soil compaction and cover crops. *Soil and Tillage Research*. 117: 17-27.

Chen, Y., Huang, Y. and Sun, W. 2017. Using organic matter and pH to estimate the bulk density of afforested/reforested soils in northwest and northeast China. *Pedosphere*. 27: 890-900.

Dlamini, P., Chivenge, P., Manson, A. and Chaplot, V. 2014. Land degradation impact on soil organic carbon and nitrogen stocks of sub-tropical humid grasslands in South Africa. *Geoderma*. 235: 372-381.

Elliott, E.T. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *Soil Science Society of America Journal*. 50: 627-633.

García-Oliva, F., Sanford Jr, R.L. and Kelly, E. 1999. Effects of slash-and-burn management on soil aggregate organic C and N in a tropical deciduous forest. *Geoderma*. 88: 1-12.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*. 26: 9-121.

Greenwood, K.L. and McKenzie, B.M., 2001. Grazing effects on soil physical properties and the consequences for pastures: A review. *Australian Journal of Experimental Agriculture*. 41: 1231-1250.

Haynes, R.J. and Swift, R.S. 1990. Stability of soil aggregates in relation to organic constituents and soil water content. *Journal of soil science*. 41: 73-83.

Hiernaux, P., Bielders, C.L., Valentin, C., Bationo, A. and Fernandez-Rivera, S. 1999. Effects of livestock grazing on physical and chemical properties of sandy soils in Sahelian rangelands. *Journal of Arid Environments*. 41: 231-245.

Hillel, D. 1998. Environmental Soil Physics. Academic Press: London.

Jastrow, J.D. 1996. Soil aggregate formation and the accrual of particulate and mineral associated organic matter. *Soil Biology and Biochemistry*. 28: 665-676.

Jiang, X., Bol, R. and Willbold, S. 2015. Speciation and distribution of P associated with Fe and Al oxides in aggregate-sized fraction of an arable soil. *Biogeosciences*. 12: 9879-9903.

Kinnell, P.I.A. 2001. Comments on “Vertical Hydraulic Gradient and Run-On Water and Sediment Effects on Erosion Processes and Sediment Regimes”. *Soil Science Society of America Journal*. 65: 953-956.

Lal, R. 1987. Tropical Ecology and Physical Edaphology. Wiley: New York.

Lal, R., Brevik, E.C., Dawson, L., Field, D., Glaser, B., Hartemink, A.E., Hatano, R., Lascelles, B., Monger, C., Scholten, T. and Singh, B.R. 2020. Managing soils for recovering from the COVID-19 pandemic. *Soil Systems*. 4: 46.

Liao, J.D., Boutton, T.W. and J.D. Jastrow. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. *Soil Biology and Biochemistry*. 38: 3184-3196.

Lugato, E., Lavallee, J.M., Haddix, M.L., Panagos, P. and Cotrufo, M.F. 2021. Different climate sensitivity of particulate and mineral-associated soil organic matter. *Nature Geoscience*. 14: 295-300.

Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S., Gweon, H.S., Peyton, J.M., Mason, K.E., van Agtmaal, M. and Blaud, A. 2018. Land use driven change in soil pH affects microbial carbon cycling processes. *Nature communications*. 9: 1-10.

Mayer, S., Kühnel, A., Burmeister, J., Kögel-Knabner, I. and Wiesmeier, M. 2019. Controlling factors of organic carbon stocks in agricultural topsoils and subsoils of Bavaria. *Soil and Tillage Research*. 192: 22–32.

Mills, A.J. and Fey, M.V. 2004. Frequent fires intensify soil crusting: physicochemical feedback in the pedoderm of long-term burn experiments in South Africa. *Geoderma*. 121: 45-64.

Moyo, C.S., Frost, P.G.H. and Campbell, B.M. 1998. Modification of soil nutrients and micro-climate by tree crowns in a semi-arid rangeland of south-western Zimbabwe. *African Journal of Range & Forage Science*. 15: 16-22.

Mwendera, E.J., Saleem, M.M. and Woldu, Z. 1997. Vegetation response to cattle grazing in the Ethiopian highlands. *Agriculture, ecosystems & environment*. 64: 43-51.

Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma*. 56: 377-400.

Reichert, J.M., da Rosa, V.T., Vogelmann, E.S., da Rosa, D.P., Horn, R., Reinert, D.J. Sattler, A. and Denardin, J.E. 2016. Conceptual framework for capacity intensity physical soil properties affected by short long-term (14 years) continuous no-tillage and controlled traffic. *Soil and Tillage Research*. 158: 123-136.

Reis, D.A., Lima, C.L.R.D., Pauletto, E.A., Dupont, P.B. and Pillon, C.N. 2014. Tensile strength and friability of an Alfisol under agricultural management systems. *Scientia Agricola*. 71: 163-168.

Rietkerk, M., Ketner, P., Burger, J., Hoorens, B. and Olff, H. 2000. Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. *Plant ecology*. 148: 207-224.

Rutherford, M.C., Mucina, L., Lotter, M.C. and Bredenkamp, G.J. 2006. The vegetation of South Africa, Lesotho and Swaziland, in Strelitzia 19. South African National Biodiversity Institution: Pretoria.

Savadogo, P., Sawadogo, L. and 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 & Environment*. 118: 80-92.

Shen, J. and Zhang, F. 2011. Phosphorus dynamics: from soil to plant. *Plant Physiology*. 156: 997-1005.

Six, J. Conant, R.T. Paul, E.A. and Paustian, K. 2002. Stabilization mechanisms of organic matter: implications for C-saturation of soils. *Plant and Soil*. 241: 155-176.

Tisdall, J.M. 1994. Possible role of soil microorganisms in aggregation in soils. *Plant Soil*. 159: 115-121.

Tisdall, J.M. and Oades, J.M. 1982. Organic matter and water-stable aggregates in soils. *Journal of Soil Science*. 33: 141-163.

Van Wilgen, B.W., Biggs, H.C., O'Regan, S.P. and Marè, N. 2000. A fire history of the savanna ecosystems in Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Sciences*. 96: 167-178.

Venter, F.J., Scholes, R.J. and Eckhardt, H.C. 2003. The abiotic template and its associated vegetation pattern. Island Press: Washington, DC.

Walkley, A. and Black, I.A. 1934. An examination of the method for determining soil organic matter and a proposed chromic acid titration method. *Soil Science*. 37: 29-38.

Wang, J., Liu, L., Qiu, X., Wei, Y., Li, Y. and Shi, Z. 2016. Contents of soil organic carbon and nitrogen in water-stable aggregates in abandoned agricultural lands in an arid ecosystem of Northwest China. *Journal of Arid Land*. 8: 350-363.

Webster, R. 2001. Statistics to support soil research and their presentation. *European Journal of Soil Science*. 52:331-340.

Wiesmeier, M., Steffens, M., Mueller, C.W., Kölbl, A., Reszkowska, A., Peth, S., Horn, R. and Kögel-Knabner, I. 2012. Aggregate stability and physical protection of soil organic carbon in semi-arid steppe soils. *European Journal of Soil Science*. 63: 22-31.

Zinn, Y.L., Lal, R. and Resck, D.V.S. 2005. Changes in soil organic carbon stocks through agriculture in Brazil. *Soil and Tillage Research*. 84: 28-40.

Zuur, A.F., Ieno, E. and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology Evolution*. 1: 3-14.

CHAPTER 5

SUMMARY AND CONCLUSION

In recent years, there has been a growing concern on the impact of recurrent prescribed burning and herbivore grazing on soil quality and forage productivity. This dissertation aimed to investigate the effects of late burning and herbivore grazing on soil nutrients and carbon dynamics in a savanna grassland at KNP. Accordingly, the second chapter reviewed literature on prescribed burning and herbivore grazing as land management practices in savannas and their impacts on soil physical and chemical properties. The third chapter evaluated changes in soil carbon and nutrients as a consequence of frequent burning and herbivore grazing in savanna grassland soils. Lastly, the fourth chapter assessed the distribution of SOC in bulk soil and within aggregate size fractions of grassland soils.

Taken together, the results obtained from this study revealed that frequent burning and herbivore grazing adversely affected some soil nutrients and altered carbon dynamics in savanna grasslands. Specifically, chapter 3 results showed a decrease in total C and total N accompanied by a decrease in aggregate stability and a consequent reduction in Ca, ECEC and Zn. This was mainly because of combustion and trampling effects brought about by fire and grazing, which altogether led to disrupted and weaken aggregates and this led to a subsequent depletion of some soil nutrients. Chapter 4 further revealed that frequent burning and herbivore grazing decreases SOC within bulk soil and aggregate fractions. Specifically, SOC in large macroaggregates was reduced by 40%, while silt+clay associated SOC slightly decreased by 3%. The different thresholds of SOC depletion are probably driven by the residence time and surface area of the different sized aggregate fractions. The silt+clay fraction of the soil has a larger specific surface area and longer residence time compared to large macroaggregates. Large macroaggregates are prone to disturbance and provide less adsorption sites for SOC because of the smaller specific surface area associated with them. The decline in SOC and soil nutrients poses serious concerns for grassland productivity in savanna grasslands considering the ability of acidic loamy sand soils to maintain primary ecosystem functions, such as soil fertility for biomass (grass) production.

Importantly, this work enhanced our understanding of the effects of frequent burning and herbivore grazing on soil nutrients and carbon dynamics in savanna grasslands. An attempt at underpinning the precise mechanisms governing the deterioration of soil quality, was one of the contributions of this work. Previous studies have focused on the mechanisms of SOC stabilization and the underlying SOC dynamics. Less attention has been paid to destabilization mechanisms of SOC, particularly in grassland soils where SOC is held in larger proportions in the uppermost layer of the soil. The findings of this study shed light on the destabilization mechanisms of SOC associated with frequent burning and herbivore grazing in savanna grasslands. This work also contributed to improved understanding on the fire-herbivory feedbacks on soil nutrient dynamics within the pedoderm layer, which is the main stock of nutrients and SOC in grassland soils. Future work should focus on how fire-herbivory interactions influence the vertical distribution of soil nutrients and SOC stock. Furthermore, our experiment was ongoing for about 7 years which is normally considered medium term in ecological studies. Studies conducted over such a medium-term period often provide limited understanding of the mechanisms operative and dynamics at play compared to long term studies. Long term experimentation would provide a more comprehensive understanding of the interaction effects of fire and herbivory on soil nutrients and carbon dynamics in savanna grasslands.

APPENDICES

Appendix 1: T-test analysis results for soil nutrients in the control and burnt+grazed grassland sites

Nutrients	Control (mean)	Burnt+grazed (mean)	P value
Total C	30.12	22.44	0.1339
Total N	1.60	1.32	0.2782
C/N ratio	18.65	18.21	0.8327
P	29.20	33.80	0.4807
Exch. Acidity	0.04	0.06	0.2371
ECEC	29.00	28.26	0.8386
Ca	4196.20	3926.60	0.6858
Mg	809.20	874.80	0.5789
K	530.60	549.60	0.5785
Zn	1.94	1.84	0.8441
Mn	8.40	11.80	0.2059
Cu	10.02	13.06	0.4189
MWD	0.85	0.80	0.5806
SOC	24.22	16.81	0.0867

$P < 0.05$ shows significant differences between the variables.

Appendix 2: Classes of stability depending on the values of mean weight diameter after disaggregation

MWD	Stability	Sealing	Overland flow and erosion
<0.4 mm	Very unstable	Always	High and constant risk for all topographic positions
0.4-0.8 mm	Unstable	Very frequent	Frequent risk for all conditions
0.8-1.3 mm	Partly stable	Frequent	Risk depending on climatic and topographic parameters
1.3-2.0 mm	Stable	Rare	Low risk
>2.0 mm	Very stable	Very rare	Very low risk

Source: Le Bissonnais *et al*. (2003)

Appendix 3: Interpretation of Pearson's correlation coefficient (r)

Correlation Coefficient Value (r)	**Direction and Strength of Correlation**
-1	Perfectly negative
-0.8	Strongly negative
-0.5	Moderately negative
-0.2	Weakly negative
0	No association
0.2	Weakly positive
0.5	Moderately positive
0.8	Strongly positive
1	Perfectly positive

Source: Ratnasari *et al*. (2015)

Appendix 4: Two-way analysis of variance showing the effect of prescribed burning and herbivore grazing on the distribution of SOC within aggregate fractions

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Treatment Factor	1	126.0	126.0	4.767	0.0365	*
Fraction Factor	3	1791.6	597.2	22.594	0.00000338	***
Treatment factor: Fraction factor	3	34.6	11.5	0.437	0.7283	
Residuals	32	845.8	26.4			

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1