

**THE EFFECT OF FIRE HISTORY ON SOIL NUTRIENTS, SOIL ORGANIC
CARBON AND SOIL RESPIRATION IN A SEMI-ARID SAVANNA WOODLAND,
CENTRAL NAMIBIA**

BY

ELISE N. NGHALIPO



**NAMIBIA UNIVERSITY
OF SCIENCE AND TECHNOLOGY**

Thesis submitted to the Namibia University of Science and Technology, School of
Natural Resources and Spatial Sciences, Department of Agriculture and Natural
Resources Sciences in partial fulfilment of the requirements for the Degree of Master
in
Natural Resources Management

Supervisor: Dr. Dave Joubert (Agriculture and Natural Resources Sciences
department, Namibia University of Science and Technology)
Co-Supervisor: Prof. Heather L. Throop (School of Earth & Space Exploration and
School of Life Sciences, Arizona State University)
Co-Supervisor: Dr. Alex Groengroeft (Institute of Soil Science, University of
Hamburg)

JUNE 2016

DEDICATION

This thesis is dedicated to my family (Nghalipo's family) for believing in me and having so much faith in me and therefore supporting me in the decision to do this Masters. I appreciate your constant love and support that shaped both my social and academic life.

ACKNOWLEDGEMENTS

My deepest gratitude goes to my Heavenly Father, who is my source of wisdom and strength. Secondly, I would like to thank the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) for funding my studies and the Namibia University of Science and Technology for giving me this opportunity. Permission to carry out research in the Waterberg Plateau Park was granted by the Ministry of Environment and Tourism, to whom I am very much thankful.

I would like to express my gratitude and appreciation to my supervisor Dr. Dave Joubert, my Co-Supervisors Prof. Heather Throop and Dr. Alex Groengroeft, for their mentorship, support and motivation throughout the project and for doing so with patience. I would not forget my Waterberg crew (Herman Aindongo, Nekulilo Uunona, Vistorina Amputu, Siphwe Lutibezi, Allan Kandjai & Quanita Daniels); they were my family away from home. Special thanks to the soil laboratory staff in the Ministry of Agriculture, Water and Forestry, (especially Mrs. Albertha Sipapo) for their great help and support during the soil analyses. To my family and friends, if it was not for your faith in me, and your constant reminders that “I can do it” this thesis would not have been complete. Last but not least, I would like to express my gratitude to the people who directly or indirectly assisted with this thesis in one way or another and whose names are not listed above, thank you very much and may God richly bless you.

DECLARATION

I, Elise N. Nghalipo, declare hereby that this study is a true reflection of my own research, and that this work, or part thereof has not been submitted for a degree in any other institution of higher education. No part of this thesis may be reproduced, stored in any retrieval system, or transmitted in any form, or by means (e.g. electronic, mechanical, photocopying, recording or otherwise) without the prior permission of the author, or the Namibia University of Science and Technology in that behalf.

I, Elise N. Nghalipo, grant the Namibia University of Science and Technology the right to reproduce this thesis in whole or in part, in any manner or format, which the Namibia University of Science and Technology may deem fit, for any person or institution requiring it for study and research; providing that the Namibia University of Science and Technology shall waive this right if the whole thesis has been or is being published in a manner satisfactory to the University.

..... Date

Elise N. Nghalipo

TABLES OF CONTENTS

DEDICATION	i
ACKNOWLEDGEMENTS	ii
DECLARATION.....	iii
TABLES OF CONTENTS.....	iv
LIST OF FIGURES.....	vi
LIST OF TABLES.....	vii
ABSTRACT	viii
ACRONYMS	x
REPORTED RESULTS FOR THIS DISSERTATION.....	xi
CHAPTER 1: INTRODUCTION.....	1
1.1 BACKGROUND AND RATIONALE OF THE STUDY	1
1.2 PROBLEM STATEMENT / SIGNIFICANCE OF THE STUDY	5
1.3 OBJECTIVES.....	6
1.3.1 Research objectives	6
1.3.2 Research questions.....	6
1.4 ETHICAL CONSIDERATION	6
CHAPTER 2: THE EFFECTS OF FIRE HISTORY ON SOIL NUTRIENTS AND SOIL ORGANIC CARBON IN A SEMI-ARID SAVANNA, CENTRAL NAMIBIA	7
2.1 INTRODUCTION.....	7
2.2 STUDY OBJECTIVES.....	9
2.3 STUDY SITE AND METHODS.....	10
2.3.1 Site description	10
2.3.2 Data collection and soil chemical analyses.....	12
(i) Soil Texture.....	12
(ii) Soil Organic Carbon (SOC)	12
(iii) Available Phosphorus	12

(v) Exchangeable cations.....	13
2.5 RESULTS.....	13
2.6 DISCUSSION	19
CHAPTER 3: EFFECTS OF FIRE HISTORY AND VEGETATION PATCH TYPE ON SOIL RESPIRATION IN A SEMI-ARID SAVANNA, CENTRAL NAMIBIA	22
3.1 INTRODUCTION.....	22
3.2 STUDY OBJECTIVES.....	24
3.3 MATERIALS AND METHODS.....	25
3.3.1 Site description	25
3.3.2 Experimental design and measurement of soil respiration	25
3.3.3 Soil temperature and soil moisture	28
3.3.4 Laboratory incubation	29
3.4 DATA ANALYSIS	29
3.5 RESULTS.....	30
3.5.1 Field Experiment.....	30
3.6 DISCUSSION	35
3.7 CONCLUSIONS	38
CHAPTER 4: CONCLUSION AND RECOMMENDATIONS.....	39
4. REFERENCES.....	42
APPENDIX	53
Appendix1. Chemical analyses methods.....	53
(i) Soil Texture	53
(ii) Organic Carbon (SOC).....	53
(iii) Available Phosphorus	54
(iv) Total Nitrogen	54
(v) Exchangeable cations	55
Appendix 2.	56

Appendix 3.	57
Appendix 4.	58

LIST OF FIGURES

Fig. 2.1: Location of Waterberg Plateau Park in Namibia and WPP map showing the fire blocks where the field experiment was conducted.	11
Fig. 2.2: Mean ($\pm$ SE; N = 13) SOC (%), total N (%) and P (ppm) in fire blocks with different time since last burn (1, 2, 14, and 24 y) measured under two vegetation patch types (inter-canopy and tree canopy). Means with different superscripts and numbers are significantly different at $P < 0.05$	16
Fig. 2.3: Mean ($\pm$ SE; N = 13) cations ions (K, Na, Mg and Ca; ppm) in fire blocks with different time since last burn (1, 2, 14, and 24 yrs) measured under two vegetation patch types (inter-canopy and tree canopy). Means with different superscripts and numbers are significantly different at $P < 0.05$	18
Fig. 3.1: Soil collar being inserted into the soil for a bare ground patch. The collar is inserted carefully to minimize soil surface disturbance and it is inserted 15 minutes prior to measurements.....	28
Fig. 3.2: Measuring soil CO ₂ flux on bare ground. The soil chamber is placed over the collar and measurements complete a 3 cycle without moving or interfering with the machine.....	29
Fig. 3.3: Mean ($\pm$ SE; [Feb: N = 24; April: N = 38]) soil CO ₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in fire blocks with different time since last burn (2, 3, 15 and 25 yrs) measured under three vegetation patch type (bare, grass and shrub) for A) February, during a dry period, and B) April, during a wet period. Means with different superscripts and numbers are significantly different at $P < 0.05$	32
Fig. 3.4: Mean ($\pm$ SE; N = 75) soil CO ₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) during laboratory incubations from soil samples collected in fire blocks with different time since last burn (2, 3, 15 and 25 yrs) under three vegetation patch types (bare, grass and shrub) during two sampling periods for A) February (dry period) and B) April (wet period). The samples were incubated over 3 weeks. Means with different superscripts and numbers are significantly different at $P < 0.05$	34
Fig. 3.5: Correlation between soil respiration and water content among vegetation patch types.....	36

LIST OF TABLES

Table 2.1: Fire history (time since last burn) of different fire blocks recorded at Waterberg between 1989 and 2013.....	12
Table 2.2: The soil texture content for different fire blocks. Means with different lower-case letters are significantly different at $P < 0.05$	19
Table 3.1: Fire history (time since last burn) of different fire blocks recorded at Waterberg between 1989 and 2013.....	26

ABSTRACT: Fire is recognized as an integral part of savanna ecosystems that shaped and continues to shape savannas since the Miocene. The prevalence of fire in this system influences nutrient cycling and soil (carbon) C pools. Fire may affect ecosystem productivity and biogeochemical processes through nutrient volatilization, altered organic matter quantity, and indirectly through altered vegetation structure. Despite the resulting effects on soil resources, substantial uncertainty about fire history effects exists, especially in semi-arid ecosystems. I explored the independent and interactive effects of fire history and vegetation patch types (bare ground, under grass and under shrub) on soil nutrients, soil organic carbon (SOC) and soil respiration in a semi-arid ecosystem, central Namibia. To determine the independent and interactive effects of fire history and vegetation patch types on soil nutrients and SOC, I collected soil samples in four fire blocks with different fire history (time since last burn ranging from 1- 25 years and fire interval ranging from 6.2 – 18.5 years). In each fire block, six transects (200 m) were laid out randomly, and soil samples were collected at every 40 m along each transect in the 0-10 cm soil layer. Chemical analyses for soil nutrients (total N, P, K, Na, Ca & Mg) and SOC were performed at the soil Laboratory. To determine the effect of fire history on soil respiration and how it responds under different vegetation patch types, I used a LI-6400XT instrument. Eight sampling sites were established in all four fire blocks, with three treatments per site. The treatments represented the vegetation patch types (bare ground, under grass and under shrub). Additionally, I collected soil cores from each sampling point for later determination of gravimetric water content and laboratory incubation experiment that allowed me to investigate potential carbon mineralization, to control water content and temperature and other environmental conditions that occur under field conditions. In the incubation experiment, soil cores were incubated for 3 weeks at 60% water holding capacity (WHC), under room temperature. Soil CO₂ efflux was measured for 15 days with an infrared gas analyzer (Licor 6400).

Soil organic carbon was not significantly different among fire blocks and vegetation patch types. The blocks that burned 2 and 24 years ago had low total N relative to the 1 and 14 blocks. The block that burned 2 years ago had the lowest available P relative to other fire blocks. Sodium showed a consistent trend, decreasing with increasing time since last burn. There was no clear trend for other exchangeable

cations K, Mg and Ca; however they were high in the recently burned area. These cations typically increase after fire because of their presence in the ash as a result of high threshold temperature at which these elements volatilize, which may have not been reached during the fire. Soil respiration responded to time since last burn differently under different vegetation patch types with under shrub having generally high soil CO₂ efflux relative to under grass and bare ground, suggesting fire may have important indirect effects on soil respiration through its alteration of vegetation cover. In the laboratory experiment, soil CO₂ efflux was high relative to the field experiment, and was not significantly different among vegetation patch types. Based on my field and incubation results, this study concluded that the higher soil respiration observed under shrubs in the field experiment is largely attributed to root respiration, suggesting fire did not significantly hurt soil microbes.

Fire history had a limited and inconsistent effect on soil nutrients, SOC and soil respiration. This suggests that soil resources return rapidly to pre-fire conditions. In addition, these fires were likely to have not been sufficiently intense to cause long-term detrimental impacts and impair the recovery of soil resources. Moreover, site to site spatial variation may have had a stronger controlling influence on soil nutrients, soil organic carbon and soil respiration. Therefore there should be no concern in using fire within the experienced frequencies (6.2 – 18.5 years) as a tool to improve positive resource utilization.

Keywords: *cations; dystrophic sandy; fire blocks; LI-6400XT; microbial activity; organic matter; soil CO₂ efflux; time since last burn; vegetation patch type*

ACRONYMS

ANOVA	Analysis of variance
Ca	Calcium
C	Carbon
CO ₂	Carbon dioxide
Mg	Magnesium
nm	nanometres
N	Nitrogen
ppm	parts per million
K	Potassium
P	Phosphorus
PVC	Polyvinyl Chloride
Na	Sodium
SOC	Soil Organic Carbon
SOM	Soil Organic Matter
SASSCAL	Southern African Science Service Centre for Climate Change and Adaptive Land Management
WHC	Water Holding Capacity
WPP	Waterberg Plateau Park

REPORTED RESULTS FOR THIS DISSERTATION

The following section lists the chapters, submitted for the purpose of this thesis, that emanate from the “the effect of fire history on soil nutrients, soil carbon and soil respiration in a semi-arid savanna woodland, central Namibia” project. For each chapter, the title is provided. In addition, a short statement regarding the rationale of each chapter and the author’s contribution to it is provided.

Each chapter of this thesis was prepared as an individual report.

Chapter 1: I present a detailed background and rationale for the study.

Chapter 2: Focuses on the effects of fire history on soil nutrients and soil organic carbon in a semi-arid savanna. I investigate how fire history and vegetation patch type, and their interaction influence soil nutrients and soil organic carbon.

My contribution: I was responsible for the project design (partly), including the design of the data sheets, and for the collection of all the data used in writing the paper. I compiled the preliminary results, analysed data and wrote the manuscript.

Chapter 3: Focuses on the effects of fire history on soil respiration in a semi-arid savanna. I investigate how soil respiration responds to time since last burn under different vegetation patch types (bare ground, under grass and under shrub).

My contribution: I was responsible for the project design (partly), including the design of the data sheets, and for the collection of all the data used in writing the paper. I compiled the preliminary results, analysed data and wrote the manuscript.

Chapter 4: Conclusions and recommendation. I summarize the findings of this study.

CHAPTER 1: INTRODUCTION

1.1 BACKGROUND AND RATIONALE OF THE STUDY

Fire is a natural disturbance that occurs in most ecosystems but it is of particular importance in grasslands, savannas, and Mediterranean ecosystems (Trollope, 2007). It is recognised as a key factor that shaped and continues to shape savannas (Neary *et al.*, 2005; Oktay *et al.*, 2009) since the Miocene (Osborne, 2008). Savannas occupy about 20% of the land surface of the Earth and 40% of Africa's land surface (Scholes & Hall, 1996). Savannas have about 10-50% canopy coverage of woody plants and a well-developed grass layer (Scholes & Hall, 1996). They are the basis of major industries in Africa including livestock, biodiversity conservation and wildlife-related tourism (van Wilgen, 2009). Savannas have a distinctive dry season, which in combination with the grassy understory fuels make savannas extremely flammable during the dry season (Scholes & Hall, 1996). Fires of both natural and anthropogenic origin can increase available soil nutrients (Snyder, 1986), and regulate ecosystem productivity and diversity (DeBano *et al.*, 1998). Fire regimes have been altered by human activities (such as fire suppression and early or late burning practices) particularly in recent times, by either reducing or increasing fire intensity, fire severity and fire return interval (Nguyen, 2011; Satyam & Jayakumar, 2012). The effects of anthropogenic transformations of fire regimes are not well understood and documented, especially in arid and semi-arid savanna ecosystems (Sheuyange *et al.*, 2005). Fire regimes and their changes are a critical foundation in understanding and describing effects of fire on soil resources, vegetation structure and composition as well as the global carbon cycle under the changing climate (Grissino-Mayer *et al.*, 2004; Schoennagel *et al.*, 2004; Pechony & Shindell, 2010).

Early views on the role and use of fire in the management of savanna ecosystems were divergent in Southern Africa (Van Wilgen, 2009). Some believed fire to be something undesirable that should totally be avoided. This led to the establishment of Fire Protection Committees in 1946, which focused on the protection and suppression of any burning in arid savanna areas (Trollope, 1984 as cited in Van

Wilgen, 2009). Others recognised that deliberate burning had several ecological benefits (Busse, 1908; Staples, 1926 as cited in Van Wilgen, 2009). In the 1950s, it was recognised that the role of fire needed to be better understood, and views toward fire as an extreme enemy have changed slowly over the ensuing decades (Van Wilgen, 2009). Many came to view fire as something that was not always detrimental to the ecosystems, and had to be properly understood and appreciated (Van Wilgen, 2009). This led to the initiation of many critically important long-term burning experiments in Southern Africa (e.g. in Etosha National Park, Kruger National Park and Pilanesberg National Park (Van Wilgen, 2009)). As ecological understanding advanced further among land managers, fire has become recognized as an integral part of savanna ecosystems that is both inevitable and necessary (Van Wilgen, 2009). In addition, land managers have increasingly viewed fire as a legitimate land management tool, if carefully timed and used (Goldammer, 1999).

Whether naturally or anthropogenically applied, fire influences vegetation communities. Fire is important in determining the composition and structure of the savanna ecosystems (Bond & Van Wilgen, 1996; Anderson *et al.*, 2003). This is so because in the absence of fire, considerable areas of savannas could potentially develop into closed woodlands (Van Wilgen, 2009). Fire reduces the chances of woody establishment events by drastically increasing the mortality of seedlings and saplings and by maintaining woody species at a browsable level (Joubert *et al.*, 2008). Fire may indirectly influences soils by changing vegetation composition and structure, and litter cover, which in turn influences organic matter inputs and the amount of bare ground exposed. The degree of fire impact in an ecosystem depends largely on fire regimes (DeBano *et al.*, 1998). Fire regimes are characterized by the combination of fire frequency, intensity, severity, seasonality, vegetation composition, physical characteristics of fuel load, size of burn that prevail in a given area (Oba, 1990; DeBano *et al.*, 1998; Trollope, 1999). The concept of fire regime provides an integrated way of understanding the patterns of fire and the impacts of fire on ecosystem composition and structure (Hardy *et al.*, 1998; Morgan *et al.*, 2001; McKenzie *et al.*, 2011).

Fire can directly alter chemical, biological and physical properties of the soil (Menaut *et al.*, 1993; Certini, 2005) and therefore influence soil carbon properties, nutrient cycling patterns and soil surface carbon dioxide (CO₂) efflux. Fire may influence the rate of soil surface CO₂ efflux by altering the contribution of above and belowground plant respiration to total soil CO₂ emissions and by modifying the amount of soil organic matter (Sawamoto *et al.*, 2012). In low intensity fires, combustion of litter and soil organic matter increases plant available nutrients, which results in rapid growth of herbaceous plants and a significant increase in plant storage of nutrients (Satyam & Jayakumar, 2012). On the other hand, high intensity fires can result in the complete loss of soil organic matter, volatilization of nitrogen (N), phosphorus (P), sulphur (S), potassium (K) and the death of microbes (Satyam & Jayakumar, 2012). The loss of these soil macronutrients may have a direct impact on ecosystem productivity because they are essential for plant growth and nutrition and needed in relatively large quantities (Satyam & Jayakumar, 2012). Fire effects can vary among soil types; depending on the temperature reached at different soil depths as well as the degree of heating they can withstand (Certini, 2005). Sandy soils are more prone to the effects of fire because of their loose structure and texture whereas clay is less vulnerable due to its cohesiveness structure (DeBano, 2000). In addition to soil type, different inherent temperature thresholds under which soil nutrients volatilize determine the response of nutrients to fire (Neary *et al.*, 1999; Certini, 2005). In a synthesis of fire responses in an African savanna, Scholes & Walker (1993) reported that in sandy soils, N may be completely lost in a soil surface at 600°C fire temperature. In contrast, only half of the N may be lost in a soil surface at 200°C fire temperature. DeBano *et al.*, (1998) reported that in savanna soils loss of organic carbon by burning can occur even at relatively low temperatures such as 200°C, but complete combustion is only observed at high temperatures 450°C – 500°C. Thus the effects of fire on soil resources may be influenced by several factors that ultimately determine the degree of its impact.

One of the most evident effects of fire on soils is the direct combustion of organic matter located on, or near, the soil surface (DeBano, 2000). Soil organic matter contains approximately 58% carbon (Post *et al.*, 1999) and other important elements (such as N, P, S etc.) that are bound to organic matter and released when the

organic matter is decomposed or combusted (DeBano, 2000). Modification of organic matter by fire may also influence soil microbial populations and some microbial species may be favoured over others (Macadam, 1989). Fire may increase the ratio of bacterial relative to fungi because bacteria are generally more heat tolerant than fungi (Bollen, 1969;; Widden & Parkinson, 1975; Bissett & Parkinson, 1980;Vazquez *et al.*, 1993). This may be due to the difference in lethal temperature between the two microbial taxa. In a montane forest fire study, Dunn & DeBano, (1977) reported that bacteria lethal temperature was 210°C in dry soil and 110°C in wet soil and for fungi it was 155°C and 100°C, respectively. Widden & Parkinson (1975) also found a water-soluble substance in the soil after a fire, which was toxic for fungi. As a result, fire may inhibit or accelerate microbially mediated processes through the modification of organic matter (Macadam, 1989).

The effects of fire on soils have been extensively studied in different ecosystems worldwide; however there has been controversy as to whether fire increases or decreases soil nutrients (Scholes & Walker, 1993; Ross, 1997; Neff *et al.*, 2005; Castaldi *et al.*, 2010; Novara *et al.*, 2013; Molla *et al.*, 2014). In particular, we know little about what happens to soil nutrients after fire in some semi-arid savanna ecosystems, including Namibian savannas. The response of soil properties to fire varies even in similar ecosystems (Neary *et al.*, 2005). Some studies reported an increase in soil organic carbon (SOC) following the combustion of organic matter in savanna soils (Raison, 1979; Kovacic *et al.*, 1986;Anderson *et al.*, 2003; Prieto-Fernandez *et al.*, 2004), whereas Kavdir *et al.*, (2005) reported no significant change or even an increase in soil organic carbon content. Fire may also affect nutrient forms differently; Kutiel & Naveh (1987) found post-fire decreases in overall soil nutrient availability but increases in plant available forms. Similarly, in Nylsvley, a poor nutrient (sandy soils) semi- arid savanna ecosystem, Scholes & Walker (1993) reported that after fire, nutrients such as N, P and S are returned to the soil in the form of ash, readily available for plant use. This temporarily enhances the primary production and promotes an improvement in grass quality in recently burnt areas (Scholes & Walker, 1993).

1.2 PROBLEM STATEMENT / SIGNIFICANCE OF THE STUDY

Waterberg Plateau Park (WPP) is at the arid end of the woodland savanna biome (Giess, 1971) and like most savanna ecosystems, WPP experiences natural fires due to its extended dry season, which in combination with the grassy understorey fuels make it extremely flammable much of the year. The known recent fire history at WPP (1976 to 2013) includes naturally-igniting fires, accidental fire and intentional application to improve productivity and grazing quality. WPP has a diverse fire history throughout the plateau. For example, my study area has a fire history ranging from 1 to 25 years of time since last burn (Table 2.1 & 3.1). However, there is a knowledge gap on the effects of fire history on soil resources at WPP. Fire research has not received much attention in Namibian savannas and thus not much has been documented scientifically. In Namibia, fire studies have been limited to investigating certain aspects such as the effect of fire frequency on savanna woodlands (Sheuyange *et al.*, 2005); the role of fire in preventing bush thickening (Joubert *et al.*, 2012) and the assessment of fire frequency, fire seasonality and fire intensity within the Okavango region (Stellmes *et al.*, 2013).

A critical gap in our understanding of the effects of fire history remains, in that we have limited understanding of responses of SOC, soil nutrients and soil respiration in semi-arid woodland savanna ecosystems. Previous work in similar woodland savannas, e.g. Nylsvley and Kruger National Park, have focused on different questions such as how fire impacts nutrient cycling (Scholes & Walker, 1993); the interactive response of herbivores, soils and vegetation to annual burning (Mills & Fey, 2005) and the impacts of long-term fire treatments on in situ soil hydrology (Riddell *et al.*, 2012). These studies have limited data on the effects of fire history on soil resources. Therefore, the key element in this research project was to investigate the effects of fire history on soil organic carbon, soil nutrients and soil respiration and build on the current knowledge and understanding of fire effects on soils in savanna ecosystems. This project is part of a broader project looking at the impacts of fire on biodiversity and ecosystem processes, as well as the interactive response of

herbivores, soils and vegetation to fire history in woodland savannas, at the WPP.

1.3 OBJECTIVES

1.3.1 Research objectives

- To determine the effects of time since last burn on soil organic carbon and soil nutrients in semi-arid woodland savannas.
- To determine whether soil respiration responds to time since last burn the same way under different vegetation patch types (bare ground, under grass and under shrub) semi-arid woodland savannas.

1.3.2 Research questions

- Will soil organic carbon and soil nutrients increase in response to time since last burn semi-arid savannas?
- How does soil respiration respond to time since last burn under different vegetation patch types (bare ground, under grass and under shrub) semi-arid savannas?

1.4 ETHICAL CONSIDERATION

The research was conducted under the authority of the Ministry of Environment and Tourism, specifically the WPP management. Since the study was conducted in a conservation area, the research was carried out in line with the rules as well as the objectives of the park to ensure that no harm was imposed on biodiversity. Large leaf and stem litter was gently removed with hands during sampling to minimizing soil disturbance. In addition, all areas where soil samples were taken were rehabilitated to prevent small invertebrates from falling in the sampled holes.

CHAPTER 2: THE EFFECTS OF FIRE HISTORY ON SOIL NUTRIENTS AND SOIL ORGANIC CARBON IN A SEMI-ARID SAVANNA, CENTRAL NAMIBIA

2.1 INTRODUCTION

Soils are important reserves of carbon and nutrients in the biosphere (Neary *et al.*, 2008). Soil nutrients and carbon: nutrient ratios play significant roles in regulating the productivity of terrestrial ecosystems and soil carbon (C) pools (Parton *et al.*, 1987; Vitousek & Howarth, 1991). Many of the terrestrial ecosystems, notably savannas, grasslands and Mediterranean ecosystems are fire-prone, with both natural ignition and anthropogenically applied fires (Trollope, 2007). In particular, savannas are characterized by grassy understory fuels which, in combination with the characteristic of extended dry season, make them extremely flammable much of the year (Scholes & Hall, 1996). The prevalence of fire in these systems influences nutrient cycling and soil C pools (Holt & Coventry, 1990). This may have long-term effects on site productivity as a result of nutrient losses (e.g. nitrogen (N) and phosphorus (P) volatilization) and redistribution via the translocation of nutrients downward in the soil profile during fire (Kauffman *et al.*, 1994; DeBano, 2000). Additionally, savannas have a variable amount of tree cover (Scholes & Walker 1993; Scholes & Archer, 1997) which may influence the size of soil nutrients and soil C pools under their canopy (Belsky *et al.*, 1989; Belsky, 1994; Ludwig *et al.*, 2004). Campbell *et al.* (1988) and Scholes & Walker (1993) reported that in savannas, concentrations of soil nutrients and SOC are substantially higher under tree canopies as compared to inter-canopy (referred to as “vegetation patch type” hereafter). Variations in soil nutrients and SOC between vegetation patch types may be a function of nitrogen fixation, high litter quality and modification of soil microclimate (e.g. moisture and temperature) under tree canopies, which in turn influences decomposition rates and microbial community composition (Belsky *et al.*, 1989; Belsky *et al.*, 1993; Hudak *et al.*, 2003). These vegetation patch type effects can potentially interact with fire by regulating the intensity of fire through the effects of grass biomass and moisture content (Higgins *et al.*, 2000; Holdo, 2005). A key question, then, is: What are the independent and interactive effects of fire and vegetation patch types on soil nutrients and SOC in woodland savannas? This is

especially relevant given that fire is an active agent of nutrient cycling (Holt & Coventry, 1990) and an important determinant of tree canopy cover in these ecosystems.

Previous studies have explored fire effects on soil nutrients [mainly N and to a lesser extent P and cations (K, Mg, Ca & Na)] and C dynamics in different savanna ecosystems. (Scholes & Walker, 1993; Cook, 1994; Ojima *et al.*, 1994; Ross, 1997; Neff *et al.*, 2005; Ansley *et al.*, 2006; Khavhagali, 2008; Castaldi *et al.*, 2010; Hurteau & Brooks, 2011; Holdo *et al.*, 2012; Novara *et al.*, 2013; Molla *et al.*, 2014). However, fire effects on soils vary greatly amongst savannas because some ecosystems are on nutrient-rich soils whereas some are on nutrient-poor soils (Khavhagali, 2008; Holdo *et al.*, 2012). Additionally, this variability may also be a function of factors such as fire intensity, fire severity, type of burned vegetation, distribution of fuel on the soil surface and regional climate (Certini, 2005; Novara *et al.*, 2013) which vary over time and landscape space (Neary *et al.*, 2005). Some studies reported a decline in SOC following the combustion of organic matter in savanna soils (Fynn *et al.*, 2003; Knicker, 2007), whereas Kavdir *et al.*, (2005) reported no significant change in SOC content after fire. In a study done in the poor soil nutrient Australian savannas, Cook (1994) reported a flush of nutrients (P, K, Ca, & Mg) and a high loss of nitrogen due to volatilization. In another nutrient poor soils savanna ecosystem, Aranibar *et al.*, (2003) and Mills & Fey (2004) reported a decline in soil organic matter (SOM) due to frequent burning which increases mineralization of organic matter and microbial activities.

Recent fire studies have considered the interactive effects of fire frequency and vegetation patch types effects on soil nutrients and soil C content in both poor and rich-nutrient soils in semi-arid ecosystems, specifically in the Kruger National Park (Coetsee *et al.*, 2010; Holdo *et al.*, 2012; Khavhagali, 2008). These studies reported no effect of fire on soil nutrients and soil C content; however they reported strong positive effects of tree canopies on soil nutrients and soil C content (Khavhagali, 2008; Coetsee *et al.*, 2010; Holdo *et al.*, 2012). Generally, fire reduces tree canopy cover in these ecosystems, thus in their studies they concluded that fire may affect

nutrients and C content in soils indirectly; by altering vegetation structure (Khavhagali, 2008; Coetsee *et al.*, 2010; Holdo *et al.*, 2012). The expansion on these earlier studies would improve our understanding of managing semi-arid woodland savanna ecosystems in the region. Here I used fire history data (with time since last burn ranging from 1 to 24 years) of different fire management blocks (Table 2.1) in a semi-arid woodland savanna to determine the independent and interactive effects of fire and vegetation patch types on soil nutrients and SOC. This is an important step for a better comprehension of the dynamics of carbon and soil nutrients in semi-arid woodland savanna ecosystems in response to ecosystem disturbances such as fire, to promote land management practices that may improve site productivity and terrestrial carbon sequestration (Concilio *et al.*, 2006). In this study, I aimed at determining how soil nutrients and SOC are affected by (i) fire history (time since last burn ranging from 1 - 24 y) (ii) vegetation patch type (tree canopy and inter canopy) in four different fire blocks (Table 2.1).

2.2 STUDY OBJECTIVES

In order to determine how soil nutrients and SOC are affected by (i) fire history (time since last burn ranging from 1 - 24 y) (ii) vegetation patch type (tree canopy and no tree canopy) and (iii) the interaction of fire and vegetation patch type, I collected soil samples along six transects in each of the four fire blocks (1, 2, 3 & 4; Table 2.1). I hypothesized that 1) soil nutrient status and SOC would differ among fire blocks; the block that burned 24 years ago would have higher SOC and soil nutrient contents relative to the recently burned area (1 year), 2) soil nutrient and SOC contents under tree canopies would be enhanced relative to inter-canopy under the assumption that beneath canopies, there is high litter quality and shade cast would reduce light intensity, modify soil microclimate (e.g. moisture and temperature) and therefore enhance nutrient mineralization (Weltzin & Coughenour, 1990) and 3) there would be a significant interactive effect between fire and vegetation patch types in recently (1 and 2 years) burned areas relative to the areas burned 14 and 24 years ago, because fire have reduced tree canopy in recently burned areas than in the blocks that burned 14 and 24 years ago. In a study done in the same area along the same

transects, Amputu (2016) reported that woody cover increased with time since last burn [1 y = 20. 3%; 2 y = 39. 7%; 14 y = 51. 0% and 24 y= 67. 5%].

2.3 STUDY SITE AND METHODS

2.3.1 Site description

The research was conducted in Waterberg Plateau Park (WPP) a semi-arid woodland savanna in the north central part of Namibia (between 20° 37'S, 17° 08' E and 20° 11'S, 17° 26' E), about 280 km northeast of Windhoek and 64 km east of Otjiwarongo (Fig. 2.1) at an elevation of 1650 m above sea level. The sandstone plateau rises up to 200 m above the surrounding plain, extending 50 km in length and 16 km in width (Schneider, 1993). The park is about 45 000 ha. The top of the plateau is made up of solidified dunes, known as aeolianite, which belongs to the Etjo formation and forms part of the Karoo sequence (Hegenberger, 1990). The sandstone is covered by Kalahari sand from the Kalahari Basin and is brownish to light grey and medium grained (Erb, 1993). The soil is dystrophic sandy with relatively low clay content ($\leq 3.7\%$) with pH ranging from 3.6 to 6.0 (Erb, 1993; Erckie, 2007). The vegetation is classified as "tree savanna and Kalahari woodland" (Giess, 1971). The woodland overstorey is mostly dominated by *Terminalia sericea* (Schneider, 1993). *Burkea africana*, *Ochna pulchra* and *Combretum* spp. are also common on the plateau (Schneider, 1993). The understorey consists of grass species such as *Eragrostis pallens*, *Brachiaria nigropedata*, and *Digitaria seriata*.

The climate is strongly seasonal (Erckie, 2007). Average annual rainfall is 450.2 ± 75.4 mm (Mukaru, 2009). Rain falls predominantly in summer, of which 90% of this summer rain falls between October and March (Erb, 1993). The annual number of days with rainfall range between 40 and 50 (Erb, 1993). Potential annual evaporation ranges between 2800-3000 mm (Erb, 1993). The daily minimum temperature for winter months ranges between 4°C and 5°C but during June, the temperatures can go as low as -9°C (sasscal weatherNet, 2015), whereas in summer, the daily

minimum temperature ranges between 9°C and 13°C (Erckie, 2007). The daily maximum temperature ranges between 31°C to 39.4°C (Erckie, 2007).

Waterberg Plateau Park (WPP) was proclaimed as a national park in 1972. The main objective of the park is to breed and maintain populations of rare and endangered mammal species (e.g. black & white rhino, buffalo, sable antelope, tsessebe, and roan antelope (Schneider, 1993). As part of the management, the park is divided into different fire blocks (Fig. 2.1). These fire blocks have different fire history (time since last burn ranging from 1 - 25 years and mean fire interval ranging from 6.2 – 18.5 years; Thalwitzer *et al.*, 2011). The fire history in the park is fairly known, however, there is a knowledge gap on the effects of this fire history on the soil resources.

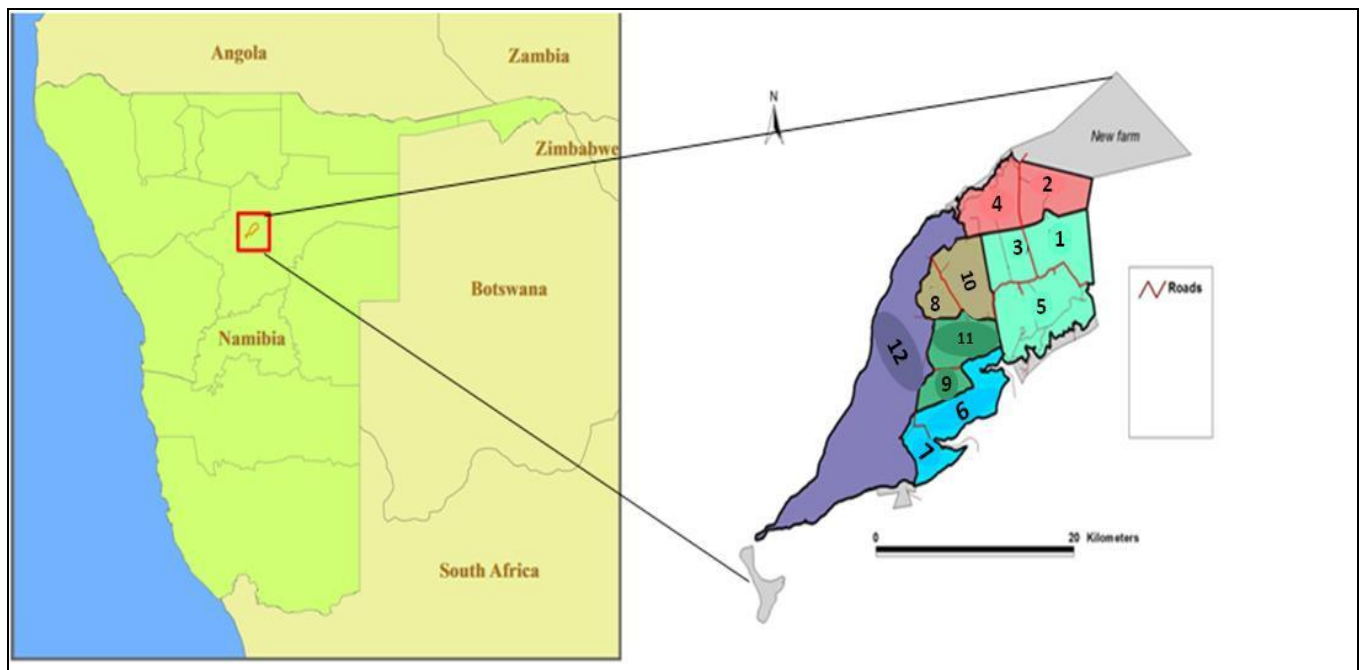


Fig. 2.1: Location of Waterberg Plateau Park in Namibia and WPP map showing the fire blocks where the field experiment was conducted.

Table 2.4 Fire history (time since last burn and mean fire return interval) of different fire blocks recorded at Waterberg between 1989 and 2013.

Fire block	Time since last burn (year)	Mean fire interval
1	1	6.2
2	2	9.3
3	14	9.3
4	24	18.5

2.3.2 Data collection and soil chemical analyses

In each fire block, six transects were laid out randomly and soil samples (10 cm depth x 7.7 cm width) were collected at every 40 m along each 200 m transect using a soil auger (n = 5 samples per transect). The transect starting location was selected randomly. Some samples were collected under canopies (tree canopy) whereas some were collected in open space (inter canopy) based on where 40 m point fell on the transect. Surface litter was removed prior to sampling. Soil samples were sealed in plastic bags and taken to the Soil Laboratory of the Ministry of Agriculture, Water and Forestry, Namibia for chemical analyses. Sampling period was from February to April 2014. The study follows space-for-time substitution which assumes that spatial and temporal variation is equivalent, hence analyses a temporal trend from a series of different aged-sites (Pickett, 1989).

(i) Soil texture

Soil texture was determined using the pippete method (Day, 1965). See the appendix for full method description.

(ii) Soil Organic Carbon (SOC)

Soil organic carbon was determined using the colorimetric Walkley-Black method (Walkley & Black, 1934). See the appendix for full method description.

(iii) Available Phosphorus

Soil available phosphorus was determined using the Olsen method (Olsen *et al.*, 1954). See the appendix for full method description.

(iv) Total Nitrogen

Total nitrogen was determined using an elemental analyzer (CHN) (LECO Corporation, St. Joseph, Michigan, USA). See the appendix for full method description.

(v) Exchangeable cations

Exchangeable cations (Na, Mg, Ca & K) were determined using Ammonium Acetate Solution, 1 M and pH 7. See the appendix for full method description.

2.4 DATA ANALYSIS

Statistical analyses were done in R 2.11.1 (R Development Core Team). Two-way analysis of variance (ANOVA) followed by Tukey's multiple comparison tests were used to assess whether soil nutrient and SOC differed among fire blocks and between vegetation patches types as well as the interaction effects between fire blocks and vegetation patch types.

2.5 RESULTS

Mean SOC ranged from 0.32 - 0.39%, whereas mean total N and available P ranged from 0.08 - 0.12% and 0.38 - 1.7 ppm respectively. Mean K ranged from 22.8 - 39 ppm whereas mean Na and Mg ranged from 4 - 30 ppm and 14 - 28 ppm respectively. Mean Ca ranged from 43 – 66 ppm. This falls within an expected range as that reported by Scholes & Walker (1993) as well as Boys (2015) in similar dystrophic sandy soils.

Soil organic carbon content (% by mass) was not significantly different ($P > 0.05$) among fire blocks (Fig. 2.2 A). Additionally, differences were not significant between vegetation patch types ($P > 0.05$) and there was also no significant interaction between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.2 A). Total N content (% by mass) showed a significant difference ($P < 0.001$) among fire blocks

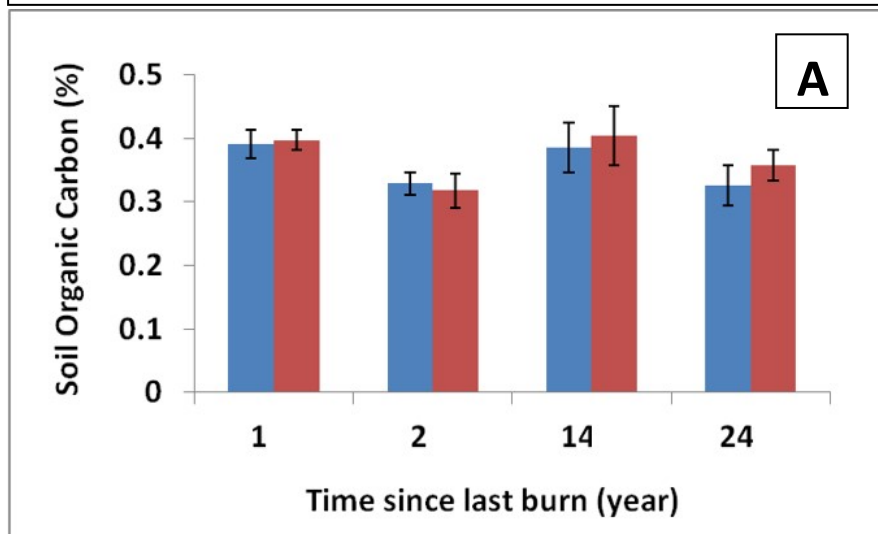
but there were no significant vegetation patch type effects ($P > 0.05$) or interaction effects between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.2 B). The block that burned 14 years ago had high total N (%) relative to other fire blocks (Fig. 2.2 B). Phosphorus (ppm) showed a significant difference ($P < 0.001$) among fire blocks but there were no significant effects between vegetation patch types ($P > 0.05$) or interaction effects between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.2 C). The fire block that burned 2 years ago had lower P (ppm) relative to other fire blocks (Fig. 2.2 C).

Potassium (K) was significantly different among fire blocks ($P < 0.001$) but there were no significant effects between vegetation patch types ($P > 0.05$) or interaction effect between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.3 A). The fire blocks that burned 1 and 14 years ago had high K relative to those that burned 2 and 24 years ago (Fig. 2.3 A). Sodium (Na) was significantly different among fire blocks ($P < 0.001$) but there were no significant effects between vegetation patch type ($P > 0.05$) or interaction effect between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.3 B). There was a sharp decrease in Na with increasing time since last burn (Fig. 2.3 B). Magnesium (Mg) was significantly different among fire blocks ($P < 0.05$). There were significant differences in Mg between vegetation patch types ($P < 0.05$) but no interaction effect between time since last burn and vegetation patch type ($P > 0.05$; Fig. 2.3 C). The fire block that burned 1 year ago had high Mg relative to the block that burned 2 years ago and Mg was significantly higher under tree canopies relative to inter canopy (Fig. 2.3 C). Calcium (Ca) was not significantly different among fire blocks ($P > 0.05$) but there was a significant effect between vegetation patch types ($P < 0.05$). There was also no interaction effect between time since last burn and vegetation patch types ($P > 0.05$; Fig. 2.3 D). Ca was significantly higher under tree canopy relative to inter-canopy.

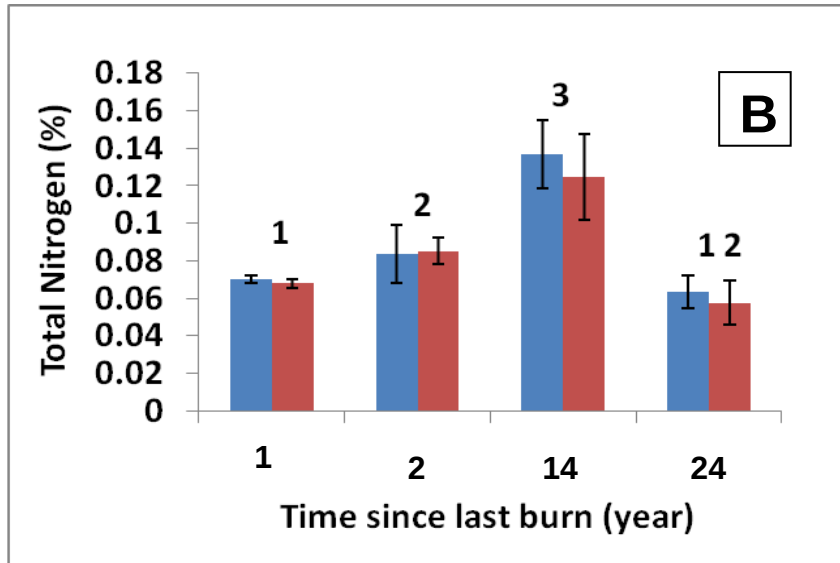
Table 2.5: The soil texture content for different fire blocks. Means with different superscript are significantly different at $P < 0.05$.

Time since last burn (year)	Sand content (%)	Clay content (%)	Silt content (%)
1	94.9 $\pm$ 0.21	3.41 $\pm$ 0.13 ^a	1.66 $\pm$ 0.18 ^a
2	94.4 $\pm$ 0.18	2.95 $\pm$ 0.17 ^b	2.66 $\pm$ 0.21 ^b
14	94.7 $\pm$ 0.39	3.69 $\pm$ 0.16 ^a	1.61 $\pm$ 0.39 ^a
24	94.9 $\pm$ 0.18	3.45 $\pm$ 0.13 ^a	1.68 $\pm$ 0.12 ^a

$FB = F_{3, 109} = 2.635$
 $VPT = F_{1, 109} = 0.268$
 $FB * VPT = F_{3, 109} = 0.165$



FB = $F_{3, 109} = 12.00^{***}$
VPT = $F_{1, 109} = 0.728$
FB * VPT = $F_{3, 109} = 0.793$



11

FB = $F_{3, 109} = 13.89^{***}$
VPT = $F_{1, 109} = 0.282$
FB * VPT = $F_{3, 109} = 0.112$

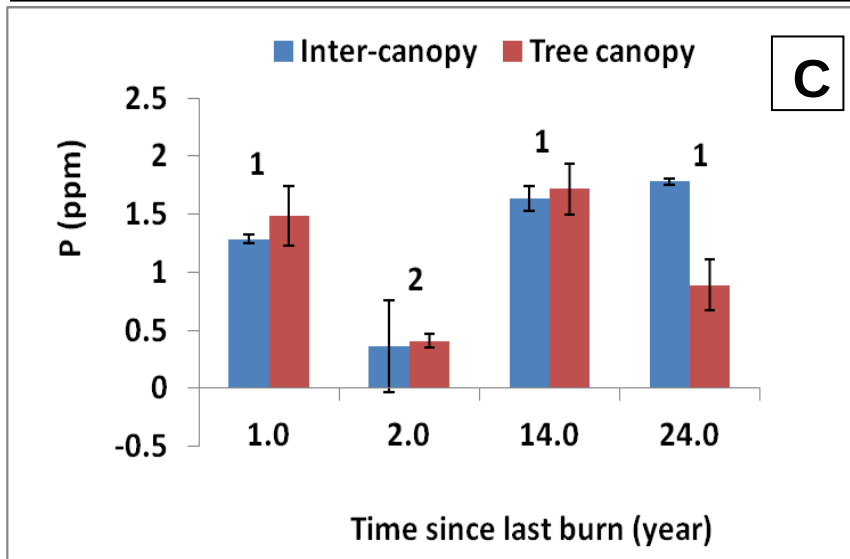
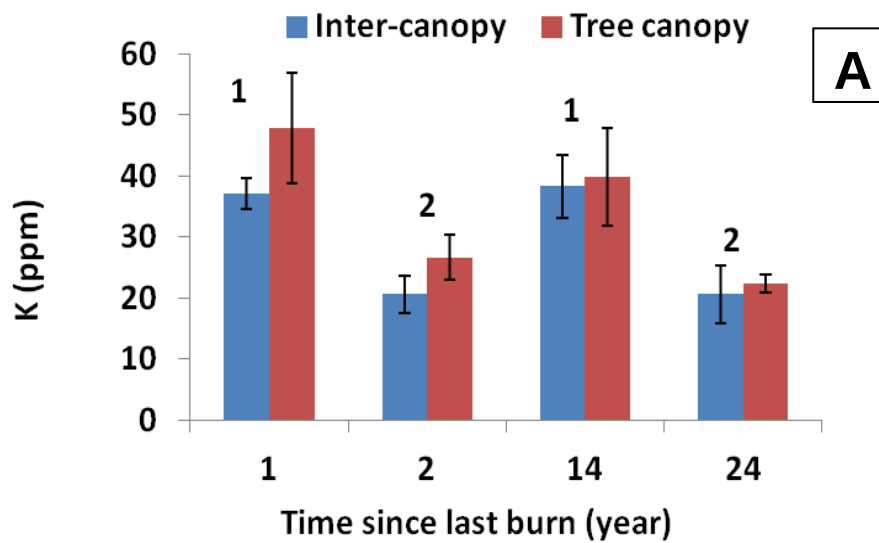
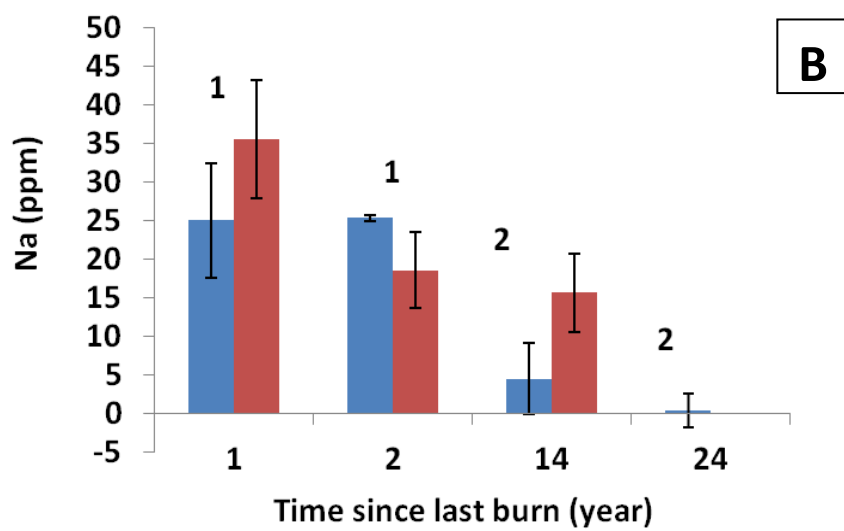


Fig 2.2: Mean ($\pm$ SE; N = 6) SOC (%), total N (%) and P (ppm) in fire blocks with different time since last burn (1, 2, 14, and 24 y) measured under two vegetation patch types (■ inter-canopy and ■ tree canopy). The ANOVA tables show F and df values in a two-way ANOVA, where FB is fire block, VPT is vegetation patch type. *P < 0.05; **P < 0.01; ***P < 0.001. Means with different superscripts and numbers are significantly different at P < 0.05.

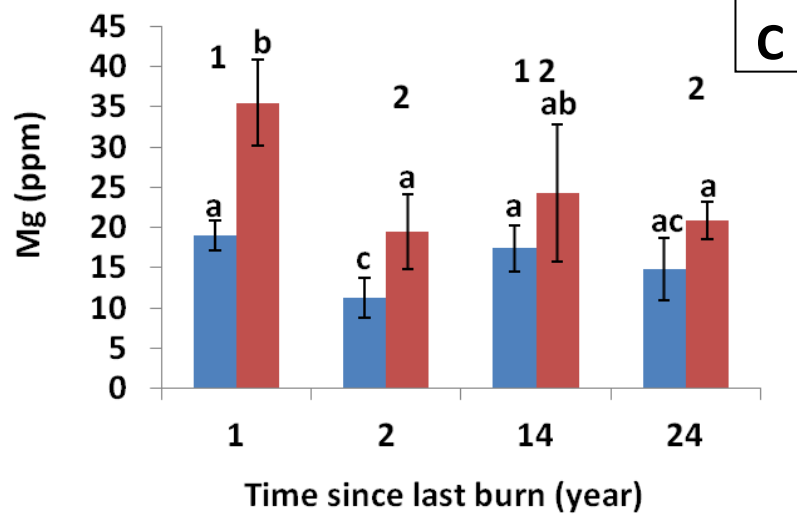
$FB = F_{3, 109} = 9.965^{***}$
 $VPT = F_{1, 109} = 1.993$
 $FB * VPT = F_{3, 109} = 0.379$



$FB = F_{3, 109} = 14.94^{***}$
 $VPT = F_{1, 109} = 1.080$
 $FB * VPT = F_{3, 109} = 1.508$



FB = $F_{3, 109} = 3.290^*$
VPT = $F_{1, 109} = 9.305^{**}$
FB * VPT = $F_{3, 109} = 0.602$



FB = $F_{3, 109} = 1.272$
VPT = $F_{1, 109} = 6.060^*$
FB * VPT = $F_{3, 109} = 0.279$

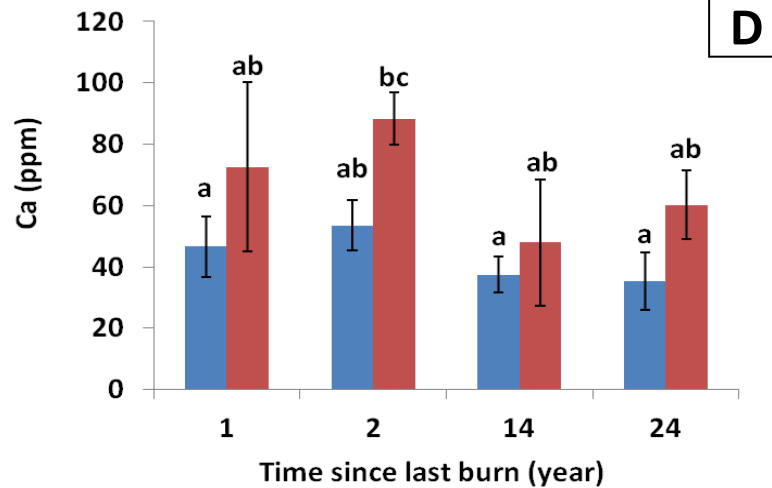


Fig. 2.3: Mean ($\pm$ SE; N = 6) cations (K, Na, Mg and Ca; ppm) in fire blocks with different time since last burn (1, 2, 14, and 24 yrs) measured under two vegetation patch types (■ inter-canopy and ■ tree canopy). The ANOVA tables show F and df values in a two-way ANOVA, where FB is fire block, VPT is vegetation patch type. *P < 0.05; **P < 0.01; ***P < 0.001. Means with different superscripts and numbers are significantly different at P < 0.05.

2.6 DISCUSSION

The results show that time since last burn ranging from 1 - 24 years and fire interval of 6.2 – 18.5 years had limited and inconsistent effect on soil nutrients and SOC content. This suggests that soil resources return rapidly to pre-fire conditions. In addition, these fires were likely to have not been sufficiently intense to cause long-term detrimental impacts and impair the recovery of soil resources. A further explanation as to why fire had limited effect on soil resources in my study could be that fire intensity was low during these fires due to low fuel loads and could not cause a detrimental impact on soil nutrients and SOC content. This is the case because growing seasons preceding all the fires had low rainfall (2012 = 39.6 mm; 2013 = 36.3 mm; 1987/88 = 366 mm; (sassa weatherNet, 2015) and therefore likely low fuel load. The results support previous savanna research showing that fire rarely causes detrimental effects on soil resources. Results from Kruger National Park, a similar dystrophic sandy soils ecosystem to my study site, also showed no significant direct fire effects on SOC, but instead suggest that fire affects soil nutrients and SOC indirectly by altering vegetation structure, particularly tree cover (Coetsee *et al.*, 2010; Holdo *et al.*, 2012; Khavhagali, 2008; Mills & Fey, 2004). Although SOC content was not significantly different between vegetation patch types (Fig. 2.2 A), my results show that SOC increases under tree canopy (Fig. 2.2 A). This may be a function of high litter quality and modification of soil microclimate (e.g. moisture and temperature) under tree canopies, which in turn increase organic matter decomposition rates (Belsky *et al.*, 1993, Belsky *et al.*, 1989). Total N and P (Fig. 2.2 B and C) differed among fire blocks; however the pattern was not consistent. Total N was high in 14 years block as total organic C (thus organic substances) was also higher in this block. Relevant is the relatively (to C organic) low total N in the 1 year block, indicating the short term influence of fire on total N.

The blocks that burned 2 years ago had the lowest available P relative to other fire blocks (Fig. 2.2 C). The enlarged P content in the 1 year block due to burning of organic matter is plausible. There is a correlation in P to clay, indicating the extraction of exchangeable P from clay silicates. My total N and P results did not support the well-known phenomenon that nutrients increase under tree canopies

(Coetsee *et al.*, 2010; Holdo *et al.*, 2012; Scholes & Walker, 1993). This contradictory finding could be due to the fact that most of the soil samples collected under tree canopies were collected under *Terminalia sericea* (which is a dominant species in the park) and *Combretum* spp. which do not fix nitrogen in the soil unlike *Acacia* spp. and other leguminous plants.

Sodium (Fig. 2.3 B), showed a consistent decrease with increasing time since last burn. The sharp decrease in Na with increasing time since last burn may be due to vegetation utilization by herbivores in recently burned areas relative to the areas that burned long ago (14 and 24 years). Uunona (2014) in a study on the impact of fire on vegetation utilization by herbivores in the park reported that animals preferred recently burned areas relative to those that have not been burned in 14 and 24 years. This herbivore preference may have deposited Na (in addition to the Na in the ash) in the soil through urine and droppings from the salt licks provided in the park.

There was no clear trend for other exchangeable cations K (Fig. 2.3 A), Mg (Fig. 2.3 C) and Ca (Fig. 2.3 D), however they were high in the recently burned area. Cations typically increase after fire because of their presence in the ash as a result of high threshold temperature at which these elements volatilize (Satyam & Jayakumar, 2012), which may have not been reached during the fire. It is likely that these fires had low intensities as mentioned earlier. Cations were significantly higher under tree canopies relative to inter canopy. This may be due to accumulation of high quality litter under tree canopy that leaves a layer of ash on soil surface after fire relative to inter canopy. There is some spatial variation between fire block 2, 14 & 24 with parallel relations of clay – organic C – N – P – K – Mg. Thus, differences among these blocks (and soil properties) are not linked to time since last burn but rather to spatial variation. The insignificant interactive effect between time since last burn and vegetation patch type on soil nutrients and SOC is also likely to be due to insufficiently intense fires and that the fires occurred in WPP were surface fires (which are more common in savanna systems) and therefore could not significantly interact with tree canopy to have an interactive impact in soil resources. The soil nutrients and SOC mean values are within the range of comparable measurements

in semi-arid savanna ecosystems of similar dystrophic sandy soils (Boys, 2015; Coetsee *et al.*, 2010; Scholes & Walker, 1993).

2.7 CONCLUSIONS

My results suggest that the current fire regime in Waterberg Plateau Park has little and inconsistent impact on soil nutrients and SOC content. This suggests that these fires were not sufficiently intense and/or not frequent enough to cause detrimental impacts and impair soil resources recovery. These results are similar to those found previously in Kruger National Park, a similar dystrophic ecosystem (Coetsee *et al.*, 2010; Holdo *et al.*, 2012; Khavhagali, 2008). Vegetation patch type influenced soil resources; with under tree canopy having high soil nutrients and SOC relative to inter-canopy in most cases. Although I did not observe a significant interactive effect between fire and vegetation patch type, it is important for studies looking at fire effects on soil properties to consider the interaction effect between fire and vegetation patch type because fire may indirectly influence soil resources by altering vegetation structure. Improvement of our understanding of the independent and interactive effects of fire and vegetation patch types on soil nutrients and SOC in semi-arid woodland savannas where fire is an active agent of nutrient cycling (Holt & Coventry, 1990) and an important determinant of tree canopy cover in these ecosystems (Holdo *et al.*, 2012) will ultimately aid in understanding of nutrient cycling and estimating global C pools. This may be an important step for a better comprehension of the dynamics of carbon and soil nutrients in semi-arid ecosystems in response to ecosystem disturbances such as fire, to promote land management practices that may improve site productivity and terrestrial carbon sequestration (Concilio *et al.*, 2006).

CHAPTER 3: EFFECTS OF FIRE HISTORY AND VEGETATION PATCH TYPE ON SOIL RESPIRATION IN A SEMI-ARID SAVANNA, CENTRAL NAMIBIA

3.1 INTRODUCTION

Soil respiration represents a significant source of CO₂ in the biosphere, constituting the second largest carbon (C) flux in the global C cycle (Raich & Schlesinger, 1992) and it contributes about 20 - 40% of annual C input to the atmosphere (Raich & Schlesinger, 1992; Schlesinger & Andrews, 2000). Soil respired CO₂ is a function of a number of belowground sources including root respiration, decomposition of soil organic matter, plant litter and root exudates (sugar, amino acids, vitamins, long chain carbohydrates, etc.) by soil micro-organisms (Shibistova *et al.*, 2002). Soil respiration can be used as a proxy to understand microbial biomass in an ecosystem because it describes the level of microbial activity and therefore reflects the capacity of soil to support soil life including vegetation, soil faunas and microorganisms (Parkin *et al.*, 1996). Rates of soil respiration may be indirectly influenced by disturbances such as fire, through changes in structure and composition of plant communities and by modifying the amount of soil organic matter in the top soil (Castaldi *et al.*, 2010). However, the effects of fire on this major biogeochemical process are poorly understood (Concilio *et al.*, 2003). The effects of fire on soil respiration are common in fire-prone ecosystems especially in arid and semi-arid savannas where fire is widely used as a land management practice (Trollope, 2007).

Arid and semi-arid savannas cover about one-third of the terrestrial land surface (Dregne, 1976) and they are important to global biogeochemical cycles (Lee *et al.*, 2004). Arid and semi-arid savannas ecosystems account for approximately 20% of the soil organic carbon pool (Conant *et al.*, 2000; Lee *et al.*, 2004). Despite the significance of arid savannas ecosystems in the global carbon cycle, soil respiration in these systems has not received much consideration (Raich & Schlesinger, 1992). This key knowledge gap is increasingly critical given the rise in atmospheric CO₂ concentrations which may change biogeochemical cycles and may also increase microbial and plant physiological responses; therefore ultimately influencing ecosystem structure (de Graaff *et al.*, 2014). Change in biogeochemical cycles and

microbial physiological responses vary among vegetation patch types. For instance, under shrub patches are known to strongly influence the physical environment around the canopy through its effects on biotic and abiotic processes. This creates an “island of fertility” relative to bare ground and under grass patches (Daryanto *et al.*, 2013; Throop & Archer, 2008). Long-term climate projection studies suggest that with increased temperatures, litter decomposition will increase more than production in arid savannas ecosystems (Jenkinson *et al.*, 1991; Schimel, 1995; West *et al.*, 1994) and this may degrade the ecosystem through organic matter depletion. An improved understanding of time since last burn effects on soil respiration and its response to time since last burn under different vegetation patch types may help to improve the management of savanna ecosystems.

The rate of soil CO₂ efflux is determined by a range of environmental factors, including temperature, soil moisture and vegetation productivity (Reichstein *et al.*, 2003). These factors differ among vegetation patch types such as under shrubs, under grass and on bare ground (referred to as “vegetation patch types” hereafter). This may be due to soil microclimates that are modified by vegetation patch types. Microclimates are sensitive to ecosystem disturbances or land management practices such as fire, which may positively or negatively influence soil respiration under different vegetation patch types (Raich & Schlesinger, 1992; Schlentner & Van Cleve, 1985; Singh & Gupta, 1977). For instance, reduction in tree canopy cover by fire can affect several factors such as solar radiation, air and soil temperature, soil moisture and relative humidity; these abiotic factors can in turn reduce the rate of soil CO₂ efflux (Chen *et al.*, 1999; Ma *et al.*, 2004; Zheng *et al.*, 2000). Uncertainties on how soil respiration responds to time since last burn under different vegetation patch types and soil microclimate can hinder our ability to understand the level of microbial activity in arid and semi-arid savannas ecosystems.

Determining the effects of time since last burn on soil respiration and how it responds under different vegetation patch types is an important step for a better comprehension of microbial biomass and carbon dynamics in arid and semi-arid savannas ecosystems; to identify and encourage land management practices that promote microbial activity and growth, and terrestrial carbon sequestration (Concilio

et al., 2006) as atmospheric CO₂ concentrations continues to rise. In this study, I aimed at determining how soil respiration is affected by (i) fire history (time since last burn ranging from 2 - 25 y and mean fire interval ranging from 6.2 – 18.5 y) (ii) vegetation patch types (bare ground, under grass and under shrub) and (iii) the interaction of fire and vegetation patch types in the field and lab experiments.

3.2 STUDY OBJECTIVES

In order to determine how soil respiration is affected by (i) fire history (time since last burn ranging from 2 - 25 y and mean fire interval ranging from 6.2 – 18.5 y) (ii) vegetation patch types (bare ground, under grass and under shrub) and (iii) the interaction of fire and vegetation patch types, I conducted two experiments, a field experiment and a controlled laboratory incubation experiment. In the field experiment, soil CO₂ efflux was measured in two different sampling periods that differed in antecedent precipitation. The experiment was done in four different fire blocks (Fire block 1, 2, 3 & 4; Table 3.1). The incubation experiment allowed me to measure potential carbon mineralization, to control water content and temperature and other environmental conditions that occur under field conditions. For the field experiment, I hypothesized that 1) soil respiration would increase with time since last burn because of the high root density of woody plant that increases total soil respiration as a result of root respiration, the well-established tree canopy (Kramer & Kozlowski, 1960) that can modify the microclimate, and the high quality litter layer that may enhance microbial activity and 2) soil respiration will be high under shrubs and grasses relative to bare ground because of root respiration, high soil C and litter influence. For the laboratory incubation experiment I hypothesized that 1) there would be high soil CO₂ efflux from the incubation experiment relative to the field experiment because room temperature and 60% water holding capacity are optimal conditions for microbial activities, however the pattern among fire blocks would not be different. I tested these hypotheses in the field by measuring CO₂ flux under three different vegetation patch types (under grass, bare ground, and under shrubs) in four fire blocks with different fire history (time since last burn ranging from 2 - 25 years and mean fire interval ranging from 6.2 – 18.5 y; Table 3.1). I collected soil cores at

each sampling point during field experiment and used these soils for the laboratory incubation experiment.

3.3 MATERIALS AND METHODS

3.3.1 Site description

Refer to chapter 2 (page 10-11)

Table 6.1: Fire history (time since last burn) of different fire blocks recorded at Waterberg between 1989 and 2013

Fire block	Time since last burn (year)	Mean fire interval
1	2	6.2
2	3	9.3
3	15	9.3
4	25	18.5

3.3.2 Experimental design and measurement of soil respiration

Soil respiration was measured using the LI-6400XT portable photosynthesis system (LICOR Inc., Lincoln, Nebraska, USA) fitted with a 6400-09 soil CO₂ flux chamber (Fig. 3.2) in February and April 2015. Measurements were done in areas that were last burnt 2, 3, 15, and 25 years ago (Table 3.1). Soil CO₂ flux measurements were done with PVC collars (interior area of 80 cm²) that were inserted 2 – 2.5 cm into the soil surface layer to prevent outside air from penetrating in during measurements. The collars were carefully inserted into the soil to minimize soil surface disturbance and measurements were done 15 minutes after inserting the collars. This was done to allow CO₂ flux to stabilize because when the collar is inserted, a burst of CO₂ may be released causing excessively high flux readings when the actual undisturbed flux may be small (Li-cor, 1993). In each fire block, eight sampling points were

established for measurements, with three collars per point to measure the response of soil respiration to time since last burn under different vegetation patch types. These three treatments per sampling point represented three different vegetation patch types: bare ground (open areas away from shrub canopies and devoid of grasses), under grass (underneath grass tufts) and under shrub (beneath shrub canopies) (Fig. 3.2). *Terminalia sericea* was chosen for the shrub vegetation patch types because it is the dominant species on the plateau. Sampling point locations were selected by generating random numbers based on the length of the fire block and the distance from the edge of the block. This was done to ensure that sampling points were at least 50 m away from the edge of the block, to avoid an impact that may result from the roads that demarcate the blocks. Soil collars were placed within 5 m of the sampling point and one replicate of each of the three vegetation patch types was selected per sampling point. Vegetation patch types that were most representative of the vegetation patches surrounding the sampling point were selected. For under shrubs, collars were placed mid-way between the shrub center and the dripline and away from sub-canopy grasses. For grasses, collars were placed beneath the leaves. For bare ground, collars were placed mid-way in an open area.

Before taking respiration measurements, the soil chamber was placed near the soil surface to determine ambient soil surface CO₂ concentration. The concentration (390 ppm) was used as the 'target' concentration. A chamber drawdown of 10 ppm below target concentration was used as the starting point for all respiration measurements, then CO₂ concentration in the chamber started building up 10 ppm above the target concentration as a result of soil respiration, and then final measurements were made at 390 ppm CO₂ concentrations (Li-cor, 1993).



Fig. 3.1: Soil collar being inserted into the soil for a bare ground patch. The collar is inserted carefully to minimize soil surface disturbance and it is inserted 15 minutes prior to measurements (Photo by H. Throop, 2015).



Fig. 3. 2: Measuring soil CO₂ flux on bare ground. The soil chamber is placed over the collar and measurements complete a 3 cycle without moving or interfering with the machine (Photo by H. Throop, 2015).

3.3.3 Soil temperature and soil moisture

Since soil respiration is influenced by soil moisture and temperature, these variables were recorded during respiration measurements. Soil temperature was monitored simultaneously with soil CO₂ efflux with a thermocouple soil temperature probe (LICOR 6000-09TC) inserted in the soil to a depth of 10 cm near the soil flux chamber. Soil cores (10 cm deep) were extracted from each collar with a soil corer (interior diameter: 5 cm) and were sealed in plastic bags for later determination of gravimetric soil moisture content and for the lab incubation experiment. Gravimetric soil moisture content was determined according to Black (1965). Approximately 100 g of soil from each soil sample was dried in the oven at 110°C for 48 hours. The water mass (or weight) was then calculated as the difference between the weights of the wet and oven dry samples. The oven drying process was repeated until there was no further mass loss.

3.3.4 Laboratory incubation

The soil cores ($n = 125$ samples) collected within the collars during field experiment were incubated for 3 weeks at 60% water holding capacity (WHC) (Linn & Doran, 1984), under room temperature. I put 75 g of soil in small containers (interior area: 42.25 cm², height: 2.5 cm). Large (± 3 mm) litter pieces (e.g. leaves, grass, branches and roots) were removed manually, so the incubated samples were roots-free. Soil CO₂ efflux was measured for 15 days with an infrared gas analyzer (Licor 6400). The soil container was placed inside a PVC collar, with a cap covering the bottom part of the collar to prevent leakage. The soil chamber was placed over the collar for measurements. On the second week of the incubation, there were variations in moisture content; some samples had minimal moisture and some were dry, so I re-wetted them to 60% water holding capacity. To determine how much water to add to each sample, I weighed the samples to determine the water content moisture in each sample and calculate how much water was needed to make 60% water holding capacity.

3.4 DATA ANALYSIS

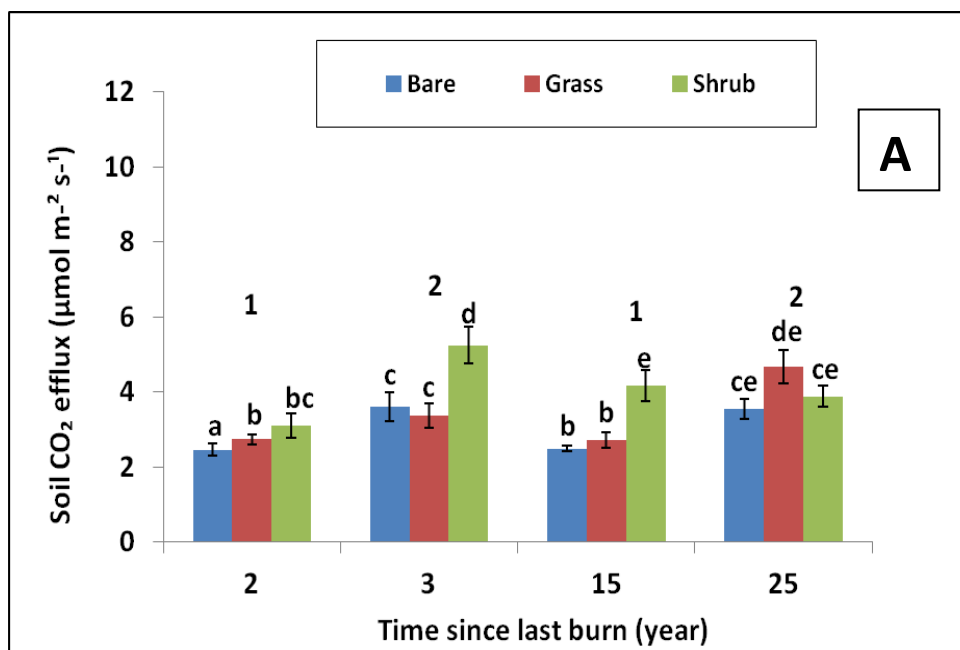
Statistical analyses for soil respiration were done in R 2.11.1 (R Development Core Team). Two-way analysis of variance (ANOVA) followed by Tukey's multiple comparison tests were used to assess whether soil respiration differed among fire blocks and vegetation patch types, as well as the interaction between fire blocks and vegetation patch types. The correlation analysis between soil CO₂ efflux and soil moisture among vegetation patch types were made in STATISTICA 12 (StatSoft, Inc).

3.5 RESULTS

3.5.1 Field Experiment

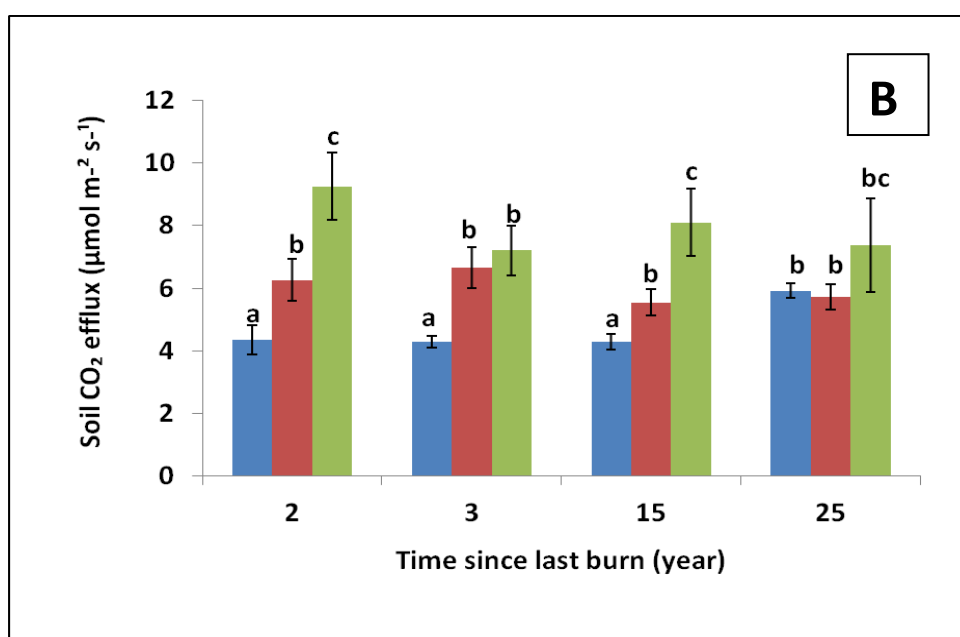
Mean soil respiration was almost 2 times lower ($2.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the recently burned block relative to the block burned 25 years ago ($4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the dry period (February, Fig 3.3 A). Among vegetation patch types, mean soil respiration ranged from 2.5 (on bare ground) to $5.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ (under shrub). In a wet period (April, Fig. 3.3 B), mean soil respiration ranged from $6.62 \mu\text{mol m}^{-2} \text{s}^{-1}$ in a recently burned block to $6.32 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the block burned 25 years ago. This falls within an expected range as that reported by Veenendaal *et al.*, (2014) in a similar semi-arid woodland savanna in Botswana.

There was a significant difference in mean soil respiration observed between two sampling periods. Greater CO_2 efflux (mean = $6.25 \pm 0.23 \mu\text{mol m}^{-2} \text{s}^{-1}$) was observed in April when there was high soil moisture (gravimetric water content mean = $3.07 \pm 0.12 \%$) than in February (mean = $3.51 \pm 0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 3.3 A) when soil moisture was minimal (gravimetric water content mean = $0.47 \pm 0.06 \%$). There was a significant difference ($P < 0.01$) in soil CO_2 efflux among fire blocks in February (Fig. 3.3 A). A significant difference ($P < 0.01$) in soil CO_2 efflux was observed between the fire block that was burned 25 years ago and the recently burned (2 years ago) block. However, there was no significant difference ($P > 0.05$) in soil CO_2 efflux among fire blocks during April (Fig. 3.3 B). Soil CO_2 efflux differed among vegetation patch types in both sampling periods (April $P < 0.001$; February $P < 0.001$), with under shrubs having higher soil CO_2 efflux relative to other vegetation patch types (Fig. 3.3 A and B). There was a significant interaction between fire block and vegetation patch types in February ($P < 0.05$; Fig. 3.3 A) and in April ($P < 0.05$; Fig. 3.3 B). In February (Fig. 3.3 A), the interaction was inconsistent among fire blocks with the 2, 3 and 15 y fire blocks having high soil CO_2 efflux under shrub whereas in the 25 y fire blocks under grass had high soil CO_2 efflux. The interaction was consistent among fire blocks in April (Fig. 3.3 B); with under shrub having higher soil CO_2 efflux, followed by under grass and bare ground had the lowest.



ANOVA Table

FB = $F_{3, 276} = 14.121^{***}$
VPT = $F_{2, 276} = 14.013^{***}$
FB * VPT = $F_{6, 276} = 3.373^{**}$



FB = $F_{3, 439} = 0.495$
VPT = $F_{2, 439} = 73.029^{***}$
FB * VPT = $F_{6, 439} = 2.234^*$

Fig. 3.3: Mean ($\pm$ SE; [Feb: N = 24; April: N = 38]) soil CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in fire blocks with different time since last burn (2, 3, 15 and 25 yrs) measured under three vegetation patch type (bare, grass and shrub) for A) February, during a dry period, and B) April, during a wet period. The ANOVA tables show F and df values in a two-way ANOVA, where FB is fire block, VPT is vegetation patch type. *P < 0.05; **P < 0.01; ***P < 0.001. Means with different lower-case letters and numbers are significantly different at P < 0.05.

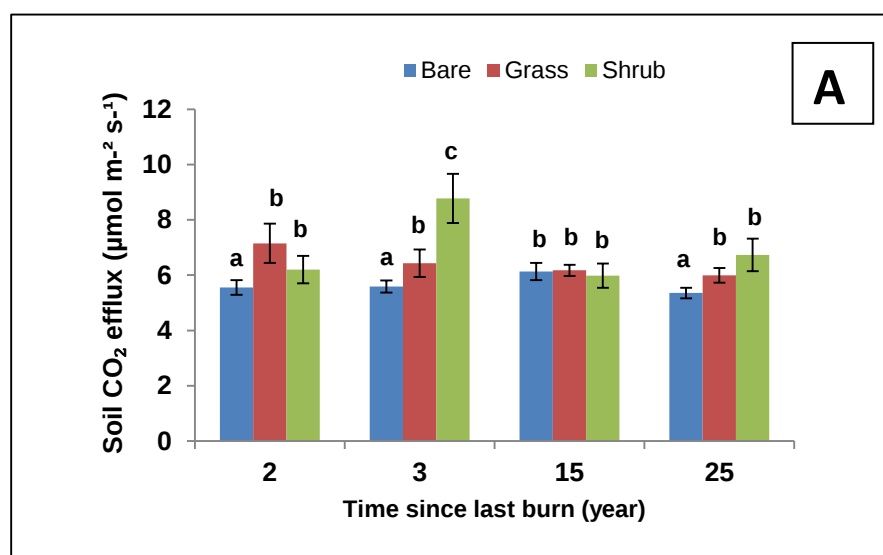
3.5.2 Laboratory incubation experiment

Mean soil respiration in the lab incubation was almost 70 % ($5.85 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.4 A) more than in the field experiment ($3.50 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.3 A) in February (the dry period). In April (wet period), no significant difference was observed in mean soil respiration between the experiments (incubation: $6.34 \mu\text{mol m}^{-2} \text{s}^{-1}$ and field experiment: $6.64 \mu\text{mol m}^{-2} \text{s}^{-1}$). Among vegetation patch types, mean soil respiration in the incubation experiment ($5.35 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.4 A) was twice as much on bare ground relative to the field experiment ($2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.3 A) and slightly increased from $5.8 - 6.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ under shrubs, in February. In April, mean soil respiration in the lab incubation was almost 20 % ($4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.4 B) more than in the field experiment ($5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig 3.3 B) on bare ground and decreased by 30 % ($7.98 - 6.13 \mu\text{mol m}^{-2} \text{s}^{-1}$) under shrubs.

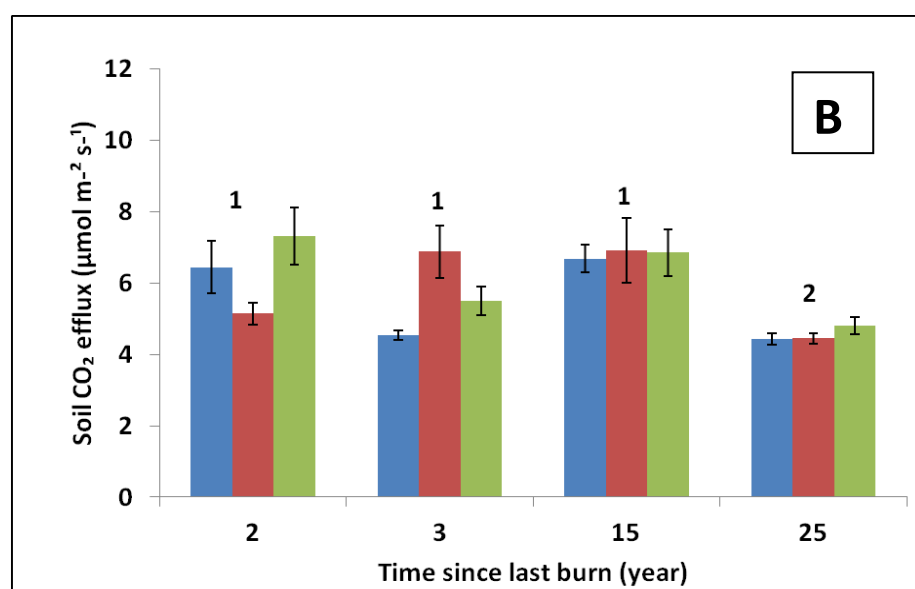
In lab incubations, there was no significant difference ($P > 0.05$) in soil CO_2 efflux between the sampling periods (Fig. 3.4). Soil CO_2 efflux was not significantly different among fire blocks in February ($P > 0.05$) but was significantly different in April ($P < 0.01$). The blocks that burned 2, 3 and 15 years ago had high soil CO_2 efflux relative to the block burned 25 years ago. There was a significant difference (February, $P < 0.05$; April, $P < 0.01$) in soil CO_2 efflux among vegetation patch types during both sampling periods, with under shrub soils generally having higher soil CO_2 efflux relative to bare ground and under grass (Fig. 3.4). There was a significant interaction ($P < 0.05$) between fire blocks and vegetation patch types in February. In February (Fig. 3.4 A), the interaction was inconsistent among fire blocks with the 3 y and 25 y fire blocks having high soil CO_2 efflux under shrub whereas there was no difference in soil CO_2 efflux among vegetation patch types in a 2 y and 15 y fire blocks. Similarly, the interaction was inconsistent among fire blocks in April (Fig. 3.4 B). In the 2 y fire block, under grass soils had the lowest soil CO_2 efflux whereas in the 3 y under soils shrub had the highest soil CO_2 efflux. In the 15 y and 25 y all vegetation patch types had the same soil CO_2 efflux. Moisture content had a significant effect ($P < 0.01$) on soil CO_2 efflux among vegetation patch type; however there was no strong correlation [bare ground: $r^2 = 0.071$; under grass: $r^2 = 0.151$ & under shrub: $r^2 = 0.062$] between soil CO_2 efflux and water content among

vegetation patch type (Fig. 3.5). The correlation was improved when outliers (○) were removed (bare ground: $r^2 = 0.230$; under grass: $r^2 = 0.172$ & under shrub: $r^2 = 0.098$).

ANOVA Table



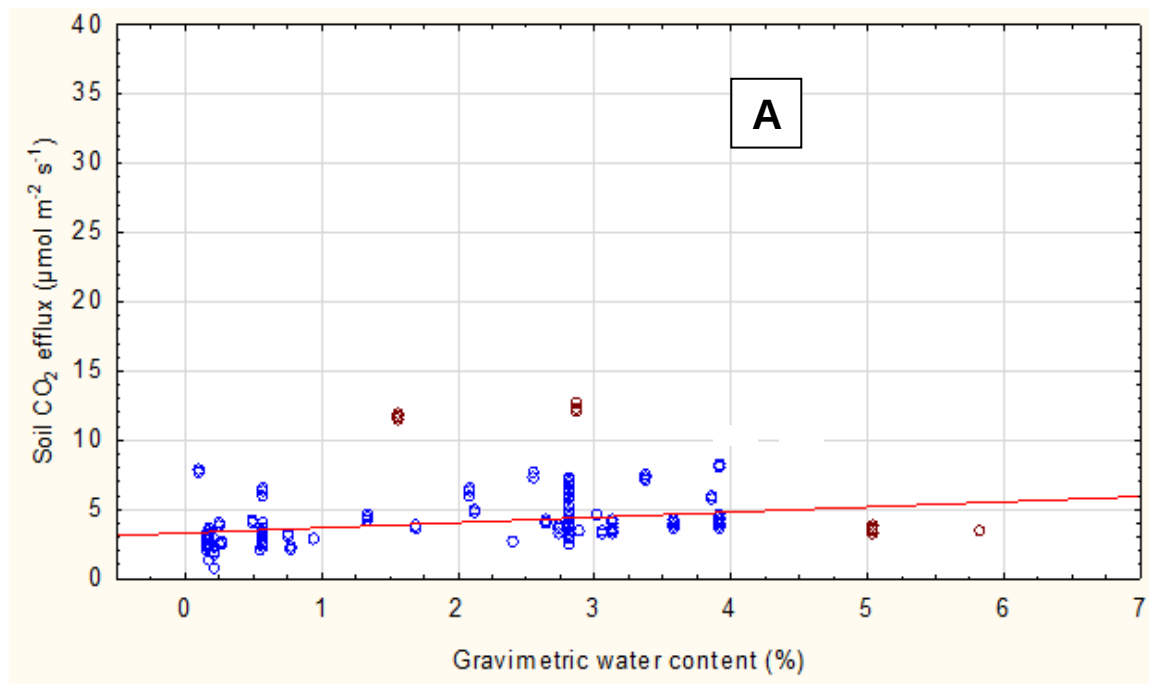
FB = $F_{3, 877} = 2.241$
VPT = $F_{2, 877} = 4.976^{**}$
FB * VPT = $F_{6, 877} = 2.662^{**}$



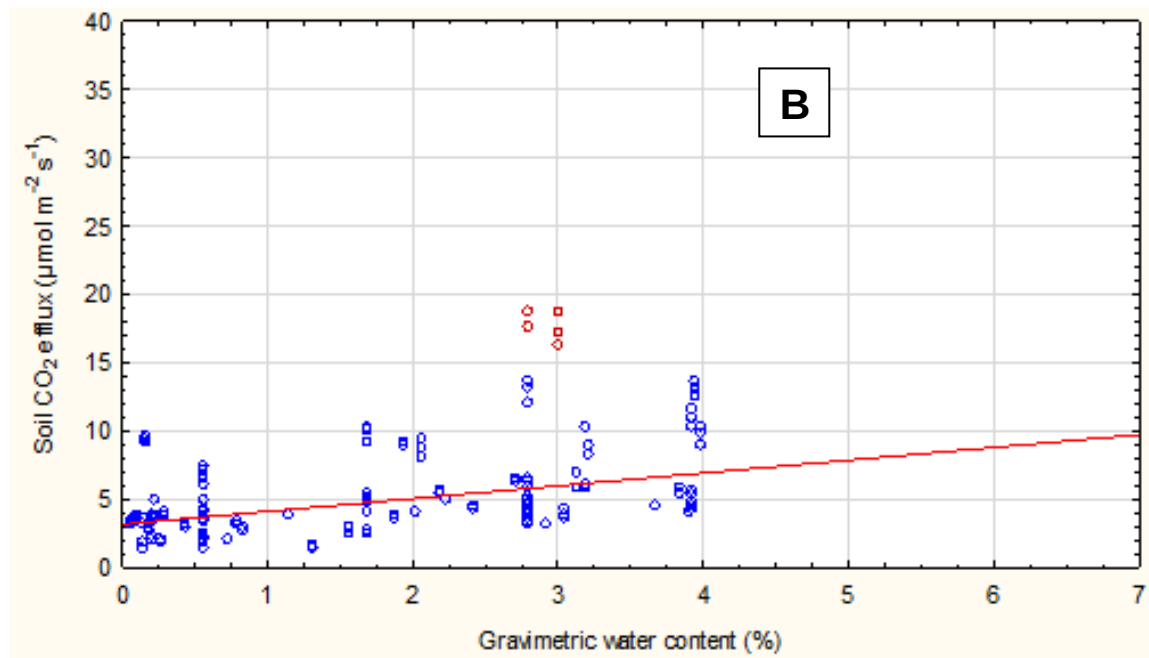
FB = $F_{3, 838} = 8.307^{***}$
VPT = $F_{2, 838} = 1.091$
FB * VPT = $F_{6, 838} = 2.234^*$

Fig. 3.4: Mean ($\pm$ SE; N = 75) soil CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) during laboratory incubations from soil samples collected in fire blocks with different time since last burn (2, 3, 15, and 25 yrs) under three vegetation patch types (bare ■, grass ■ and shrub ■) during two sampling periods for A) February (dry period) and B) April (wet period). The samples were incubated over 3 weeks. The ANOVA tables show F and df values in a two-way ANOVA, where FB is fire block and VPT is vegetation patch types. *P < 0.05; **P < 0.01; ***P < 0.001. Means with different superscript and numbers are significantly different at P < 0.05.

$P < 0.01$, $r^2 = 0.23$



$P < 0.01$, $r^2 = 0.172$



$P < 0.01$, $r^2 = 0.098$

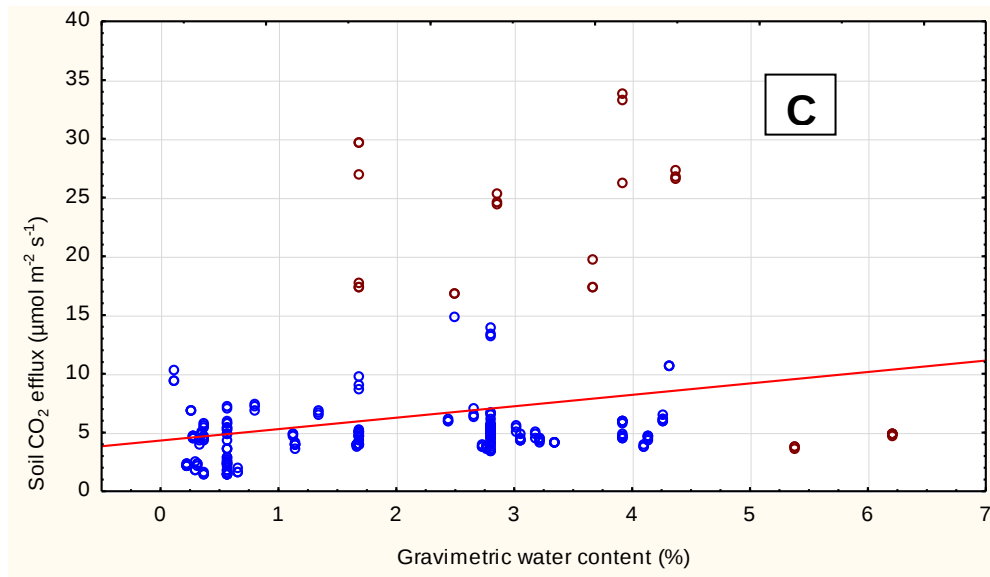


Fig. 3.5: Correlation between soil respiration and water content among vegetation patch types (A = bare ground; B = under grass and C = under shrub).

3.6 DISCUSSION

I hypothesized that soil respiration may increase with time since last burn but there was no consistent pattern among fire blocks. This may suggest that soil microbes return rapidly to pre-fire conditions or that some microbes were not significantly affected by time since last burn because microbes like bacteria are generally heat tolerant (Vazquez *et al.*, 1993; Widden & Parkinson, 1975; Bissett & Parkinson, 1980; Bollen, 1969). In addition, these fires were likely to have not been sufficiently intense, and therefore lethal temperature for different microbes may not have been reached during these fires to cause long-term detrimental impacts and impair their recovery. Moreover, site to site spatial variation may have had a stronger controlling influence on soil respiration among fire blocks. Although my findings regarding soil CO₂ efflux reduction in recently burned areas by fire (due to canopy removal) were in contrast with other studies (Holt *et al.*, 1990; Sawamoto *et al.*, 2012; Nakane *et al.*, 1983), a consistent trend was more apparent among vegetation patch types, with under shrub soils generally having high soil CO₂ efflux relative to other patch types. This suggests that fire may indirectly influence soil CO₂ efflux by reducing vegetation

cover, as Amputu (2016) reported that woody cover increased with time since last burn [2 y = 20. 3%; 3 y = 39. 7%; 15 y = 51. 0% and 25 y = 67. 5%] in the same area. Change in canopy may have long-term legacy effects on the magnitude and pattern of litter inputs, and reduces decomposer communities at the former canopy site, hence directly affecting decomposition rates (Throop & Archer, 2007). Soil respiration may decrease due to a decline in tree root respiration as a result of tree damage or death after fire. Plant top-kills reduce photosynthesis rates which ultimately influences tree root respiration (Sawamoto *et al.*, 2012). Without specifically quantifying the contribution of root respiration and respiration from microbes to total respiration, I cannot be sure of how each component contributed to the observed total soil respiration. However, Holt *et al.*, (1990); and Nakane *et al.*, (1983) reported that root respiration typically contributes between 40 - 60% to total soil respiration. This seems to be evident considering the field and incubation experiment results; it suggests that soil respiration observed under shrub in the field experiment is largely attributed to root respiration. In contrast to Sawamoto *et al.*, (2012) findings that there is higher soil CO₂ efflux in an area that has not been burned for long due to higher woody plant density, my results do not suggest that consistent trend. This could be explained by the fact that I did not separate out woody patches as 'old' (existing before fire), regrowth of old trees post fire, or new plants establish post-fire. This may cause a lot of inconsistent variance among blocks and among woody patches within fire blocks (Throop & Archer, 2008).

Higher soil CO₂ efflux was observed in April (wet period) relative to February (dry period). This difference may be a function of soil moisture differences observed during the sampling periods as indicated by the correlation. Under shrubs had high soil CO₂ efflux relative to bare ground and under grass, this could be attributed to deposition of high-quality litter on the soil surface beneath shrubs, which enhances carbon cycling activity, significant growth of woody root biomass, and generally a favourable microclimate beneath shrubs (Belsky, 1994; Hibbard *et al.*, 2001; Liu *et al.*, 2010; Makhado & Scholes, 2011; McCulley *et al.*, 2004; Schlesinger *et al.*, 1996; Zou *et al.*, 2007). Shrubs have a dense lateral root system from the trunk which decreases with distance from the trunk. In other words, a gradient exists in root

density and root respiration as the distance increases from the trunk (Belsky, 1994; Cable *et al.*, 2012; Khavhagali, 2008).

My hypothesis that soil CO₂ efflux increases in laboratory incubation experiment relative to the field experiment was strongly supported (incubation [mean = $6.10 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$]; field [mean = $5.17 \pm 0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$]). Lab incubation results suggest that room temperature and 60% water holding capacity are optimal conditions for microbial activity. The results are in agreement with other studies conducted from other soil types (Zhou *et al.*, 2014; Linn & Doran, 1984). In an incubation experiment of tilled and non-tilled clay soils, Linn & Doran (1984) found that a soil water content equivalent to 60% of a soil's water holding capacity maximises aerobic microbial activity. Zhou *et al.*, (2014) also found microbial activity to be at maximum at 60% water holding capacity. The WHC in soil may be a useful indicator of the relative potential for aerobic and anaerobic microbial activity in soil (Linn & Doran, 1984). High soil CO₂ efflux observed from incubation experiments in Feb (Fig. 3.4 A) provided a better reflection of the potential carbon mineralization (under room temperature and 60% WHC conditions), which did not come out in the field experiment (Fig. 3.3 A); nonetheless it showed how much CO₂ efflux there is in dry versus wet conditions. This then, suggests that lower soil respiration observed in the field experiment was not limited by microbial populations and their activities. This disparity is rather a function of low moisture content that was observed during field sampling. Additionally, environmental factors such as variations in soil-surface temperatures, intensity of solar radiation and vegetation structure which were present in the field (and not in the incubation experiment) may have contributed to this disparity. The different pattern among vegetation patch type between the field and incubation experiments (Fig. 3.3 & 3.4) strongly reflects how root respiration under grass and shrub contributed to total respiration in the field experiment because the soil cores were roots free in the incubation experiment.

Although moisture content had a significant effect on soil CO₂ efflux as expected, the correlation between the two was rather weak, particularly under shrubs. This is likely to be due to the fact that under shrub soil respiration is dependent upon various factors such as root density, high litter quality and hence this reduces the

proportional dependence of soil respiration on soil moisture under shrub relative to other patch types. Additionally, other factors such as light intensity, soil temperature, time of the day etc may have influenced soil CO₂ efflux other than moisture content, hence causing a weak correlation. Outliers that were observed could be a function of high root density, animal respiration (especially termite mounds) under sampling points.

3.7 CONCLUSIONS

The results suggest that time since last burn ranging from 2 - 25 years and mean fire interval of 6.2 – 18.5 years had limited and inconsistent significant direct effect on soil respiration, suggesting no significant effect on soil microbial biomass. Soil respiration responded to time since last burn differently under different vegetation patch types, but it was generally highest under shrubs. This suggests that fire may have important indirect effects on soil respiration if it alters vegetation cover. Additionally, my results suggest that studies and models emphasizing the rates of soil respiration (as a proxy for microbial biomass) and its response to disturbances such as fire in arid and semi-arid savannas ecosystems must take vegetation patch types into account. This is the case because of heterogeneity in microclimates modified among different vegetation patch types, which in turn influences soil respiration. Additionally, Buchmann (2000) and Raich & Tufekcioglu (2000) reported that there is a difference in the amount of carbon under each vegetation patch type, which influences soil respiration. Improvement of our understanding of the effects of fire on soil respiration and how it responds in different vegetation patch types in arid and semi-arid savanna ecosystems where there are very few measurements of soil CO₂ efflux (Epule, 2015; Raich & Schlesinger, 1992), will ultimately aid in understanding microbial activities in the ecosystem as well as estimating global soil respiration. These relationships may be a critical component for a better comprehension of microbial biomass and activities as well as carbon dynamics in semi-arid savanna ecosystems and will assist in identifying and encouraging land management practices that promote soil health system and reflects the soil capacity to support soil life.

CHAPTER 4: CONCLUSION AND RECOMMENDATIONS

This study sets out to fill a critical gap in our understanding of the effects of fire history on soil resources in dystrophic sandy soils. Therefore, the main aim of this study was to investigate the effect of time since last burn on soil nutrients, SOC and soil respiration in an arid and semi-arid woodland savanna ecosystem, central Namibia. I used fire history data of four fire blocks (with time since last burn ranging from 1 - 25 years and mean fire interval of 6.2 – 18.5 years) to explore the response of soil nutrients, soil organic carbon and soil respiration to time since last burn and vegetation patch type, and to explore the interaction between these two variables.

Results in chapter 2 showed that time since last burn had a limited and inconsistent effect on soil nutrient and soil organic carbon, supporting results of earlier work in semi-arid savanna ecosystems (Coetsee *et al.*, 2010; Holdo *et al.*, 2012; Khavhagali, 2008). This suggests that soil resources return rapidly to pre-fire conditions. In addition, these fires were likely to have not been sufficiently intense due to low fuel loads as a result of low rainfall during the growing seasons preceding all the fires; therefore could not cause long-term detrimental impacts and impair the recovery of soil resources. Additionally, in this study other factors such as soil texture and topography may have had a stronger controlling influence on soil nutrients and soil organic carbon. Moreover, site to site spatial variation may have had a stronger controlling influence on soil nutrients, soil organic carbon and soil respiration among fire blocks. Vegetation patch type showed no significant effects on SOC, total N and P; however, exchangeable cations (K, Na, Mg and Ca) were significantly higher under tree canopies relative to inter-canopy. This is likely to be due to the accumulation of high quality litter under tree canopies that leaves a layer of ash on the soil surface after fire. No significant interactive effects between fire and vegetation patch type on soil nutrients and SOC were observed.

Results in chapter 3 also showed that time since last burn had a limited and inconsistent effect on soil respiration. This may suggest that soil microbes return rapidly to pre-fire conditions or that some microbes were not significantly affected by time since last burn because microbes like bacteria are generally heat tolerant

(Vazquez *et al.*, 1993; Widden & Parkinson, 1975; Bissett & Parkinson, 1980; Bollen, 1969). In addition, these fires were likely to have not been sufficiently intense, and therefore lethal temperature for different microbes may not have been reached during these fires to cause long-term detrimental impacts and impair their recovery. There was a strong effect of vegetation patch type on soil respiration, where soils under shrubs generally had higher respiration relative to other vegetation patch types. There was also an interactive effect between time since last burn and vegetation patch type. This suggests that fire may have important indirect effects on soil respiration through its alteration of vegetation cover. Based on my field and incubation results, this study concluded that the higher soil respiration observed under shrubs in the field experiment is largely attributed to root respiration, suggesting fire did not significantly affect soil microbes.

The current fire regime in the park does not have a significant impact on soil nutrients and soil microbes; therefore there should be no concern in using fire, within the frequencies experienced (6.2 – 18.5 years) as a tool to improve positive resource utilization. This study improves our understanding of the effects of fire on soil resources and how these resources respond across different vegetation patch types in arid and semi-arid savannas. The results may assist in identifying and promoting land management practices that may improve site productivity in the park. Additionally, the results can be useful in estimating global soil respiration. This study has also shown that investigations of soil nutrients, soil organic carbon and soil respiration in response to disturbances such as fire in arid and semi-arid savanna ecosystems must take vegetation patch types into account. This is the case because each vegetation patch type modifies its microclimate differently, and there is a difference in the amount of carbon under each vegetation patch type, which in turn may influence soil microbial activities.

This study serves as a baseline for soil resources monitoring in the park. Therefore, long-term monitoring of the response of soil resources to fire history in these fire blocks need to be considered for better park management practices. The long-term monitoring data will not only be restricted to the management of Waterberg Plateau Park but could be useful to land managers in other semi-arid savanna ecosystems in

the region. Future studies should consider the sampling season, fire intensity and topography as factors that may also influence the response of soil resources to fire.

4. REFERENCES

- Amputu, V. (2016). Fire history and frost in a semi-arid savanna woodland: Understanding their impacts on vegetation structure and species composition in the Waterberg Plateau Park. Unpublished MSc. thesis, Namibia University of Science and Technology, Windhoek, Namibia
- Anderson, A. N., Cook, G. D., & Williams, R. J. (2003). Burning for Conservation in Australian Tropical Savannas: Implications from the Kapalga Fire Experiment. Retrieved from <http://www.fire.uni-freiburg.de/summit-2003/3-IWFC/Papers/3-IWFC-051.pdf>
- Ansley, R. T., Boutton, T. W., & Skjemstad, J. O. (2006). Soil organic carbon and black carbon storage and dynamics under different fire regimes in temperate mixed-grass savanna. *Global Biogeochemical Cycles*, 20, GB3006.
- Aranibar, I. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R., & Shugart, H. H. (2003). Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as indicated by stable isotope analysis. *Isotopes in Environmental and Health Studies*, 39(2), 141-158.
- Belsky, A. J. (1994). Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. *Ecology*, 75(4), 922 - 932.
- Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R., & Mwonga, S. M. (1989). The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology*, 26(3), 1005 - 1024.
- Belsky, A. J., Mwonga, S. M., Amundson, R. G., Duxbury, J. M., & Ali, A. R. (1993). Comparative effects of isolated trees on their undercanopy environments in high-rainfall and low-rainfall savannas. *Journal of Applied Ecology*, 30(1), 143 - 155.
- Beyers, J. L., Brown, J. K., Busse, M. D., DeBano, L. F., Elliot, W. J., Ffolliott, P. F., ...Knoepp, J. D. (2005). Wildland Fire in Ecosystems: Effects of Fire on Soil and Water. General Technical Report RMRS-GTR, 42(4). Department of Agriculture, Forest Service, Rocky Mountain Research Station, USA
- Bisset, J., & Parkinson, D. (1980). Long-term effects of fire on the composition and activity of the soil microflora of a subalpine coniferous forest. *Canadian Journal of Botany*, 58(1), 1704 -1721.
- Black, C. A. (1965). Methods of Soil Analysis: Part I: Physical and mineralogical properties. *American Society of Agronomy*, 9(1), 50 - 51.

- Bollen, G. J. (1969). The selective effect of heat treatment on the microflora of a greenhouse soil. *Netherlands Journal of Plant Pathology*, 75(1), 157-163.
- Bond, W. J., & Van Wilgen, B. W. (1996). *Fire and Plants*. Chapman & Hall, London, UK
- Boys, J. M. (2015). Rangeland dynamics at increasing distances from the Kavango river, Northern Namibia. Unpublished MSc. thesis, University of Free State, Bloemfontein, South Africa
- Buchmann, M. (2000). Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology and Biochemistry*, 32(11-12), 1625-1635.
- Cable, J. M., Barron-Gafford, G. A., Ogle, K., Pavao-Zuckerman, M., Scott, R. L., Williams, D. G., & Huxman, T. E. (2012). Shrub encroachment alters sensitivity of soil respiration to temperature and moisture. *Journal of Geophysical Research Biogeosciences*, 117(1), G01001.
- Campbell, B. D., Swift, M., Hatton, J., & Frost, P. (1988). Small scale pattern and nutrient cycling in Miombo woodland. In Verhoeven, G. W. H., & Werger, M. J. A. (eds.). *Vegetation structure in relation to carbon and nutrient economy* (pp. 69-85). SPB Academic Publishing, The Hague, Netherlands
- Castaldi, S., de Grandcourt, A., Rasile, A., Skiba, U., & Valentini, R. (2010). CO₂, CH₄ and N₂O fluxes from soil of a burned grassland in Central Africa. *Biogeosciences*, 7, 3459 - 3471.
- Certini, G. (2005). Effect of fire on properties of soil - A review. *Oecologia*, 143, 1-10.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D.,...Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology. Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, 49(4), 288 – 297.
- Coetsee, C., Bond, W. J., & February, E. C. (2010). Frequent fire affects soil nitrogen and carbon in an African savanna by changing woody cover. *Oecologia*, 162, 1027-1034.
- Conant, R. T., Klopatek, J. M., & Klopatek, C. C. (2000). Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Science Society of America Journal*, 64(1), 383 - 390.
- Concilio, A., Ma, S., Ryu, S., North, M., & Chen, J. (2006). Soil respiration response to experimental disturbances over 3 years. *Forestry Ecology and Management*. Elsevier Publisher, 228, 82 - 90.

- Cook, G. D. (1994). The fate of nutrients during fires in a tropical savanna. *Australian Journal of Ecology*, 19(4), 359 - 365.
- Daryanto, F., Eldridge, D. J., & Wang, L. (2013). Spatial patterns of infiltration vary with disturbance in a shrub-encroached woodland. *Geomorphology*, 194, 57- 64.
- Day, P. R. (1965). Particle fractionation and particle-size analysis. In Black, C. A. (ed.). *Methods of Soil Analysis* (pp. 545-567). Agronomy No. 9, Part I, American Society of Agronomy, Madison, WI.
- Davidson, E. A., Trumbore, S. E., & Amundson, R. (2000). Biogeochemistry: soil warming and organic carbon content. *Nature*, 408, 789 - 790.
- DeBano, L. F. (2000). The role of fire and soil heating on water repellency in wildland environments: A review. *Journal of Hydrology*, 231, 195 - 206.
- DeBano, L. F., Neary, D. G., & Folliott, P. F. (1998). *Fire's Effects on Ecosystems*. John Wiley and Sons, Inc. New York
- Dregne, H. E. (1976). *Soils of arid regions*. Amsterdam/ Holland: Elsevier Publisher
- Dunn, P., & DeBano, L. F. (1977). Fire's effect on biological and chemical properties of chaparral soils. In Mooney, H. A., & Conrad, C. E. (eds.). *The environmental consequences of fire and fuel management in mediteranean ecosystems* (pp. 75-84). Symposium conducted at the meeting of the Forest Washington of Palo Alto, CA. USDA, DC. General technical report WO-3
- Erb, K. P. (1993). The Roan Antelope (*Hippotragus equinus*, Desmarest 1804), its ecology in the Waterberg Plateau Park. Unpublished MSc. thesis, University of Stellenbosch, Cape Town, South Africa
- Erckie, J. B. (2007). Assessing the effects of grazing intensity by large herbivores on species diversity and abundance of small mammals at Waterberg Plateau Park, Namibia. Unpublished MSc. thesis, University of Namibia, Windhoek, Namibia
- Fang, C., & Moncrieff, J. B. (2001). The dependence of soil CO₂ efflux on temperature. *Soil Biology and Biochemistry*, 33, 155 - 165.
- Frost, P., Medina, E., Menaut, J. C., Sobrig, O., Swift, M., & Walker, B. (1986). *Responses of savannas to stress and disturbance* (pp, 28). International Union of Biological Sciences Publisher, Paris, France
- Giess, W. (1971). A preliminary vegetation map of South West Africa, *Dinteria*, 4, 1-144

- Goldammer, J. G. (1999). Environmental problems arising from land use, climate variability, fire and smog in Indonesia: Development of policies and strategies for land use and fire management. In WMO Workshop on Regional transboundary smoke and haze in Southeast Asia, Singapore, 2, 13 – 88. World Meteorological Organization, Global Atmosphere Watch Report Ser. No. 131, WMO TD No. 948, Geneva
- Grissino-Mayer, H. D., Romme, W. H., Floyd, M. L., & Hanna, D. D. (2004). Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology*, 85, 1708 – 1724.
- Hibbard, K. A., Archer, S., Schimel, D. S., & Valentine, D. W. (2001). Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna, *Ecology*, 82(7), 1999 - 2011.
- Higgins, S. I., Bond, W. J., & Trollope, W. S. W. (2000). Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2), 213 – 229.
- Holdo, R. M. (2005). Stem mortality following fire in Kalahari sand vegetation: effects of frost, prior damage, and tree neighbourhoods. *Plant Ecology*, 108(1), 77 – 86.
- Holdo, R. M., Mack, M. C., & Arnold, S. G. (2012). Tree canopies explain fire effects on soil nitrogen, phosphorus and carbon in a savanna ecosystem. *Journal of Vegetation Science*, 23, 352–360.
- Holt, J. A., & Coventry, R. J. (1990). Nutrient cycling in Australian savannas. *Journal of Biogeography*, 17(4/5), 427– 432.
- Holt, J. A., Hodgen, M. J., & Lamb, D. (1990). Soil respiration in seasonally dry tropics near Townsville, North Queensland. *Australian Journal of Soil Research*, 28, 737-745.
- Hurteau, M. D., & Brooks, M. L. (2011). Short- and Long-term Effects of Fire on Carbon in US Dry Temperate Forest Systems. *BioScience*, 61(2), 139 - 144.
- Jenkinson, D. S., Adams, D. E., & Wild, A. (1991). Model estimates of CO₂ emissions from soil in response to global warming. *Nature* (London), 351, 304 - 306.
- Joffre, R., Ourcival, J. M., Rambal, S., & Rocheteau, A. (2003). The key-role of topsoil moisture on CO₂ efflux from a Mediterranean Quercus ilex forest. *Annals of Forest Science*, 60, 519 - 526.
- Joubert, D. F., Rothauge, A. & Smit, G. N. (2008). A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular

- reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments*, 72, 2201–2210.
- Joubert, D. F., Smit, G. N., & Hoffman, M. T. (2012). The role of fire in preventing transitions from grass dominated state to a bush thickened state in arid savannas. *Journal of Arid Environments*, 87, 1-7.
- Kavdir, Y., Ekinici, H., Yüksel, O., & Mermut, A. R. (2005). Soil aggregate stability and ¹³C CP/MAS-NMR assessment of organic matter in soils influenced by forest wildfires in Canakkale, Turkey, *Geoderma*, 129 (3-4), 219 – 229.
- Kauffman, J. B., Till, K. M., & Shea, R. W. (1992). Biogeochemistry of deforestation and biomass burning. In Dunnette, D. A. (Ed.). *The impact of human activities on the environment* (pp. 45-58). Symposium (series, 483) conducted at the meeting of American Chemical Society of Washington, USA,
- Khavhagali, V, P. (2008). Forest Colonization of Savannas: Patterns and Process. Unpublished MSc. thesis, University of Cape Town, Cape Town, South Africa
- Kovacic, D. A., Swift, D. M., Ellis, I. E., & Hankonson, T. E. (1986). Immediate effects of prescribed burning on mineral soil N in ponderosa pine of New Mexico. *Soil Science*, 141(1), 71-76.
- Kramer, P. J., & Kozlowski, T. T. (1960). *Physiology of trees*. McGraw – Hill Book Publisher, New York
- Kutiel, P., & Naveh, Z. (1987). The effect of fire on nutrients in a pine forest soil. *Plant and Soil*, 104 (2), 269 - 274.
- Lee, H., Fitzgerald, J., Hewins, D. B., McCulley, R. L., Archer, S. R., Rahn, T., & Throop, H. L. (2014). Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment. *Soil Biology & Biochemistry*, 72, 123 -132.
- LI-COR. (1993). Soil Respiration Chamber Instruction Manual. Lincoln, NE 68504, Nebraska USA
- Linn, D. M., & Doran, J. W. (1984). Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. *Soil Science Society of American Journal*, 48, 1267-1272.
- Liu, F., Wu, X. B., Bai, E., Boutton, T. W., & Archer, S. R. (2010). Spatial scaling of ecosystem C and N in a subtropical savanna landscape. *Global Change Biology*, 16(8), 2213 - 2223.

- Ludwig, F. de Kroon, H. Berendse, F. & Prins, HHT. 2004. The influence of savanna trees on nutrients, water and light availability and the understorey vegetation. *Plant Ecology*, 170(1), 93 -105.
- Ma, S., Chen, J., North, M., Erikson, H., Bresee, M., & LeMoine, J. (2004). Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed conifer forest. *Environmental Management*, 33(1), 148 - 159.
- Macadam, A. (1989). Effects of prescribed fire on forest soils. Ministry of Forestry Research Report 89001, Victoria, B.C
- Makhado, R. A., & Scholes, R. J. (2011). Determinants of soil respiration in a semi-arid savanna ecosystem, Kruger National Park, South Africa, *Koedoe*, 53(1).
- McCulley, R. L., Archer, S. R., Boutton, T. W., Hons, F. M., & Zuberer, D. A. (2004). Soil respiration and nutrient cycling in wooded communities developing in grassland, *Ecology*, 85(10), 2804 - 2817.
- Menaut, J. C., Abbadie, L., & Vitousek, P. M. (1993). Nutrient and organic matter dynamics in tropical ecosystems. In Crutzen, P. J., & Goldammer, J. G. (eds.), *Fire in the Environment* (pp. 215-231): The Ecological, Atmospheric and Climatic Importance of Vegetation Fires. Wiley, Chichester
- Menyailo, O. V., Matvienko, A. I., Stepanov, A. L., & Makarov, M. I. (2013). Measuring soil CO₂ efflux: effect of collar depth. *Russian Journal of Ecology*, 46(2), 152 -156.
- Mills, A. J., & Fey, M. V. (2005). Interactive response of herbivores, soils and vegetation to annual burning in a South African savanna. *Austral Ecology*, 30, 435 – 444.
- Milne, E. (2012). Soil organic carbon. In Heimsath, A (ed.). *Encyclopedia of the Earth*. Retrieved from <http://www.eoearth.org/view/article/156087/>
- Molla, I., Velizarova, E., Malcheva, B., Bogoev, V., & Hadzhieva, Y. (2014). Forest Fire Impact on the Soil Carbon Content and Stock on the North Slopes of Rila Mountain (Bulgaria). *Ecologia Balkanica*, 5, 81 - 88.
- Mukaru, W. C. (2009). Impacts of large herbivores on vegetation and soils around water points in Waterberg Plateau Park, central Namibia. Unpublished MSc. thesis, University of Namibia, Windhoek, Namibia
- Nakane, K., Yamamoto, M., & Tsubota, H. (1983). Estimation of root respiration rate in a mature forest ecosystem. *Japanese Journal of Ecology*, 33, 397- 408.

- Neff, J., Harden, J., & Gleixner, G. (2005). Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. *Canadian Journal of Forest Research*, 35, 2178 - 2187.
- Nguyen, C. T. (2011) Effects of a prescribed fire on soil nutrient pools in the pine rockland forest ecosystem. PhD Thesis, University Of Florida, USA. Unpublished
- Novara, A., Gristina, L., Ruhl, J., Pasta, S., D'Angelo, G., La Mantia, T., & Pereira, P. (2013). Grassland fire effect on soil organic carbon reservoirs in a semi-arid environment. *Solid Earth*, 4, 381 - 385.
- Oba, G. (1990). Effects of wildfire on a semi desert riparian woodland along the Turkwel river, Kenya, and management implications for Turkana pastoralists. *Land Degradation and Rehabilitation*, 2, 247–259.
- Ojima, D. S., Schimel, D. S., Parton, W. J., & Owensby, C. E. (1994). Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, 24, 67 - 84.
- Osborne, C. P. (2008). Atmosphere, ecology and evolution: what drove the Miocene expansion of C₄ grasslands? Essay Review, *Journal of Ecology*, 96, 35-45.
- Parkin, T. B., Doran, J. W., & Franco-Vizcaíno, E. (1996). Field and Laboratory Tests of Soil Respiration. In Doran, J.W., & Jones, A.J. (eds.). *Methods for assessing soil quality* (p. 231-45). Madison, WI
- Parton, W. J., Schimel, D. S., Cole, C. V., & Ojima, D. S. (1987). Analysis of factors controlling soil organic-matter levels in Great- Plains grasslands. *Soil Science Society of America Journal*, 51(5), 1173 – 1179.
- Pechony, O., & Shindell, D. T. (2010). Driving forces of global wildfires over the past millennium and the forthcoming century. *PNAS*, 107(45), 19167–19170.
- Pickett, S.T. A. (1989). Space-for-time substitution as an alternative for long term studies. In Likens, G. E (ed.), *Long-term studies in Ecology: Approaches and alternatives*, (pp.110-135). Springer-Verlag New York Inc., USA.
- Pinto, A. de S., Bustamante, M. M. C., Kisselle, K., Burke, R., Zepp, R., Viana, L. T., ...Molina, M. (2002). Soil emissions of N₂O, NO, and CO₂ in Brazilian Savannas: Effects of vegetation type, seasonality, and prescribed fires. *Journal of Geophysical Research*, 107(20), 8089.
- Post, W. M., Izaurralde, R. C., Mann, L. K., & Bliss, N. (1999). Monitoring and verifying soil organic carbon sequestration. In Rosenberg, N. J., Izaurralde, R. C., & Malone, E. L. (eds.). *Carbon Sequestration in Soils. Science, monitoring and beyond*. Battelle Press. Washington D. C., USA

- Prieto-Fernandez, A., Carballas, M., & Carballas, T. (2004). Inorganic and organic N pools in soils burned or heated: Immediate alterations and evolution after wildfires. *Geoderma*, 121(3), 291 - 306.
- Raich, J. W., & Schlesinger, W. H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B*, 44(2), 81-99.
- Raich, J.W., & Tufekcioglu, A. (2000). Vegetation and soil respiration: Correlations and controls. *Biogeochemistry*, 48, 71 - 90.
- Raison, R. J. (1979). Modification of the soil environment by vegetation fires with particular reference to nitrogen transformations: a review. *Plant and Soil*, 51(1), 73 -108.
- Reichstein, M., A. Rey, A. Freibauer, J. Tenhunen, R. Valentini, J. Banza et al. (2003). Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature, and vegetation productivity indices. *Global Biogeochemical Cycles*, 17(4), 1104.
- Riddell, E. S., Khan, A., Mauck, B., Ngcobo, S., Pasi, J., & Pickles, A. (2012). Preliminary assessment of the impact of long-term fire treatments on *in situ* soil hydrology in the Kruger National Park, *Koedoe*, 54(1), 1 - 7.
- Rochette, P., B. Ellert, E. G., Gregorich, R. L., Desjardins, E. Pattey, R. Lessard, and B.G. Johnson. (1997). Description of a dynamic closed chamber for measuring soil respiration and its comparison with other techniques. *Canadian Journal of Soil Science*, 77, 195 - 203.
- Ross, D. J., Speir, T. W., Tate, K. R., & Feltham, C. W. (1997). Burning in a New Zealand snow-tussock Grassland: Effects on soil microbial biomass and nitrogen and phosphorus availability. *New Zealand Journal of Ecology*, 21 (1), 63 - 71.
- Satyam, V. & Jayakumar, S. (2012). Impact of forest fire on physical, chemical and biological properties of soil: A review. Proceedings of the *International Academy of Ecology and Environmental Sciences*, 2(3), 168 -176.
- Sawamoto, T., Hatano, R., Yajima, T., Takahashi, K., & Isaev, A. P. (2012). Soil respiration in Siberian Taiga ecosystems with different histories of forest fire. *Soil Science and Plant Nutrition*, 46(1), 31 - 42.
- Schimel, D. S. (1995). Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, 1, 77 - 91.
- Schlentner, R. E., & Van Cleve, K. (1985). Relationships between soil CO₂ evolution from soil, substrate temperature, and substrate moisture in four mature

- forest types in interior Alaska. *Canadian Journal of Forest Research*, 15(1), 97-106.
- Schlesinger, W. H., & Andrews, J. A. (2000). Soil respiration and the global carbon cycle. *Biogeochemistry*, 48(1), 7 – 20.
- Schlesinger, W. H., Raikes, J. A., Hartley, A. E., & Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems, *Ecology*, 77(2), 364 - 374.
- Schneider, I. (1993). *Waterberg Plateau Park*. Shell Namibia
- Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience*, 54(7), 661–76.
- Scholes, R. J., & Archer, S. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28, 517 - 544.
- Scholes, R. J., & Hall, D. O. (1996). 'The carbon budget of tropical savannas, woodlands and grasslands'. In Breymer, A. I., Hall, D. O., Melillo J. M., & Agren, G. I (eds.). *Global change: Effects on coniferous forests and grasslands* (pp. 69 – 100). Wiley, Chichester
- Scholes, R. J., & Walker, B. H. (2004). *An African Savanna: Synthesis of the Nylsvley Study* (pp, 300), Cambridge Studies in Applied Ecology and Resources Management. Cambridge University Press
- Scholes, R. J. & Walker, B. H. (1993). *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge
- Sheuyange, A., Oba, G., & Weladjib, R. B. (2005). Effects of anthropogenic fire history on savanna vegetation in northeastern Namibia. *Journal of Environmental Management*, 75, 189 –198.
- Shibistova, O., Lloyd, J., Evgrafova, S., Savushkina, N., Zrazhevskaya, G., Arneeth, A., ...Kolle, O. (2002). Seasonal and spatial variability in soil CO₂ efflux for a central Siberian Pinus sylvestris forest. *Tellus B*, 54(5), 552 - 567.
- Singer, M. J., & Munns, D. N. (1999). *Soils: An Introduction*, (4th ed.). pp. 163 - 226: Macmillan Publishing Company, New York, USA
- Singh, J. S., & Gupta, S. R. (1977). Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review*, 43(4), 449 – 528.
- Stellmes, M., Frantz, D., Finckh, M., Revermann, R., Röder, A., & Hill, J. (2013). Assessment of fire frequency, fire seasonality and fire intensity within the Okavango region derived from MODIS fire products. *Biodiversity & Ecology*, 5, 351-362

- Snyder, J. R. (1986). The impact of wet and dry season prescribed fire on Miami Rock Ridge Pineland, South Florida. Report SFRC 86/06. Everglades national Park: South Florida Research Center.
- Thalwitzer, S., Joubert, D., Johann, L., Alberts, M. & Förtsch, M. (2011). Waterberg Plateau Park Management and Tourism Development Plan. Unpublished paper. Ministry of Environment and Tourism. Windhoek. Namibia
- Throop, L. H., & Archer, S. R. (2008). Shrub (*Prosopis velutina*) encroachment in semidesert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. *Global Change Biology*, 14, 2420 – 2431.
- Throop, L. H., & Archer, S. R. (2007). Interrelationships among shrub encroachment, land management, and litter decomposition in a semi desert grassland. *Ecological Applications*, 17(6), 1809 - 1823.
- Trollope, W. S. W. (2007). Fire—a key factor in the ecology and management of African grasslands and savannas. In Masters, R. E. & Galley, K. E. M. (eds.). Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems (pp. 2-14). Tall Timbers Research Station, Tallahassee, Florida, USA
- Trollope, W. S. (1999). Veld burning in different vegetation types: savanna. In Tainton, N. M. (ed.). *Veld management in South Africa* (pp. 236–242). University of Natal Press, Pietermaritzburg, South Africa
- Uunona, N. M. (2014). Impacts of fire on resource utilization of grazers and browsers in the Waterberg Plateau Park. Unpublished Work Integrated Learning (WIL) report, Namibia University of Science and Technology, Windhoek, Namibia
- Van Wilgen, B. W. (2009). The evolution of fire management practices in savanna protected areas in South Africa: a review. *South African Journal of Science*, 105, 343 – 349.
- Vásquez, F. J., Acea, M. J., & Carballas, T. (1993). Soil microbial populations after wildfire. *FEMS Microbiology Ecology*, 13(2), 93 - 104.
- Veenendaal, E. M., Kolle, O., & Lloyd, J. (2014). Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. *Global Change Biology*, 10, 318 – 328.
- Vitousek, P. M., & Howarth, R. W. (1991). Nitrogen limitation on land and sea: how can it occur? *Biogeochemistry*, 13(2), 87–115.
- Walkley, A., & Black, I. A. (1934). An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science*, 37, 29-38.

- West, N. E., Stark, J. M., Johnson, D. W., Abrams, M. M., Wright, J. R., Heggem, D., & Peck, S. (1994). Effects of climatic change on the edaphic features of arid and semiarid lands of western North America. *Arid Soil Research and Rehabilitation*, 8(4), 307 - 351.
- Widden, P., & Parkinson, D. (1975). The effect of a forest fire on soil microfungi. *Soil Biology Biochemistry*, 7(2), 125 - 138.
- Yildiz, O., Esen, D., Sarginci, M., & Toprak, B. (2009). Effects of forest fire on soil nutrients in Turkish pine (*Pinus brutia*, Ten) Ecosystems. *Journal of Environmental Biology*, 31, 11-13.
- Zheng, D., Chen, J., Song, B., Xu, M., Sneed, P., & Jensen, R. (2000). Effects of silvicultural treatments on summer forest microclimate in south-eastern Missouri Ozarks. *Climate Research*, 15, 45 - 59.
- Zhou, W., Hui, D., & Shen, W. (2014). Effects of soil moisture on the temperature sensitivity of soil heterotrophic respiration: A laboratory incubation study. *PLOS ONE*, 9(3). doi: 10.1371/journal.pone.0092531
- Zou, C. B., Barron-Gafford, G. A., & Breshears, D. D. (2007). Effects of topography and woody plant canopy cover on near-ground solar radiation: Relevant energy inputs for ecohydrology and hydrogeology. *Geophysical Research Letters*, 34(24), L24S21.

APPENDIX

Appendix1. Chemical analyses methods

(i) Soil Texture

Soil samples were air dried and passed through a 2 mm sieve. Soil texture was determined by the Pipette Method (Particle Size Analysis). Approximately 20.00 g of air-dry soil from each sample was weighed into an identical 250 ml polyethylene bottles plus the blank. About 20 ml of dispersing agent followed by 100 ml of water (de-ionised water) was added. The solution was shaken for two separate 30 minute periods at 180 oscillations per minute during the day. The solution was left to stand overnight. Three sets of dry aluminium weighing dishes were weighed. One set for sand, clay and another for silt. About 80 ml of water was added to the bottles and stand bottles were put in a location at constant temperature and that is vibration free. The bottles were shaken by hand for 30 seconds, and placed onto the bench, the inner lid was carefully remove the inner lid to allow sedimentation to settle. The samples were then placed in the aluminium weighing dish and dried in an oven at 100 °C for about 3 hours. Set of dishes containing the clay and silt samples were placed in the oven and weigh when dry to determine the clay and silt content. Sand fraction were separated by washing the contents of the bottle onto a 53 μ sieve with several portions of tap water. The sand was washed free of silt, clay and dispersing solution by playing a fine jet of water over the sieve for about 60 seconds. The washed sand was carefully transferred into a weighed aluminium dish and dry at 100 °C overnight.

(ii) Organic Carbon (SOC)

Soil samples were air dried and passed through a 2 mm sieve. Soil organic carbon was determined using the colorimetric Walkley-Black method (Walkley & Black, 1934). Approximately 1 mg of air-dry soil from each sample was weighed and glucose standards of different concentrations (0.1, 0.2, 0.3, 0.4 and 0.5 parts per million (ppm)) were prepared. The weighed soil samples and glucose standards were then transferred into a 16 x 120 mm test tube with 1 ml of 1N potassium

dichromate ($K_2Cr_2O_7$) solution; 2 ml of concentrated sulfuric acid (H_2SO_4) was gradually added. The solutions were mixed using a vortex mixer set at low speed. The samples were heated at 80°C for 60 minutes in an oven. After the samples cooled down, 7 ml of de-ionised water was added. The solutions were allowed to settle overnight in a refrigerator. The following day, absorbance was measured at 600 nm, using a UV/VIS spectrophotometer (model 916; GBC Scientific Equipment, Melbourne, Australia). A calibration curve was prepared using glucose standards concentrations.

(ii) Available Phosphorus

Soil available phosphorus was determined using the Olsen method (Olsen *et al.*, 1954). Approximately 5 g of the sieved, air-dried soil from each sample was weighed into a 125 ml flask. Standard phosphate solutions of different concentrations (0, 0.4, 0.8, 1.2, 1.6, 2.0 mg/l) were prepared and subject to the same procedures as sample solutions. Roughly 0.3 g of activated charcoal (to increase the surface area of adsorption) and 50 ml of extracting solution (sodium bicarbonate) were added to each flask and the solutions were shaken for 30 minutes. The solutions were filtered through a Whatman #40 filter paper, and 5 ml from each sample was pipetted into a 25 ml volumetric flask. Each flask was filled to 10 ml with de-ionised water and 1 drop of p-nitrophenol indicator was added. An amount of 300 μ l 4M sulphuric acid and 4 ml colour reagent were also added to each flask and the solutions were shaken for 30 minutes. De-ionised water was added to each flask to make to volume and the absorbance was measured at 882 nm using a UV/VIS spectrophotometer (model 916; GBC Scientific Equipment, Melbourne, Australia). A calibration curve was prepared using standard phosphate solution concentrations.

(iv) Total Nitrogen

Total nitrogen was determined using an elemental analyzer (CHN) (LECO Corporation, St. Joseph, Michigan, USA). Approximately 1 mg from each soil sample was pre-weighed and encapsulated (in foil). The samples were placed in the CHN

machine's loader and transferred to the instrument's purge chamber directly above the furnace, eliminating the atmospheric gases from the transfer process. The samples were then introduced to the primary furnace containing only pure oxygen, resulting in a rapid and complete combustion (oxidation) at 950°C. At this stage, carbon, hydrogen, and nitrogen present in the sample were oxidized to carbon dioxide (CO₂), water (H₂O) and nitrogen dioxide (NO₂) respectively, and are swept by the oxygen carrier through a secondary furnace for further oxidation and particulate removal. The NO₂ is passed through a reduction tube filled with copper to reduce the gases to N₂ and remove any excess oxygen present from the combustion process. The total nitrogen results were given in percent by weight values (LECO, 2013).

(v) Exchangeable cations

The standard solutions used in the cation analysis were prepared as below; and they were subject to the same procedures (after preparation) as sample solutions. A 1000 mg/l stock standard 50 ml of Ca stock, 50 ml of Na, 20 ml of K and 5 ml of Mg were pipetted into a 200 ml volumetric flask and de-ionised water was added to make to volume. These stock standards were used to prepare working standards; for Ca and Mg, the combined stock solution (0-5-10-15-20-25 ml) was pipetted into 250 ml volumetric flask. To each flask, 25 ml of NH₄OAc 1 M solution and 125 ml 1 % of lanthanum solution were added, and de-ionised water was also added to make to volume. The standard series were 0-5-10-15-20-25 mg/l Ca and 0- 0.5- 1.0- 1.5- 2.0- 2.5 mg/l Mg. For Na and K, the combined stock solution (0-5-10-15-20-25 ml) was pipetted into 250 ml volumetric flask. To each flask, 25 ml of NH₄OAc 1 M solution and 125 ml 1 % of lanthanum solution were added, and de-ionised water was also added to make to volume. The standard series were 0-5-10-15-20-25 mg/l Na and 0- 2-4-6-8-10 mg/l K. These standards were used to calibrate the spectrometry machine.

Approximately 5 g of sieved, air-dry soil from each sample was weighed into extraction flasks. A 50 ml ammonium acetate solution was added from a reagent dispenser and the solutions were shaken at 180 oscillations per minute for 30

minutes. The solutions were allowed to stand for a few minutes and then filtered into test tubes. The solutions were stored in the refrigerator overnight. The absorbance was read at different wavelengths for different elements [Ca = 315.887, Mg = 279.079, Na = 589. 592 and K = 766. 490 nm] using an Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES; Thermo Fisher Scientific, Cambridge, UK). A calibration curve was prepared using standard solution concentrations.

Appendix 2. GPS coordinates for the beginning and end of transects surveyed for soil nutrients and SOC in 2014.

Treatment	Transect	Beginning	End
1	1	S 20.34940 E 17.36468	S 20.34931 E 17.36276
1	2	S 20.34717 E 17.36301	S 20.34722 E 17.36112
1	3	S 20.33695 E 17.35962	S 20.33693 E 17.35771
1	4	S 20.32828 E 17.35189	S 20.32824 E 17.35382
1	5	S 20.32043 E 17.39806	S 20.31859 E 17.39804
1	6	S 20.34509 E 17.40938	S 20.34506 E 17.41131
2	1	S 20.29462 E 17.40840	S 20.29278 E 17.40841
2	2	S 20.29152 E 17.39159	S 20.28969 E 17.39159
2	3	S 20.29130 E 17.38774	S 20.28947 E 17.38774
2	4	S20.28523 E 17.353268	S 20.28522 E 17.35077
2	5	S 20.31055 E 17.35288	S 20.31052 E 17.35098
2	6	S 20.30417 E 17.35312	S 20.30415 E 17.35119
14	1	S 20.31953 E 17.34557	S 20.31952 E 17.34748
14	2	S 20.32588 E 17.33940	S 20.32764 E 17.33596
14	3	S 20.32657 E 17.32745	S 20.32834 E 17.32745
14	4	S 20.32821 E 17.31689	S 20.32999 E 17.31689
14	5	S 20.32523 E 17.31526	S 20.32520 E 17.31332
14	6	S 20.33197 E 17.33899	S 20.32928 E 17.31330
24	1	S 20.34939 E 17.35604	S 20.34938 E 17.35758
24	2	S 20.35646 E 17.35784	S 20.35646 E 17.35974
24	3	S 20.33073 E 17.34793	S 20.33069 E 17.34984
24	4	S 20.33423 E 17.31628	S 20.33241 E 17.31626
24	5	S 20.32704 E 17.34859	S 20.32843 E 17.34854
24	6	S 20.32930 E 17.31523	S 20.3312 E 17.33904

Appendix 3. GPS coordinates for the sites surveyed for soil respiration in February 2015.

Treatment	Point	Month	Longitude	Latitude
2	1	February	20.327951	17.353493
2	2	February	20.326910	17.352429
2	3	February	20.327272	17.352465
2	4	February	20.327156	17.352147
2	5	February	20.328630	17.352856
2	6	February	20.326939	17.353386
2	7	February	20.327177	17.353962
2	8	February	20.327177	17.353962
3	1	February	20.325513	17.353132
3	2	February	20.326076	17.351869
3	3	February	20.325780	17.351964
3	4	February	20.325650	17.351777
3	5	February	20.324834	17.351829
3	6	February	20.324807	17.352085
3	7	February	20.325540	17.352959
3	8	February	20.325656	17.352869
15	1	February	20.327956	17.350846
15	2	February	20.327664	17.350846
15	3	February	20.327636	17.350718
15	4	February	20.327392	17.350558
15	5	February	20.329205	17.351580
15	6	February	20.329135	17.351115
15	7	February	20.327737	17.349882
15	8	February	20.327581	17.349599
25	1	February	20.325853	17.351864
25	2	February	20.326003	17.350337
25	3	February	20.325845	17.350536
25	4	February	20.325974	17.349946
25	5	February	20.325049	17.350308
25	6	February	20.324948	17.349901
25	7	February	20.326187	17.349599
25	8	February	20.326230	17.349880

Appendix 4. GPS coordinates for the sites surveyed for soil respiration in April 2015.

Treatment	Point	Month	Longitude	Latitude
2	1	April	20.326943	17.352154
2	2	April	20.327070	17.352344
2	3	April	20.327561	17.352149
2	4	April	20.327690	17.352509
2	5	April	20.327974	17.352692
2	6	April	20.328129	17.352536
2	7	April	20.327154	17.353022
2	8	April	20.327395	17.353324
2	9	April	20.327326	17.352028
2	10	April	20.327296	17.352532
3	1	April	20.325768	17.351835
3	2	April	20.325558	17.351804
3	3	April	20.325577	17.351725
3	4	April	20.325300	17.352138
3	5	April	20.325192	17.352469
3	6	April	20.325405	17.352738
3	7	April	20.325697	17.352205
3	8	April	20.325787	17.352489
3	9	April	20.325782	17.352808
3	10	April	20.325456	17.352944
15	1	April	20.327165	17.350617
15	2	April	20.327178	17.350925
15	3	April	20.327627	17.350627
15	4	April	20.327389	17.350523
15	5	April	20.327246	17.350331
15	6	April	20.327491	17.350200
15	7	April	20.327262	17.349670
15	8	April	20.327409	17.349425
15	9	April	20.327301	17.349976
15	10	April	20.327638	17.349974
25	1	April	20.325954	17.350278
25	2	April	20.326090	17.350246
25	3	April	20.326152	17.350329
25	4	April	20.326286	17.350183
25	5	April	20.326154	17.350101
25	6	April	20.325957	17.350374
25	7	April	20.325680	17.350595
25	8	April	20.325321	17.350332
25	9	April	20.326224	17.349678
25	10	April	20.325885	17.349808