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Author
Dintwe, Kebonyethata

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Assessing Biogeochemical Process in Dryland Ecosystems: Potential Impacts of Climate Change

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Geography

by

Kebonyethata Dintwe

2016

ABSTRACT OF THE DISSERTATION

Assessing Biogeochemical Process in Dryland Ecosystems:
Potential Impacts of Climate Change

by

Kebonyethata Dintwe
Doctor of Philosophy in Geography
University of California, Los Angeles, 2016
Professor Gregory Stewart Okin, Chair

Drylands are drought-prone biomes in which precipitation is less than the potential evapotranspiration for the whole year, or for the most part of it. They include grasslands, shrublands, savannas, Mediterranean and deserts. Drylands cover 6.3 billion hectares (Bha) or 47% of the earth's land surface, and are home to 30% of the global human population. Collectively, drylands highly productive, contributing 30% of the global net primary productivity. Although dryland soils contain low organic carbon at local scale, globally they contain 20% of the global soil organic carbon. Furthermore, dryland are fire-prone ecosystems, with more than 80% of global wildfires occurring in drylands. The biogeochemical processes, such as soil carbon sequestration and fire regime are highly regulated by precipitation, and to some extent surface temperature.

Climate models, on the other hand, show that drylands would experience a decrease in mean annual precipitation, and an increase in surface temperature. The secondary effects of climate change include frequent extreme weather events such as strong winds, lighting and droughts. The predicted climate change and associated secondary effects are likely to alter and modify biogeochemical processes in drylands, a process that could lead drylands to become either net carbon source or sink depending on the magnitude of climate change. In light of the relationship between climate change and dryland functions, it is imperative to assess and evaluate the magnitude of the potential impacts of climate change in biogeochemical processes in drylands.

The dissertation of Kebonyethata Dintwe is approved.

Thomas Welch Gillespie

Yongkang Xue

Philip W. Rundel

Gregory Stewart Okin, Committee Chair

University of California, Los Angeles

2016

This dissertation is dedicated to Thami, Crystal and Tumi
and the rest of my family for the great support and courage they gave
me as I was working on this project

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VITA

EDUCATION

Ph.D. Candidate	Geography, University of California Los Angeles	(2012 - 2015)
Master of Arts	Geography, University of California Los Angeles	(2009 - 2012)
Bachelor of Science	Biological Sciences, University of Botswana	(1999 - 2003)

FELLOWSHIP, AWARDS and GRANTS

Graduate Student Support – Graduate Division UCLA	($ 7,000.00)	2016 - 2017
Dissertation Year Fellowship – UCLA	($35,582.09)	2015 - 2016
Graduate Student Paper Award – Depart. of Geography UCLA	($ 200.00)	2015 - 2015
Stable Isotope Biogeochemistry & Ecology NSF Award	($ 3,500.00)	2015 - 2015
Research Travel Grant – Depart. of Geography UCLA	($ 5,000.00)	2014 - 2015
Research Travel Grant Pilot – Graduate Division UCLA	($ 600.00)	2014 – 2015
Century/DayCent Model Training Award	($ 800.00)	2013 - 2013
Teaching Assistant, Associate, Fellow - UCLA	($30,000.00)	2010 - 2015
Graduate Student Support Award - UCLA	($24,675.50)	2009 - 2010

PEER-REVIEWED JOURNAL PUBLICATIONS

Junran, L., Flagg, C., Okin, G. S., Painter, T. H., **Dintwe**, K, Belnap, J. 2015. On the Prediction of Threshold Friction Velocity of Wind Erosion Using Soil Reflectance Spectroscopy. Aeolian Research 19, Part A (December 2015): 129–36. doi:10.1016/j.aeolia.2015.10.001

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Meyer, T., D'Odorico, P., Okin, G.S., Shugart, H., Caylor, K.K., O'Donnell, F., Bhattachan, A., **Dintwe, K.**, 2013. An analysis of structure: biomass structure relationships for characteristic species of the western Kalahari, Botswana. African Journal of Ecology.

Bhattachan, A., D'Odorico, P., Okin, G.S., **Dintwe, K.**, 2013. Potential dust emissions from the southern Kalahari's dunelands. Journal Geophysical Research: Earth Surface.

Bhattachan, A., Tatlhego, M., **Dintwe, K.**, O'Donnell, F., Caylor, K. K., Okin, G. S., Perrot D. O., Ringrose, S., D'Odorico, P. (2012) Evaluating eco-hydrological theories of woody root distribution in the Kalahari. PLoS ONE 7(3): e33996

Outline of my Dissertation

My dissertation investigates carbon cycling in dryland ecosystem, and the potential impacts of climate change. It is divided in to six chapters.

Chapter 1: *Introduction, What are drylands?* I described Dryland ecosystems and gave examples, and their geographical locations. I then discussed the importance of drylands, from evolution, socio-economic and ecological point of view. I also discussed potential impacts of climate change in drylands. I concluded by discussing major initiatives carried out by the science community and policy makers, in order to understand biogeochemical processes in drylands in the context climate change.

Chapter 2: *Isotopic analysis of C and N: critical insights into tree-grass interactions and soil inputs in savannas*. In 2014, I published a paper in which I estimated soil organic carbon (SOC) in drylands to be 299 x 10^{15} g C (299 Pg C). The purpose of this Chapter was to building and expanding on the previous work. Because I had estimated SOC, in this Chapter I determined the contribution of trees and grasses to soil carbon (C) input. Plants are important terrestrial primary producers. However, they are likely to face challenges posed by climate change. Therefore, it is critical to understand and quantify their contribution C cycling. To this end, analyzed stable C and nitrogen isotopic composition ($\delta^{13}C$ and $\delta^{15}N$, respectively) in the soil profile and vegetation. Stable carbon isotopic analysis has widely been used as a proxy to partition sources of C, whereas $\delta^{15}N$ had been used to assess nitrogen cycling in the ecosystems.

Chapter 3: *The contribution of biological soil crust to soil respiration in drylands.*

In the previous Chapter, I determined the contribution of trees and grasses to soil C input. However, it is important to point out that soil C pools are dynamic and change over time depending on many factors. For example, some of the soil C is lost back into the atmosphere through soil respiration. In this Chapter I assessed the two components of soil respiration: heterotrophic and autotrophic respiration. Soil respiration is single largest pathway of soil C loss into the atmosphere. Non-photosynthetic soil microbes carry out heterotrophic respiration, whereas primary producers such as plants (roots) and biological soil crusts (BSC) carry out autotrophic respiration. Biological soil crusts, on the other hand, are a common feature in drylands, covering up to about 70% of the surface area. Here, I used a combination of field measurements, $\delta^{13}C$ and $\delta^{15}N$ analysis to separate heterotrophic respiration from autotrophic respiration. I further calculated net primary productivity and chlorophyll content of the BSC.

Chapter 4: *Fire-induced albedo change and radiative forcing in Sub-Saharan Africa: implications on energy balance*.

Drylands are responsible for more than 80% of the global wildfires. Fires play an important role in modifying biogeochemical processes across the globe. For instance, they burn and convert vegetation biomass in to CO_2, charcoal and ash, a process that affect C fixation and sequestration. Further, fires deposit charcoal and ash on the ground surface, which darkens surface cover and reduces surface albedo. Surface albedo is the key component controlling surface energy balance thereby driving local climate and ecosystem functions. These two processes, biomass combustion into CO_2 and fire-induced albedo change, have potential to modify C cycling at local to global scales, as well as to modify global climate. In this Chapter, I used remote sensing technique to assess fire-induced albedo change and its radiative forcing in fire prone ecosystems, at continental scale.

Chapter 5: *Simulating soil organic carbon dynamics in African savannas using the Century model and CMIP5 climate variables*.

In this Chapter, I used Century model to simulate C fluxes in a savanna ecosystem. The purpose of this Chapter was to assess potential impacts of climate change in C fluxes in drylands. I used the results from the previous Chapters to parameterize the model. To run the model in to the future, I used CMIP5 future climate projections. I also used radiocarbon analysis ($\delta^{14}C$) to estimate the age of soil C and turnover.

Chapter 6: *Discussion and Conclusion*.

In this Chapter, I will discuss all the findings from the previous Chapters, and draw conclusion. I will also identify areas that need further research, and map the way forward. I intend to publish my Chapters as research papers.

Chapter 1: Introduction, What are dryland ecosystems?

1.1 What are dryland ecosystems?

Drylands are drought-prone biomes in which precipitation is less than the potential evapotranspiration for the whole year, or for the most part of it (D'Odorico and Porporato, 2006; Glenn et al., 1993; Lal, 2003). They include grasslands, shrublands, savannas, Mediterranean and deserts (Figure 1). According to D'Odorico and Porporato (2006), drylands are mostly located in continental areas, away from moisture sources, 2) in regions of high cells, between 20° and 40° latitudes in the southern and northern hemisphere, in rain shadow area, 4) or along western continental margins where, due to the upwelling of deep oceanic water, low surface temperature causes high atmospheric stability. Drylands cover 6.3 billion hectares (Bha) or 47% of the earth's land surface (Glenn et al., 1993; Lal, 2003). They cover 2 Bha each in Africa and Asia, 0.7 Bha in Australasia, 0.8 Bha in North America 0.6, in South America and only 0.3 Bha in Europe (Lal, 2001).

Drylands can be categorized by aridity, based on mean annual precipitation (MAP) (D'Odorico and Porporato, 2006). This approach classified drylands in to 1) Extremely arid zones, in which MAP ranges below 60 – 100 mm); Arid zones, where MAP ranges between 150 and 250 mm; 3) Semiarid zones, where MAP is about 250 – 600 mm; and 4) Dry sub-humid zones with Map in the range from 600 to 1200 mm (Mainguet, 1994; Noy-Meir, 1973).

Drylands can also be classified using aridity index, which is defined as the ratio of MAP to potential evapotranspiration (P:ET, AI, or Aridity Index) (Lal, 2003). Hyper-arid regions have AI of less than 0.05. The AI in arid- and semiarid regions is 0.05-0.2 and 0.2-0.5, respectively, while dry sub-humid regions have AI of 0.5-0.65 (Reynolds and Smith, 2002).

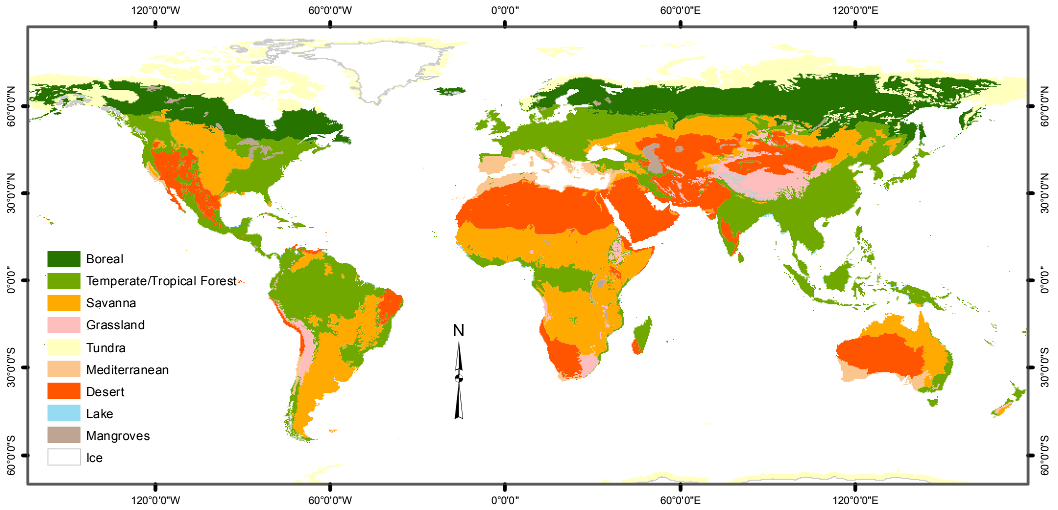

Figure 1-1. The geographical distribution of global terrestrial biomes. Data source: (Olson et al. (2001), WWF)

1.2 Why are drylands important?

1.2.1 Savanna and the evolution of hominids

Evolution theory suggests that hominids evolved in drylands, specifically in the East African savannas, some 12 million to 5 million years ago (Kingston et al. 1994). According to the savanna theory, transition from forested to a more open savanna like habitat may have prompted the early hominids to wander from trees and begin walking upright across the grass, an adaptation mechanism that freed up their fore-limbs or hands for carrying items and tool use (Reed 1997). Bipedalism and the use of tools are thought to have contributed significantly to diet improvement among our early ancestors, a process that give rise to civilization. It is important to note that there are other theories explaining the evolution of hominids. Savannas are also a place where anthropogenic fires originated and they are still the only ecosystems that burn much more frequently (Goldammer & Ronde 2004).

1.2.2 Socio-economic importance

Drylands support more than 2 billion (35%) of the world population, of which 90% live in developing countries (D'Odorico et al., 2013; MEA, 2005). Many of the drylands inhabitants practice subsistence farming and, or rely solely on commodities offered by these ecosystems (Solbrig et al. 1991). For instance, grasslands and Mediterranean are among the productive ecosystems (Parton et al., 1995; Von Fischer et al., 2008). They support arable and pastoral farming in many parts of the world (Zarovali et al., 2007). Savannas on the other hand, provide commodities such as firewood, timber and non-timber products, and constitute major resources to vast populations of the world (Solbrig et al., 1991). They also support large numbers of herbivores of all kinds ranging from invertebrates to large vertebrates such as buffalos and elephants, providing breeding grounds for them. The presence of herbivores attracts and supports other types of animals such as carnivores, which are in the higher trophic level. The unique vegetation composition and the presence of different kinds of animals make savannas an exquisite landscape and a major tourist attraction, indirectly serving as source of income for the local people, countries and regions at large. Recently, many countries had joint forces and established Transfrontier parks in many savanna ecosystems in recognition of the socio-economic importance played by these magnificent landscapes. Transfrontier Parks (or Peace Parks) are a recent concept in nature conversation based on the principle of ecosystems not recognizing national borders. This provision involves formal agreement for the joint management of conservation areas spanning international boundaries. For example, the region of Southern Africa alone established four Transfrontier Parks in the past 10 years as a way to promote conservation and improve the livelihoods of the locals as well as to increase revenues of the respective countries (van Amerom & Büscher 2005). The other goal of Peace Parks is to help bring peace to civil war victims as well as to establish amity between neighboring countries.

1.2.3 Ecological importance

1.2.3.1 Soil Organic Carbon

Soils are an important part of the biosphere, and fundamental resource of life on Earth. Globally, soils contain about 1500 Pg of carbon (1 Pg = 10^{15} g = 1 billion metric ton) in the top meter, and about 900 Pg of C in 1-2 m depth, compared to 600 Pg and 730 Pg in vegetation biomass and atmosphere, respectively (Batjes, 1996; Eswaran et al., 1993; Kirschbaum, 2000; Lal, 2008; Revelle and Suess, 1957; Schimel, 1995; Schlesinger and Bernhardt, 2013b). In drylands, the total soil organic carbon (SOC) has been estimated at 198 – 299 Pg C (Dintwe et al., 2014; Glenn et al., 1993; Grace et al., 2006; Jobbágy and Jackson, 2000). The importance of soil C sequestration is based on the assumption that enlargement of the soil C reduces the concentration of atmospheric CO_2 (Ringius, 2002). Conversely, loss of soil C could rapidly increase atmospheric CO_2 and results in detrimental effects in biogeochemical process (Townsend et al., 1997). While soil, vegetation and atmosphere C pools are largely driven by climate, soil C sequestration is mainly controlled by balance between C in plant residues returned to soil and that released into the atmosphere (Blanco-Canqui and Lal, 2004). At pedon and local scales, factors such as vegetation productivity and microbial activity control soil C sequestration, while at landscape to regional scale precipitation and temperature control soil C dynamics in drylands (White II et al., 2009).

Although dryland soils sequester large quantities of C, they also lose considerable quantities of C through soil respiration process (Box, 1978; Houghton and Woodwell, 1989). Soil respiration is a sum of autotrophic and heterotrophic respiration. Autotrophic refers to organisms that synthesize their own organic matter from CO_2 such as plants, whereas heterotrophic refers to organisms that depend on pre-formed organic matter for their energy and nutrition support (Büdel, 2005; Hibbard et al., 2005). At global scale, soil respiration releases 75 Pg C yr^{-1} to 100 Pg C yr^{-1} (Bond-Lamberty and Thomson, 2010; IPCC, 2013; Raich and Schlesinger, 1992). Compared to the emissions from fossil fuel combustion and cement production, soil respiration emissions are an order of magnitude higher (Mielnick and Dugas, 2000; Raich et al., 2002).

1.2.3.2 Primary Productivity

Global estimates of terrestrial gross primary productivity (GPP) and net primary productivity (NPP) are 120 Pg C yr^{-1} and 58 Pg C yr^{-1} (Hinsinger, 2013; Schlesinger, 1997). Savannas contributed significantly to the global NPP, contributing 17 Pg C yr^{-1}, while grasslands, Mediterranean shrublands and deserts contributed 5.3, 1.3 and 3.3 Pg C yr^{-1}, respectively (Hinsinger, 2013; Parton et al., 1994; Schlesinger, 1997). Furthermore, savannas have high fine roots biomass, second highest after temperate grassland (Jackson et al., 1996; Jackson et al., 1997).

Dryland ecosystems are also characterized by the presence of biological soil crusts (BSC), which could cover up to about 70% of the land surface (Belnap and Otto, 2003; Evans and Johansen, 1999; Garcia-Pichel et al., 2003). The BSC biomass in drylands has been estimated at ~17 Pg C, with NPP of about 3.9 Pg C yr^{-1} (Elbert et al., 2012; Sancho et al., 2016). Biological soil crusts are also important in the sense that they fix atmospheric nitrogen (N_2), thus improving soil fertility and enhancing ecosystem productivity, especially in regions where rainfall and anthropogenic inputs of N are low (Belnap, 1995, 2002). The rate of N fixation by BSC is about 40% (45 Tg yr^{-1}) of the global estimate of N fixation (107 Tg yr^{-1}) (Elbert et al., 2009; Elbert et al., 2012).

1.2.3.3 Fire regime

Fire-prone biomes cover about 40% of the Earth's land surface, and include biomes such as grasslands, savannas, Mediterranean and boreal forests (Bond et al., 2005; Chapin et al., 2011). Collectively, fire-prone ecosystems in drylands account for more than 80% of the global fires (Hao and Liu, 1994; Tansey et al., 2004).

An early European explorers to North American plains, Peter Fidler, narrated in his diary in 1793, "*These large plains either in one place or another constantly on fire and when the grass happens to be long and the wind high, the sight is grand and awful, and it drives along with amazing swiftness. The lightning in the spring and fall frequently lights the grass, and in winter it is done by the Indians. These fires among the long grass are very dangerous*" (Wright and Bailey, 1982).

Frequent fires, which characterize wet savannas, and intense fires which characterize grassland fires engulf large quantities of biomass resulting in emission of large quantities of CO_2, CO, CH_4, NO and N_2O, some trace aerosols and smoke particles, annually. The annual global C release due to biomass burning, is estimated at 8.3 Pg C yr^{-1} (IPCC, 2013).

Furthermore, fires play a significant role in regulating global energy balance by modifying surface albedo through charcoal and ash decomposition, and atmospheric composition through greenhouse gas and aerosol production (De Sales et al., 2015; Jin and Roy, 2005; Smith et al., 2005).

1.2.3.4 Dust emission and deposition

The relatively low biomass productivity in drylands, particularly deserts, makes the soil more vulnerable to wind erosion (Lal, 2001). In Jornada, New Mexico - USA it was estimated that wind erosion after disturbance of the soil surface removed up to 25% of total organic carbon (Li et al., 2007a; Li et al., 2007b). The study further showed that SOC and TN were among the first nutrients to be wind eroded and redistributed, and that soil particles deposited downwind were “nutrient-imbalanced” (Li et al., 2008).

In the southern hemisphere, in the Kalahari South, where soils are 95% sand and almost lack biological soil crusts, Bhattachan et al. (2013) calculated that the vertical dust flux was 3.0×10^{-2} g m^{-2} yr^{-1}, and the flux could increase to 2.4×10^{-1} g m^{-2} yr^{-1} and 4.8 g m^{-2} yr^{-1} if 50% and 100% of vegetation cover was lost, respectively.

Furthermore, it has been shown that drylands affect other ecosystems by way of dust deposition. Bhattachan et al. (2013) found that iron-rich dust from the Kalahari gets transported and deposited in the Southern Ocean where it enhances the productivity of the ocean. In the Sahel, a significant portion of anthropogenic dust (due to agriculture) is transported over the Atlantic to North America and deposited on snow, where it reduces surface albedo and exerts positive radiative forcing (Ginoux et al., 2010; Myhre et al., 2013; Okin et al., 2004). Furthermore, strong winds North American rangelands transport dust over long distances and deposit it on snow where it lowers albedo of the snow (Li et al., 2013; Okin et al., 2011; Okin et al., 2006; Painter et al., 2012)

1.3 Climate change in drylands

1.3.1 Future climate projections

Atmospheric CO_2 has been steadily increasing from about 270 ppm since the mid 18th century following the industrial revolution, reaching 350 ppm in 1990, approximately 367 ppm in 2000, 387 ppm in 2010 and 400 ppm in 2012 (IPCC, 2013; Schlesinger, 1993; Taub, 2010; WMO, 2010). The levels of atmospheric CO_2 are expected to reach about 600 ppm by the year 2100 (Houghton et al., 2001; Lattanzi, 2010; Vitousek, 1994). Increase in atmospheric CO_2 and associated climate change are likely to cause unprecedented modifications in biogeochemical processes in the ecosystems across the world.

Dryland ecosystems are vulnerable to climate change, and would be affected by directional changes in climate and land use (Nicholson, 2001; Nicholson and Kim, 1997). More than 70% of global climate models (GCM) predict that mean annual precipitation (MAP) in drylands, particularly savannas, will decrease by about 10 - 25% and 15 - 45% under Representative Concentration Pathway 2.6 (RCP2.6) and RCP8.5 climate scenarios, respectively, by 2100 while mean annual temperature (MAT) will increase by about 1.5 - 3

°C and >4 °C under RCP2.6 and RCP8.5 climate scenarios, respectively (IPCC 2013, Hartmann et al., 2013; Knapp et al., 2008; Shongwe et al., 2009). Vegetation-climate models have predicted change in vegetation structure and composition, with an increase in bush encroachment in drylands (Tietjen et al., 2010)

Gastineau and Soden (2009) and Young et al. (2011) predicted an increase in windstorms and wind speeds respectively in tropics and extra tropics. Sheffield and Wood (2007) had shown that drought, an extended period of anomalously low soil moisture, would increase in the drylands by the end of the 21st century. High windstorms frequency and wind speed coupled with dry soil soils could lead to increased sediment transport especially in areas with low and sparse vegetation cover (Bhattachan et al., 2013; Li et al., 2008; Li et al., 2007b).

Because drylands are likely to experience a relatively uniform increase in CO_2, the anticipated changes in biogeochemical processes would mostly be due to changes in precipitation and temperature (Lattanzi, 2010; Ringrose et al., 2008).

1.3.2 Large scale studies in drylands ecosystems

In quest to understand biogeochemical processes in drylands, a number of long-term and large-scale experiments had been established throughout the world during the last few decades, with a few established in the early 1900s. Examples of these projects include Long

Term Ecological Research (LTER) in the USA and the International Geosphere-Biosphere Program (IGBP).

1.3.2.1 Long Term Ecological Research

The LTER is the largest and longest-lived ecological network in the United States, consisting of 26 different projects covering an array of landscapes. Jornada Experimental Range (JER), established in 1982 and with data sets dating back to the mid 1800s is part of the LTER network (Havstad et al., 2006). The JER was established with an overall goal to quantify the key factors and processes that control ecosystem dynamics and biotic patterns in Chihuahuan Desert landscapes. Chihuahuan Desert, the largest desert in North America and located between short-grass prairies of the central United States and the shrub dominated ecosystems of the Sonoran and Mojave Deserts, is used as representative of arid and semi arid ecosystems of the world where dramatic changes in vegetation structure and ecosystem processes have occurred over the past several centuries (Buffington and Herbel, 1965; Gibbens et al., 1983; Gibbens and Beck, 1987; Havstad et al., 2006; Monger et al., 1998). The land surveys carried out in the 19th century augmented with recent long-term monitoring had provided substantial information and evidence that shrub and bush (mesquite and creosote) cover had increased since 1858 while grass cover had been decreasing with time especially during drought years (McClaran and Devender, 1997).

1.3.2.2 *International Geosphere-Biosphere Program*

In the early 1990s the IGBP proposed and set up a number of large-scale terrestrial transects to study the effect land use and climate change on biogeochemistry, vegetation dynamics and surface-atmosphere exchange in terrestrial ecosystems (Koch et al., 1995). Three of the IGBP transect were established in semi-arid tropical regions, covering a wide range of savanna ecosystems: Kalahari Transect (KT), North Australian Tropical Transect (NATT) and Savannas in the Long Term (SALT) in West Africa. These transects, ~1000 km long, were located in environmental and land use intensity gradient and climatic gradient.

1.3.2.3 The Kalahari Transect (KT)

The Kalahari Transect is situated in the Kalahari basin, an ancient depositional environment with complex history. The Kalahari sands cover an area of about 2.5 million ha spreading from the heart of southern Africa to the interior of central Africa between latitudes 15 – 30^0 S and longitudes 17 – 26^0 E (Shugart et al., 2004; Wang et al., 2007b). The sediments have accumulated and evolved mainly through Aeolian processes, and to some extent through fluvio-deltaic and groundwater processes. The Kalahari sands are generally nutrient poor (Dintwe et al., 2014; Thomas and Shaw, 1991b; Wang et al., 2007b), and very deep with the center of the basin reaching up to 200 m in depth.

Given the great extends of the KT, it is not surprising that the Kalahari is climatically variable, with a strong south to north mean annual precipitation gradient ranging from 150 to 1200 mm. The relatively vertical and horizontal homogeneity (poor nutrient and low fossil content) of the sandy substrate, the flat topography of about 1000 m.a.s.l., the untransformed nature of much of the land surface and lack of surface water make the Kalahari an ideal environment for studying the effect of precipitation on biogeochemical processes with minimal or no effect from soil and other biophysical factors at sub continental scale. This is the main reason why the Kalahari has qualified and been included as one of the IGBP transects.

A substantial amount of work has been done in characterizing vegetation and soil structure and to some extent fire regimes (Caylor et al., 2004; Privette et al., 2004; Scholes et al., 2004). Major findings have revealed that vegetation productivity and fire frequency increase with moisture availability. The spatial distribution varies with space, whereby trees in the drier part of the Kalahari tend be randomly distributed while those in the moist part of Kalahari tend to cluster (Caylor et al., 2003). The cause of variation in spatial distribution of trees still remains a mystery. Biogeochemical processes such nutrients cycle, microbial abundance have and are continuing to receive attention (Aranibar et al., 2004; Büdel et al., 2009; Dintwe et al., 2014; Dougill and Thomas, 2004; Shushu, 1996; Thomas et al., 2008). Existing information had shown that precipitation plays a major role in these processes. The main question that a still remains to be answered is how are these processes going to be affected by the envisaged climatic change. To this end intensive and detailed ecosystem studies have been and are still being conducted. The results coupled with model outputs could provide an insight of the future process.

1.3.2.4 North Australian Tropical Transect (NATT)

The NATT is located in northern Australia; in a savanna landscape characterized by lack or limited variation in topography. Them main distinct characteristic of the area is the constant decline of MAP from 1600 in the north to 500 mm in the south inland (Hutley et al., 2011). The NATT is 1000 km long transect with a width of 250 km. It covers large intact vegetation and wide range of soils. The great variations in soil type and MAP make NATT an ideal place to study the climatic factors and land-atmosphere interactions as well as how they could influence vegetation and floristic change (Bancroft, 1996). The variations in soil make it possible to assess landscape patchiness and soil surface condition as a predictor of nutrient availability on soils. A substantial amount of research has been done in the NATT over the past few decades.

1.3.2.5 Savannas in the Long Term (SALT)

The SALT transect is located in Sahel-Sudan zone, a region crucial to the rural economy and for the livelihoods of the region's pastoral people. SALT, which ran from 1988 through 1998, was a project funded by the French ministry of research and by CNRS in collaboration with IGBP (Abbadie et al., 2006).The Sahel is densely populated and subject to frequent drought, with associated problems of food security, environmental degradation and noticeable problems of desertification. This transect is important in the sense that it provides the opportunity to study and understand how human management practices, especially grazing and fire, impact ecological processes. The findings could help scientists, policy makers and locals to develop best practices for sound land management.

1.3.2.6 Other large-scale and long-term projects

Various countries had also established medium to large-scale experimental sites in their respective savanna ecosystems. Argentina, Brazil and South Africa are examples of such countries. The Cerrados in Brazil have started getting attention from government, NGOs and the scientific community (Cole, 1960; Eiten, 1982; Lopes and Cox, 1977; Ratter et al., 1997). One of the factors that triggered attention was the high rate at which Cerrados were being converted to cropland for cash crops, leading to massive losses some of biodiversity hotspots in the world. South Africa has two large-scale experimental sites: the Nylsvley Nature Reserve and Kruger National Park (Huntley, 1982; Huntley and Morris, 1982; Scholes and Walker, 1993). The experiments in these two sites cover a broad array of topics including the effect of fire, herbivory and precipitation on vegetation structure and composition as well as topics on biogeochemical processes such as nutrients and hydrologic cycle. Similarly, there is a big scale multi discipline research going on in the savannas o Argentina.

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Chapter 2: Isotopic analysis of C and N: critical insights into tree-grass interactions and soil inputs in savannas

Abstract

Savannas, characterized by coexistence of tree and grasses, are extensive and occur in all the continents except for Antarctica. The mechanisms that control coexistence of trees and grasses in savannas are not fully understood, and *in situ* observations of belowground components (soils and roots) are particularly sparse. Here, we used stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$, respectively) in plants and soils to examine tree-grass interactions, carbon cycling, and nitrogen inputs in a savanna ecosystem along a strong precipitation gradient (180 - 540 mm yr^{-1} mean annual precipitation, MAP). Soil $\delta^{13}C$ values at 30 cm were higher than at other depths in all the sites, suggesting a more complex interaction between trees and grasses than previously thought. Our results indicate a three-layer belowground competition model with grasses dominating in a shallow layer between surface and deep layers dominated by woody plants. Along the precipitation gradient, tree-derived soil organic carbon (SOC) was found to be highest (63.8%, 1288.1 g m^{-2}) in the wettest site (precipitation: 540 mm yr^{-1}) whereas grass-derived (SOC) was found to be highest (69.4%, 1721.0 g m^{-2}) in the middle of the transect. These results indicate that woody species are the dominant source of SOC in the driest and wettest sites, and whereas grasses dominate SOC input in the intermediate sites. Our results also confirm

that the highly abundant *Acacia* species in the Kalahari do not fix atmospheric nitrogen, despite being legumes.

2.1 Introduction

Savannas are characterized by a paradoxical coexistence of trees and grasses, covering about 23-33 million km^2 (10 - 25%) of the Earth’s land surface (Grunow et al., 1980; Sankaran et al., 2005; Scholes and Archer, 1997). They are found in the latitude band ~15° - 30° in the south and north of the equator, where the mean annual precipitation (MAP), ranges between 100 - 1500 mm yr^{-1} (Belsky, 1994; Bond and Parr, 2010).

Several theories have been put forth to explain the dual-dominant character of savannas. In areas with less than 650 mm yr^{-1}, the 'dry' savannas, several studies (Accatino et al., 2010; Dohn et al., 2013; e.g. Sankaran et al., 2005) have suggested that competition for water between woody plants and grasses is a key determinant of the coexistence of these functional types, and that climate is the principal controller of tree-grass interactions. In these areas, savannas would exist even in the absence of fire in these systems, and belowground competition is the main factor determining tree-grass coexistence. In these savannas, belowground competition is typically thought of a result of the fact trees and grasses occupy different ecological niches (Bate et al., 1982; Grubb, 1977; Hipondoka et al., 2003; Shmida and Ellner, 1984; Walker and Noy-Meir, 1982); grasses are thought to exploit moisture in the topsoil and trees are though to have exclusive access to subsoil water. This two-layer model explains how grasses influence water availability for trees (February et al., 2013a; February et al., 2013b; Manea and Leishman, 2014) because, as water from precipitation percolates through the soil, uptake high in the soil by grasses profile reduces water availability lower down. The two-layer hypothesis, however, does not satisfactorily explain how trees reduce water availability for grasses (Accatino et al., 2010; Scholes, 1987). In fact, facilitative effects of trees on grasses are observed to contribute to grass water availability (D'Odorico et al., 2007a; Moustakas et al., 2013), at least at the tree-interspace scale.

Here, we use stable isotopes of carbon to evaluate the partitioning of grass- vs. tree-derived soil carbon with depth along a precipitation gradient (180 - 540 mm yr^{-1}). Because plants are the major terrestrial producers and sources of SOC, soil carbon stocks record and reflect the long-term interactions between tree-grass (Ehleringer et al., 2000; West et al., 2006). $\delta^{13}C$ values of SOC relate to the ^{13}C of plants residues mainly through root turnover (Wang et al., 2010). Thus, the soil profile $\delta^{13}C$ signature may be used as a proxy to identify sources of SOC and thus infer the belowground trees-grasses relationships. Thus, this analysis elucidates both belowground interactions between plant functional types as well as the effect of this interaction in different precipitation regimes. Stable isotopes of nitrogen are also measured in our samples and are used to evaluate whether the abundant *Mimosaceae* contribute nitrogen to the system.

Savannas are vulnerable to climatic fluctuations such as drought, directional changes in climate, and land use pressures (Nicholson, 2001; Nicholson and Kim, 1997). Global climate models predict that savannas, particularly southern African savannas might experience a

10 to 45% decrease in mean annual precipitation (MAP) and a 1.5 to 4 °C increase in mean annual temperature (MAT) by the end of this century (IPCC 2013, Hartmann et al., 2013). Regional climate models have further predicted an increase in the frequency and magnitude of extreme weather events such as windstorm, lightning and droughts (Knapp et al., 2008; Shongwe et al., 2009). In light of the perceived climate change impact, it has become imperative to evaluate and understand how the interaction between trees and grasses would respond to climate change. Trees and grasses are the main sources of soil organic carbon; therefore, any slight impact on vegetation dynamics due to climate change could dramatically alter the massive carbon stock in the savannas. Globally, savannas are estimated to contain 198×10^{15} to 299×10^{15} g of SOC, which translates to 13% - 20% of global SOC (Dintwe et al., 2014; Jobbágy and Jackson, 2000).

2.2 Methods and Material

2.2.1 Study site description

The study was conducted in the Kalahari Desert in southern Africa (Figure 1). The Kalahari covers an area of about 2.5 million km^2 between 12° - 29°S and 14° – 28°E, along a steep north-south precipitation gradient (Batisani and Yarnal, 2010; Nicholson and Kim, 1997; Tyson and Crimp, 1998). While the mean annual precipitation (MAP) in the north could be as high as 1200 mm, the south receives as little as 150 mm.

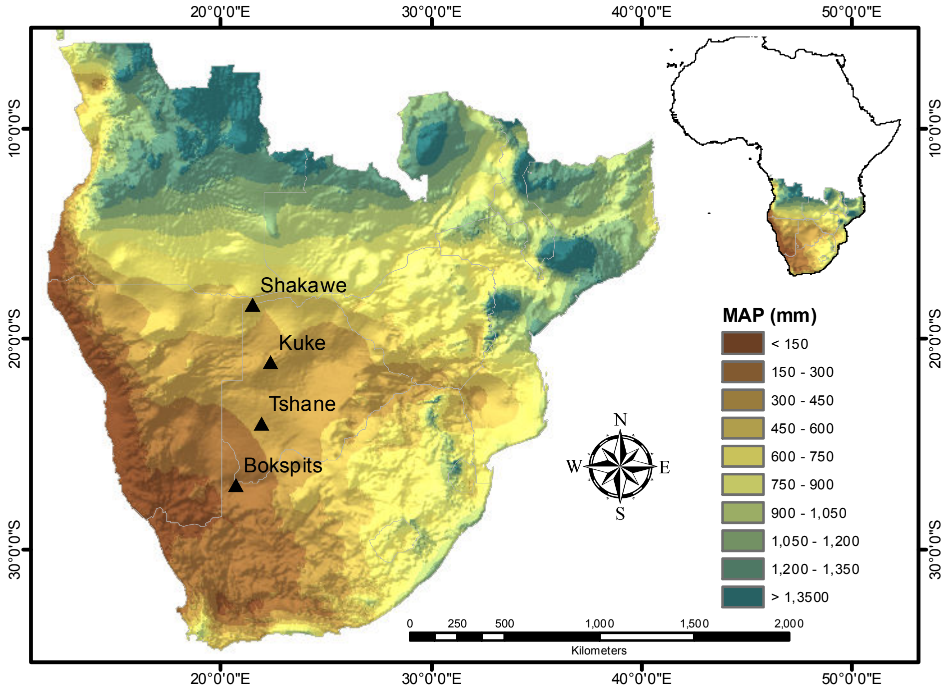

Figure 2-1. Mean annual precipitation (MAP) in southern African. The black triangles represent the study areas.

Soils in the Kalahari are characterized by a deep homogenous aeolian sand deposits, that reach about 100 – 200 m deep in the center of the basin (Scholes et al., 2002; Shugart et al., 2004; Thomas and Shaw, 1991b). The soils in Kalahari are slightly acidic, about ~ 95% sand and poor in organic carbon and total nitrogen content (Dintwe et al., 2014; Wang et al., 2007a). Throughout much of the Kalahari, groundwater is deep (> 20 m) (de Vries et al., 2000) meaning that plants rely almost exclusively on precipitation.

The vegetation structure in the Kalahari is highly tied to the north-south precipitation gradient (Caylor et al., 2003; Scholes et al., 2002). Shrubs and trees in the dry portions of the Kalahari contribute significantly to the patterning of soil resources, whereas in wet portions only trees contribute to the patterning of soil resources (Okin et al., 2008). The dominant plant species in the wettest part of Kalahari (north) are the nutrient-poor broad-leaf *Combretaceae* and *Caesalpinaceae* whilst in the driest (south) part are C_4 grasses, with sparsely distributed nutrient-rich fine-leaf *Mimosaceae* (Bhattachan et al., 2014; Bhattachan et al., 2013; Caylor et al., 2003; Meyer et al., 2013; Ringrose et al., 2003; Scholes et al., 2002; Shugart et al., 2004). Among the *Poaceae*, the *Aristidae* (*Aristida* and *Stipagrostis spp.*) dominate the arid south, the *Panicoidae* in the semi-arid center while the *Andropogonae* dominates in the mesic north (Scholes et al., 2002).

The steep precipitation gradient, homogenous and deep sandy soils of the Kalahari make it an outdoor living laboratory ideal to study the effects of precipitation on ecosystem processes with minimal background effects from abiotic and geophysical features like soil texture and relief (Koch et al., 1995; Thomas and Shaw, 1991b; Wang et al., 2007a). The International Geosphere-Biosphere Program (IGBP) has identified the Kalahari as one of the large-scale terrestrial transects to study the effects of climate change and land use on biogeochemistry, land-atmosphere interaction and vegetation dynamics of terrestrial ecosystems (Koch et al., 1995).

2.2.2 Sample design

Four study sites were selected along the Kalahari transect (KT) along the north-south moisture gradient (Table 1). Three 20 m x 20 m plots were established at each site. Vegetation was characterized on each plot before removal (Meyer et al., 2013). The cleared plots were gridded into 1 x 1 m quadrats. Eighty of the 1 m x 1 m quadrats were randomly selected and sampled in the center with a 4 inch (~10 cm) diameter sand auger (AMS Inc, Pittsburgh, PA) at four depths. The auger was inserted in the center of each quadrat until its tip was at 10, 30, 70 and 120 cm depth. Upon reaching each of these depths, the auger was removed, and a mixed sample from the auger was extracted. Thus, the average depth for the samples was approximately 5, 20, 60, and 110 cm. About 50 g of soil was taken at each depth and stored in a labeled zip-lock bag. The bags were left open for a week to air dry before shipping to the USA for laboratory analysis.

Table 2-1 Geographic coordinates, climate parameters, soil and vegetation characteristics of the study sites. The $\delta^{13}C$ values for trees and grasses obtained from Swap *et al.* (2004) and Wang *et al.* (2010). Tree $\delta^{15}N$ values obtained from Aranibar *et al.* (2004) and Wang *et al.* (2010). The numbers in brackets were calculated using equation provided by from Aranibar *et al.* (2004).

Site Feature	Bokspits	Tshane	Kuke	Shakawe
Geographic Coordinates	26°53'39"S 20°41'54"E	24°01'01"S 21°52'08"E	20°58'36"S 22°28'48"E	18°21'51"S 21°50'31"E
Mean Annual Precipitation (mm)	180	360	440	540
Mean Min Temp (°C)	2.1	3.9	4.4	5.8
Mean Max Temp (°C)	34.3	33.5	33.4	33.7
Soil pH	6.7	5.6	5.9	5.4
Carbon (g m^{-2})	1397.0	2506.0	2136.0	1982.0
Nitrogen (g m^{-2})	78.6	151.0	135.0	107.0
C_3 Foliar $\delta^{13}C_{VPDB}$ (‰)	-23.2	-25.9	-25.9	-26.7
C_4 Foliar $\delta^{13}C_{VPDB}$ (‰)	-14.0	-14.2	-13.8	-13.4
C_3 foliar $\delta^{15}N_{atm}$ (‰))	7.40 (5.4)	6.82 (4.6)	7.27 (4.2)	3.50 (3.7)

2.2.3 Laboratory analysis

Soil grain size distribution was measured in a subset of soil samples following a method outlined by Bird et al. (2010) and Kirby et al. (2015). Approximately 0.5 cm^3 of sample was boiled in DI water and pretreated with about 50 ml of 30% H_2O_2 to remove organic matter, 10 mL 1 N HCl to remove carbonates, and 10 mL 1 N NaOH to remove biogenic silica. Grain size was measured using Malvern Mastersizer 2000G large-volume sample dispersion unit. To verify the equipment's accuracy, repeatability and stability, a tuff standard (TS2) with a known distribution between 1.0 μm and 16 μm (mean = 4.53 μm ± 0.07 μm, n = 2998) was run regularly. The TS2 was run every few samples and once at the end for a final assessment. The results were reported as volume percent and divided into sand (74.00 – 2000 μm), silt (3.90 – 73.99 μm) and clay (0.02 – 3.89 μm).

Each labeled bag of soil was sieved, thoroughly mixed, and sub-sampled using a riffle sampler. Subsamples of about 4-5 cm^3 were ground into a powder using a ball mill for three minutes at 3450 rpm (Cianflone Scientific Instruments Corporation, Pittsburgh, PA). Thirty-tree samples for each depth at 10 and 30 cm, and fifteen samples each depth at 70 and 120 cm were randomly selected for each site for $\delta^{13}C$ and $\delta^{15}N$ analysis. A small portion, approximately 190 mg, of the ground, homogenized soil was placed into 9 x 10 mm tin capsules (Costech Analytical, Valencia, CA). After being sealed, the $\delta^{13}C$ and $\delta^{15}N$ of each sample was measured using Elemental Combustion System (Costech Analytical, Valencia, CA, USA) interfaced with continuous gas flow ConFlo IV (Thermo Scientific, Waltham, MA, USA) to gas isotope ratio mass spectrometer (Delta V Plus, San Jose, CA, USA). SOC and total nitrogen (TN) of the samples has previously been reported by Dintwe et al. (2014).

The $\delta^{13}C$ in the soil samples was calculated relative to the international standards USGS-40 (L-glutamic acid) and Buffalo River Sediments (SRM 2704), while ammonium sulfate (IAEA-N-1) was used as the standard for $\delta^{15}N$ (Amundson et al., 1998; Craig, 1953, 1957; Epstein et al., 1988; Mariotti, 1983; Olsson, 1970; Peterson and Fry, 1987; Stuiver and Polach, 1977). The isotope ratios were calculated using Equation 1, where R was the element measured, x was heavier isotope and y was the lighter isotope of the element measured (Amundson et al., 1998; Craig, 1953; Farquhar et al., 1989; Keeling et al., 2005; O'Leary, 1981, 1988; Wang et al., 2008).

$$\delta^{x}R\ ‰ = \left(\frac{({}^{x}R/{}^{y}R)_{sample}}{({}^{x}R/{}^{y}R)_{standard}}\right) * 10^{3} = \frac{\left(R_{sample} - R_{standard}\right)}{R_{standard}} * 10^{3} \tag{1}$$

By convention the $\delta^{13}C$ and $\delta^{15}N$ were corrected and reported as parts per thousand (per mil) relative to that for Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 respectively (Craig, 1957; Mariotti, 1983; Werner and Brand, 2001). Reproducibility of these measurements was approximately ±0.2‰.

2.2.4 Statistical analysis

Descriptive statistics such as mean, median and standard deviation were used to analyze the measured variables and to indicate the degree of overall variation. Student’s t-test and ANOVA were employed to test for differences between samples, depth, and sites. The Fisher’s least significant difference (LSD) method was used to distinguish differences following an ANOVA test. We further used linear and multiple regression techniques to evaluate the relationship between isotope values and climate variables.

2.3 Results

2.3.1 Soil Texture

No trends were observed with regard to soil texture either with depth or along the precipitation gradient. The soils in the Kalahari contained more than 93% sand at all sites and depths except in Bokspits at 120 cm where sand content was 88% (Table 2). Shakawe had the highest sand content, containing more than 98% at all depth. Clay content was highest in Tshane followed by Kuke, Bokspits and Shakawe respectively. Silt content increased with soil depth in all the sites except in Shakawe.

Table 2-2. Soil texture in the Kalahari Transect. The soils consisted of more than 90% sand, and had very poor clay content

Site (MAP)	Depth (cm)	Clay (% Composition)	Silt	Sand
Bokspits (180)	10	0.55	3.10	96.34
	30	0.67	3.56	95.76
	70	0.81	4.36	94.82
	120	1.30	10.36	88.32
	0 - 120	0.97	6.62	92.39
Tshane (350)	10	1.54	5.01	93.43
	30	1.13	6.30	92.55
	70	1.52	7.76	90.70
	120	1.58	8.17	90.22
	0 - 120	1.48	7.46	91.04
Kuke (440)	10	1.15	3.44	95.40
	30	0.87	3.88	95.23
	70	1.05	4.56	94.38
	120	1.00	4.59	94.39
	0 - 120	1.01	4.37	94.61
Shakawe (540)	10	0.00	1.02	98.98
	30	0.00	0.83	99.16
	70	0.00	0.00	99.99
	120	0.00	1.21	98.79
	0 - 120	0.00	0.73	99.27

2.3.2 Soil ^{13}C

The mean soil $\delta^{13}C$ values ranged between -22.7‰ and -17.3‰ (Table 3). The highest $\delta^{13}C$ value at 10 cm was recorded at Tshane (-18.9‰), followed by Bokspits with -18.98%. The lowest $\delta^{13}C$ value at 10 cm depth was recorded at Shakawe, -22.15‰. Similarly, Tshane had the highest depth-weighted $\delta^{13}C$ average for the soil profile, followed by Bokspits, Kuke and lastly Shakawe.

The highest δ^{13}C values occurred at 30 cm in all the sites, and the second highest values occurred at 10 cm. Soil organic carbon was highest at 10 cm in all the sites, followed by 30 cm layer. Shakawe (wettest) had the lowest mean δ^{13}C values and Tshane had the highest values. In general, soil δ^{13}C values decreased with MAP, a pattern observed in other studies around the world (Amundson, 1989; Bai et al., 2012; Bird and Pousai, 1997; Ma et al., 2012; Sanaiotti et al., 2002; Wang et al., 2008; Wang et al., 2009; Weiguo et al., 2005). The mean SOC was highest in Tshane and lowest in Bokspits (driest). There was a weak correlation between δ^{13}C and clay content in the soil profile along the KT.

Table 2-3. Soil δ^{13}C and tree-grass C input. The wettest site had lowest soil δ^{13}C values. Soil δ^{13}C values were highest at 30 cm depth in all the sites. The uncertainty is presented in standard errors.

Site	Depth	Soil $\delta^{13}C_{VPDB}$ Mean ± SE	SOC (mg g^{-1})	% Tree contribution to SOC	SOC Tree input (mg g^{-1})	% Grass contribution to SOC	SOC Grass input (mg g^{-1})
Bokspits	10	-18.98 ± 0.17	1.28 ± 0.08	54.15 ± 1.81	0.69 ± 0.07	45.85 ± 1.81	0.59 ± 0.07
	30	-18.62 ± 0.24	1.029 ± 0.06	50.18 ± 2.61	0.52 ± 0.08	49.82 ± 2.61	0.51 ± 0.08
	70	-19.25 ± 0.18	0.845 ± 0.10	57.05 ± 1.91	0.48 ± 0.13	42.95 ± 1.91	0.36 ± 0.13
	120	-19.27 ± 0.28	0.737 ± 0.10	57.24 ± 3.00	0.42 ± 0.15	42.76 ± 3.00	0.32 ± 0.15
	0-120	-19.13 ± 0.10	0.867 ± 0.02	55.74 ± 1.09	0.48 ± 0.05	44.26 ± 1.09	0.39 ± 0.05
Tshane	10	-18.92 ± 0.30	2.266 ± 0.09	40.23 ± 2.52	0.91 ± 0.07	59.77 ± 2.52	1.35 ± 0.06
	30	-17.36 ± 0.22	1.843 ± 0.09	26.94 ± 1.91	0.50 ± 0.09	73.06 ± 1.91	1.35 ± 0.06
	70	-17.34 ± 0.27	1.542 ± 0.11	26.73 ± 2.29	0.41 ± 0.11	73.27 ± 2.29	1.13 ± 0.08
	120	-18.10 ± 0.37	1.309 ± 0.12	33.22 ± 3.18	0.43 ± 0.13	66.78 ± 3.18	0.87 ± 0.10
	0-120	-17.79 ± 0.13	1.556 ± 0.03	30.59 ± 1.14	0.48 ± 0.05	69.41 ± 1.14	1.08 ± 0.04
Kuke	10	-20.02 ± 0.16	2.001 ± 0.08	51.37 ± 1.32	1.03 ± 0.05	48.63 ± 1.32	0.97 ± 0.05
	30	-19.71 ± 0.11	1.484 ± 0.04	48.83 ± 0.88	0.72 ± 0.03	51.17 ± 0.88	0.76 ± 0.03
	70	-20.34 ± 0.26	1.259 ± 0.05	54.05 ± 2.14	0.68 ± 0.06	45.95 ± 2.14	0.58 ± 0.06
	120	-20.61 ± 0.14	1.162 ± 0.08	56.24 ± 1.19	0.65 ± 0.07	43.76 ± 1.19	0.51 ± 0.07
	0-120	-20.32 ± 0.08	1.355 ± 0.02	53.87 ± 0.67	0.71 ± 0.03	46.13 ± 0.67	0.61 ± 0.03
Shakawe	10	-22.15 ± 0.27	2.50 ± 0.20	65.76 ± 2.00	1.64 ± 0.08	34.24 ± 2.00	0.86 ± 0.10
	30	-20.68 ± 0.27	2.017 ± 0.17	54.72 ± 2.07	1.10 ± 0.09	45.28 ± 2.07	0.91 ± 0.10
	70	-21.4 ± 0.30	0.83 ± 0.09	60.14 ± 2.25	0.50 ± 0.11	39.86 ± 2.25	0.33 ± 0.12
	120	-22.72 ± 0.26	0.584 ± 0.08	70.04 ± 1.97	0.41 ± 0.14	29.96 ± 1.97	0.17 ± 0.15
	0-120	-21.89 ± 0.12	1.065 ± 0.03	63.83 ± 0.91	0.66 ± 0.05	36.17 ± 0.91	0.41 ± 0.05

2.3.3 Soil ^{15}N

The mean soil δ^{15}N values ranged between 1.6‰ and 10.7‰ (Table 4). The two intermediate sites, Tshane and Kuke, had the highest δ^{15}N values of 10.7‰ and 8.6‰ respectively, at 10 cm depth. The two extreme sites, Bokspits and Shakawe, had 7.4‰ and 5.2‰ respectively. Similarly, the intermediate sites had the highest depth-weighted mean

$\delta^{15}N$ values, and the two extreme sites had the lowest depth-weighted mean $\delta^{15}N$ values. A similar pattern was observed in total nitrogen (TN) where intermediates sites had the highest total nitrogen concentration (Dintwe et al., 2014). Although mean TN in Bokspits was the same as in Shakawe, the mean $\delta^{15}N$ in Bokspits was twice as high as in Shakawe (Table 4). Shakawe had the overall lowest $\delta^{15}N$ values in the soil profile compared to other sites. There was no significant correlation between soil $\delta^{15}N$ and clay content in the soil profile along the KT.

Table 2-4. Soil and tree $\delta^{15}N$. The wettest site had the lowest soil $\delta^{15}N$ values. The difference between plant $\delta^{15}N$ and soil $\delta^{15}N$ was lowest in the second wettest site and highest in the second driest site. The uncertainty is presented in standard errors.

Site (MAP)	Depth	Soil Total Nitrogen (mg g^{-1})	Soil $\delta^{15}N_{atm}$ (‰)	(plant – soil) $\lvert(\Delta^{15}N)\rvert$	(plant – atmosphere) $\lvert(\Delta^{15}N)\rvert$
Bokspits	10	0.07 ± 0.01	7.43 ± 0.21	0.03	7.40
	30	0.05 ± 0.00	7.96 ± 0.20	0.56	
	70	0.05 ± 0.00	7.48 ± 0.27	0.08	
	120	0.04 ± 0.00	8.49 ± 0.24	1.09	
	0-120	0.05 ± 0.01	7.98 ± 0.10	0.69	
Tshane	10	0.14 ± 0.01	10.75 ± 0.17	3.93	6.82
	30	0.11 ± 0.01	10.27 ± 0.10	3.45	
	70	0.09 ± 0.01	9.99 ± 0.23	3.17	
	120	0.08 ± 0.01	8.41 ± 0.57	1.59	
	0-120	0.09 ± 0.00	9.44 ± 0.14	3.15	
Kuke	10	0.15 ± 0.01	8.59 ± 0.16	1.32	7.27
	50	0.10 ± 0.00	8.14 ± 0.18	0.87	
	70	0.09 ± 0.01	7.54 ± 0.30	0.27	
	120	0.07 ± 0.01	6.55 ± 0.24	0.72	
	0-120	0.09 ± 0.00	7.31 ± 0.11	0.65	
Shakawe	10	0.12 ± 0.01	5.19 ± 0.23	1.69	3.5
	30	0.10 ± 0.01	6.10 ± 0.23	2.60	
	70	0.04 ± 0.00	5.48 ± 0.39	1.98	
	120	0.02 ± 0.00	1.60 ± 0.81	1.90	
	0-120	0.05 ± 0.00	3.94 ± 0.22	2.03	

We calculated the difference between C_3 foliar $\delta^{15}N$ and the potential sources of plant N; soil and the atmospheric. The difference ($\Delta^{15}N$) was used to identify the dominant source of plant N as well as to estimate the isotopic composition of plant available N (Amundson et al., 2003). We assumed that foliar $\delta^{15}N$ reflected the $\delta^{15}N$ of the source and no isotopic discrimination occurs during N uptake (Craine et al., 2015; Handley and Raven, 1992; Hobbie et al., 1999). By definition, the $\delta^{15}N$ of the atmospheric N_2 is 0‰, whereas that of the soil is usually greater than 0‰. Therefore, δ^{15}N of N-fixing plants should be very close to 0‰ (±2‰), slightly modified by diffusion fractionation and isotope effect associated with N fixation (Shearer et al., 1983; Virginia et al., 1989). Non N-fixing plants should have δ^{15}N greater than >2‰. At present, there is no easy and straight forward technique for isolating and analyzing δ^{15}N in the soil pools that are available for plant uptake (Dawson et al., 2002).

Recent studies have shown that plants in Kalahari have mean folia δ^{15}N greater than 3‰, with the driest site recording as high as 7.4‰ (Table 1). Our calculations indicated that the magnitude of the difference between plant and soil δ^{15}N was highest in Tshane (the second driest site) and lowest in Kuke (Table 4). The difference between plant and atmospheric δ^{15}N was highest in the driest site and lowest in the wettest site. The difference between foliar and atmospheric δ^{15}N was higher than the difference between foliar and soil δ^{15}N in all the sites.

2.3.4 Contribution of trees and grasses to SOC

To estimate the proportion of SOC from trees and grasses, we assumed that SOC was made up of the sum of the fractions (F_i) contributed from the sources (δ_i), where the sources were C_3 and C_4 plant species (Equation 2).

$$\delta^{13}\mathrm{C}_{soil} = \sum_{i=1}^{n} F_i \delta_i \qquad (2)$$

We used a simple 2-endmember mass balance ratio to calculate the potential contribution of C_3 and C_4 plants to SOC in the 120 m soil profile (Equation 3):

$$C_x(\%) = \frac{\delta^{13}C_{soc} - \delta^{13}C_y}{\delta^{13}C_x - \delta^{13}C_y}\ x\ 100 \qquad (3)$$

where $\delta^{13}C_{soc}$ represented $\delta^{13}C$ signature in the SOC. The $\delta^{13}C_x$, $\delta^{13}C_y$ represented $\delta^{13}C$ signature of the two-end-member (Phillips and Gregg, 2003; Phillips et al., 2005). The $\delta^{13}C_{C3}$ and $\delta^{13}C_{C4}$ values were obtained from the literature (Swap et al., 2004; Wang et al., 2010).

Results from these calculations indicate that contribution of C_3 plants (trees) to SOC was highest in Shakawe (wettest), and lowest in Tshane (Table 3). The highest C_3 SOC contribution was recorded at 10 cm in all the sites (Table 3). The C_3 contribution at 70 cm was higher than at 30 cm in all the sites, except in Tshane, where C_3 contribution at 30 cm and 70 cm were statistically indistinguishable. The depth-weighted mean tree SOC contribution in Shakawe was about 64%, which translates to 0.66 mg C g^{-1}, while Tshane recorded about 31% contribution, translating into 0.48 mg C g^{-1}. The absolute C_3 SOC contribution increased with MAP, with Bokspits recording, 769.4 g C m^{-2} whereas Shakawe recorded 1288.1 g C m^{-2} (Table 5).

Table 2-5. Organic C contribution from trees and grasses. Organic C contribution from trees was highest in the wettest site, and lowest in the driest site. Carbon contribution from grasses was highest in the second driest site.

Site	Trees						Grasses	
	Co (g m^{-3})	Tree input (g m^{-2})	k (m)	e-folding depth (m)	Z_{95} (m)	Z_{50} (m)	Co (g m^{-3})	Grass input (g m^{-2})
Bokspits	965.5	769.4	0.5	2.1	6.3	1.5	881.0	648.0
Tshane	1216.7	808.4	0.9	1.1	3.4	0.8	2084.4	1721.0
Kuke	1423.2	1121.9	0.5	2.0	6.0	1.4	1470.3	1073.5
Shakawe	2729.5	1288.1	1.8	0.6	1.7	0.4	1583.9	830.6

The intermediate sites had higher C_4 (grass) SOC contribution than the extreme sites (Table 3). The highest C_4 contribution was at 30 cm in all the sites. Bokspits lowest absolute C_4 contribution while Tshane had the highest absolute contribution, 648 g C m^{-2} and 1721.0 g C m^{-2} respectively (Table 5). In contrast, tree carbon contribution had a linear relationship with MAP, where the contribution increased with an increase in MAP (Figure 2).

The SOC contribution from C_3 plants was higher than the C_4 input at 10 cm, except in Tshane where C_4 had higher contribution. The C_4 contribution was higher than C_3 contribution at 30 cm in the intermediate sites (Tshane and Kuke), lower than C_3 contribution in the two extreme sites (Bokspits and Shakawe). Grass carbon contribution had a non-linear relationship with MAP. The contribution increased with MAP, reached maximum in Tshane, and then decreased with an increase in MAP.

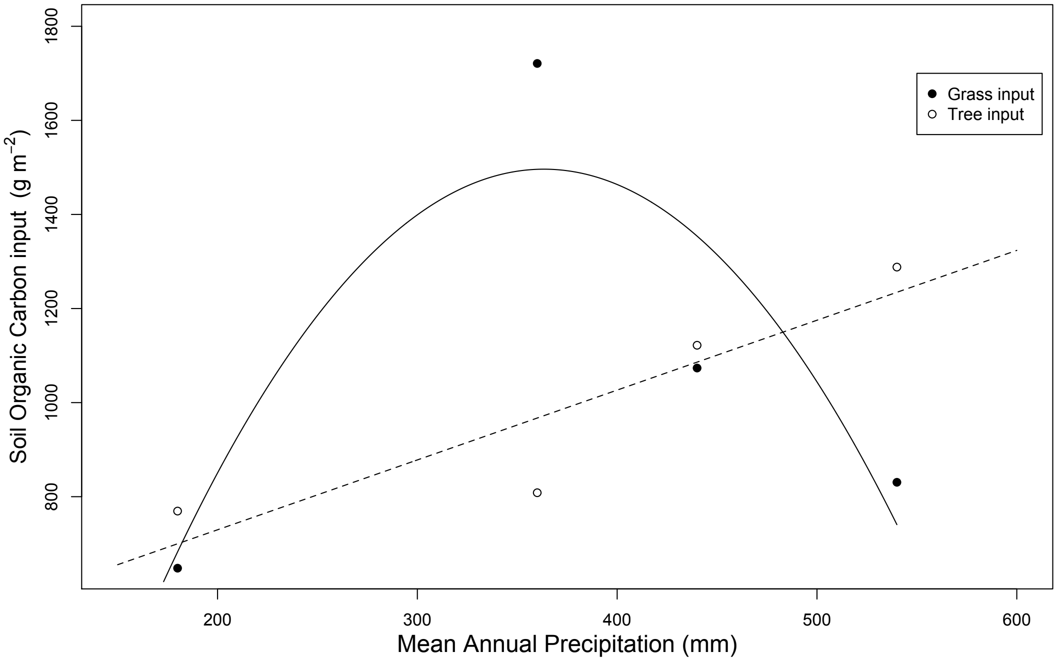

Figure 2-2. Relationship between mean annual precipitation and soil organic carbon input from trees and grasses. Tree carbon input follows a linear relationship (broken line) with MAP ($R^2 = 0.82$) whereas grass input follows a non-liner (solid line) relationship ($R^2 = 0.79$).

2.3.5 Carbon contribution in the soil profile

Because SOC declined with depth, a decaying exponential function $C = C_o e^{-kz}$, was used to estimate total C contribution from trees and grasses in the soil profile, where C and C_o were in units of g m^{-3}. The parameters of the equation, C_o and k (m^{-1}) were determined by least squares fitting of measured concentrations with depth, z. The total C contribution was calculated by taking the integral of the equation from 0 to 1 m:

$$\int C_o e^{-kz}\,dz = -C_o e^{-kz}|k\Big|_{0\,m}^{1\,m} \qquad (4)$$

We calculated Z_{50} and Z_{95} of the soil profile, which are the depths at which 50% and 95% of the total C contribution occurs, respectively. Furthermore, we calculate the e-folding depth $\left({}^{1}/_{k}\right)$, the depth at which C contribution decreases to $1/e$ of the surface value. For tree contribution, the e-folding depth was lowest in Shakawe and highest in Bokspits, 0.6 m and 2.1 m respectively (Table 5).

2.4 Discussion

2.4.1 Belowground tree-grass (C_3 - C_4) interactions

Soil $\delta^{13}C$ values at 10 cm decreased with increasing MAP, a proxy for plant- available moisture. We speculate that plant-available moisture was the primary determinant of C_3 and C_4 belowground interactions in this layer. It has been noted in many studies that as soil moisture availability increases in the topsoil, C_3 plants tend to allocate most of their roots in near sub-surface (Bhattachan et al., 2012b; Grossman and Rice, 2012; Reynolds and D'Antonio, 1996). The selective root placement (SRP) is an adaptation strategy that enables trees to switch from deeper water to superficial water depending on short- and long-term patterns of precipitation. The ability of C_3 plants to utilize SRP, implies that trees may develop an extensive lateral root system near the surface that enables them to access surface soil moisture from a larger area farther away from the tree. Grasses, on the other hand, have less adaptive root systems and therefore have limited capacity to exploit multiple sources of water (Priyadarshini et al., 2016).

This may give grasses an advantage under some intermediate precipitation regimes, below which trees' ability to exploit shallow rains with their surface roots favors water uptake by trees and above which trees' ability to exploit deeper soil moisture resulting from large, frequent rains favors water uptake by trees. In this intermediate precipitation regime, then, the trees' investment in biomass in both surface and deep root systems yields a metabolically expensive belowground network that is at a disadvantage compared to the conservative root system of grasses.

According to savanna 'bottom-up' theory and competition theory (Walter's two-layer hypothesis), grasses exploit nutrients and water in the upper soil layers whereas trees exploit deeper soil layers, resulting in a two-layer vertical distribution of grass and tree roots (Hipondoka et al., 2003; Walker et al., 1981). This concept, however, assumes that tree roots grow vertically and does not explicitly take into account the distribution of lateral roots. Furthermore, the model does not take into account the maximum rooting depth of the two plant life forms (Holdo, 2013). Field observations have shown that savanna trees usually have bimorphic type of root systems, comprised of superficial lateral root system and vertical deep-ranging roots. The *Combretaceae* and *Fabaceae* in Kalahari had been found to have straight lateral roots superficially situated just beneath the soil surface, and could extend more than 7 m from the trunk (Cole and Brown, 1976; O'Donnell et al., 2015). Observations in West and East African savannas indicated that *Fabaceae* and

Malvaceae concentrated most lateral root biomass in the top 10 to 20 cm soil depth and that grasses concentrated their root biomass between 20 and 40 cm while vertical and deep-ranging tree roots occupied the bottom layer, below 40 cm (Lawson et al., 1968; O'Donnell et al., 2015; Okali et al., 1973).

The soil δ^{13}C values, and estimated tree vs. grass C inputs, show a distinct and consistent pattern in the soil profile in all the sites. The relatively depleted δ^{13}C values in the top 10 cm and below 30 cm suggest the importance of tree input at these depths, whereas the more enriched δ^{13}C values in the 30 cm layer suggest the importance of grass input. This δ^{13}C pattern suggests that there could be more than two root niches in the soil profile, resulting in a more complex interaction between tree and grass roots, contrary to the Walter's two-layer niche hypothesis. Our findings are consistent with those of Mordelet et al. (1997), who used stable C isotope analysis in African humid savannas and found that fine roots from trees peaked at 10 cm while fine roots from grasses peaked at 20 cm. Mordelet and Roux (2006) reported overlapping rooting patterns in West African savannas, where woody roots larger than 2 mm in diameter were essentially found in the upper soil layer, contrary to Walter's two-layer hypothesis, which assumes that tree roots would be located deeper in the subsoil. Mordelet and Roux (2006) concluded that the belowground vegetation structure in Lamto savanna did not support the Walter's two-layer hypothesis. Similarly, in Sonoran desert, Nilsen et al. (1983) found that *Prosopis* developed two distinct root system, whereby root mats occurred at 10 cm and below 60 cm. Scholes and Archer (1997) pointed that shallow lateral roots can be important in plant water uptake even in phreatophytic trees.

Recent studies indicate that the Walter's two-layer hypothesis does not adequately explain woody-grass dynamics, as it works in dry savannas (Cipriotti et al., 2014; February et al., 2013a; Hipondoka et al., 2003; Holdo, 2013; Mordelet et al., 1997; Verweij et al., 2011; Ward et al., 2013). In simple experiments where woody plants were removed resulted in increased grass cover, and vice versa (Riginos, 2009; Scholes, 1987; Stuart - Hill and Tainton, 1989; Walter, 1973; Ward and Esler, 2010). If trees and grasses occupied different root zones, with grass roots higher in the profile than tree roots, then removal of grasses, would allow more water to get to the deep-rooted trees. In two-layer root system, the deep-rooted trees would not respond to the additional water because, trees would have exclusive access to the deep water. The findings where removal of grass resulted in increased tree cover challenged the two-layer root hypothesis, and indicated that there could be competition between trees and grasses. Similarly, in a two-layer root system grasses would not be expected to respond positively to the removal of deep-rooted woody plants. What is a mystery though, is why grasses respond positively to woody plants removal. Facilitation studies have actually shown that tree cover increases grass cover locally although grass cover goes down as tree cover goes up above ~450 mm yr^{-1} (Dohn et al., 2013; Moustakas et al., 2013; Scanlon et al., 2002; Synodinos et al., 2015).

In a semi-arid savanna in southern Africa, Stuart - Hill and Tainton (1989) found that removal of grasses increased moisture availability within 9 m of the trees by about 100%, whereas removal of trees increase soil moisture available to grasses by 20%, and removal of all vegetation increased the soil moisture regime by 200%. In a controlled experiment, Holdo and Brocato (2015) found that increasing grass density led to a decrease in soil moisture, which affected deep rooted trees. In light of the results from these and other experiments, we argue that tree and grasses do not occupy exclusive soil moisture niches, but rather overlap. For instance, Peláez et al. (1994) reported that shrubs in Argentina (e.g. *Condalia microphylla*) exploited the upper layer (20 cm) and the lower layer (40 cm) for soil moisture. In spite of shrubs accessing water from the upper and lower layers, the presence of grasses led to Peláez et al. (1994) to speculate that shrubs competed with grass for water in the upper soil layer.

The inadequacy of the Walter's two-layer hypothesis to explain tree-grass coexistence had motivated for a revisit of the hypotheses (Cipriotti et al., 2014; Ward et al., 2013; Yu and D'Odorico, 2015). In one of the revisits, it was suggested that grasses scavenge water lifted by woody plants through the hydraulic lift process (Ludwig et al., 2002; Ludwig et al., 2004; Yu and D'Odorico, 2015). We argue that grasses can only benefit from hydraulic lift if shrubs and trees have superficial and lateral roots to lift and redistribute water to the surface, making it available to shallow rooted grasses. The presence of shallow lateral tree roots could explain moisture availability in the inter-canopy spaces, which in most cases is occupied by grasses. That is, tree roots facilitate establishment of grasses through hydraulic lift. In a field experiment in southern African savanna, Verweij et al. (2011) showed that severing shallow lateral roots of trees resulted in rapid abscission of leaves, whereas severing deep growing taproots did not have significant effects on tree water balance even during the dry season. They concluded that trees and grasses exploit and compete for soil moisture in the upper soil layer, and that the two-layer hypothesis does not explain tree-grass coexistence in mesic savannas.

It is important to point out that previous studies categorized fine roots in to trees and grass biomass based on size and morphology (e.g. Hipondoka et al., 2003). It is possible that a bias in root characterization led to the conclusion that the upper soil layer was dominated by only grass roots and the lower layer dominated by tree roots. Recent studies, however, used stable C isotope analysis and molecular technology to distinguish between grass and tree roots. In mesic and semi arid savanna ecosystems in Australia and southern Africa, stable C isotope analysis revealed that tree and grass fine roots were concentrated in the 20 cm of the soil (February et al., 2013a; February and Higgins, 2010). Similarly, in west Africa savannas, Mordelet et al. (1997) used stable C isotope analysis and found that fine roots from trees peaked at 10 cm while fine roots from grass peaked at 20 cm. In southern Africa savanna, Kulmatiski et al. (2010) injected deuterated water (deuterium-labeled water) into four soil depths at 5, 20, 50 and 120 cm. Their analysis revealed that trees absorbed 24, 59, 14 and 4% of tracer from the 5, 20, 50 and 120 cm depths, respectively. Grasses absorbed 61, 29, 6 and 0.3% of tracer from the same depths. These results did not reflect, as suggested by Walter's two-layer hypothesis, the ability of trees to access deep soil water that was presumably not available to grasses (Kulmatiski et al., 2010).

Here, propose that there could be three root zones in dryland ecosystems, in which shallow lateral trees roots occupy the first 10 cm, followed by grass roots at 10 – 30 cm and finally tree roots below 30 cm. It is important to point out that our proposed three-layer model is different from the one proposed by Kambatuku et al. (2013), who suggested that grasses exclusively exploit the 15 cm layer, the intermediate layer (25 – 35 cm) was utilized by both tree and grass seedling roots, while the deeper subsoil exclusively tapped by tree seedling roots. The 'Kambatuku' model was based of green house experiments that were highly manipulated, using rocky and sandy soils and specific plant species. Our model, on the other hand, was based of field samples collected from a natural savanna ecosystem. The only difference between Kambatuku's model and Walter's model is that the former takes into account the maximum rooting depth, whereas the latter does not, which means that the former is still a two-tier layer model.

2.4.2 Aboveground C_3 and C_4 productivity and MAP

The C_3 content of the soil was consistent with vegetation structure in the Kalahari, where tree cover and height increase with MAP (Belsky, 1994; Caylor et al., 2003; Scholes et al., 2002). Studies from other parts of the world showed a similar pattern, where the woody contribution increased with MAP (Bai et al., 2012; Bird and Pousai, 1997; Wang et al., 2010). The e-folding depth and Z_{95} values for SOC from trees were lowest in Shakawe (Table 5), suggesting that trees in the area could be shallow rooted. This is consistent with results from both Bhattachan et al. (2012b) and O'Donnell et al. (2015) for this site. Bokspits had the highest e-folding depth for SOC from trees, indicating that trees in this area could be deep rooted. Our results are consistent with the tree root pattern being regulated by plant-available moisture, resulting in deeper roots in the drier portion and shallow roots in the wetter portion.

The C_4 contribution to SOC increased from Bokspits, reached maximum in Tshane and decreased with an increase in MAP (Figure 2). This non-linear relationship between aboveground grass biomass and MAP has been reported in previous studies (e.g. Scanlon et al., 2002). Individual bunch grasses tend to be smaller in Bokspits, and their biomass increase with an increase in MAP, reaching maximum in the intermediate sites and then decrease in Shakawe. This is consistent with the results of Scanlon et al. (2002) who reported that grass cover peaks at the location with approximately 450 mm MAP. We suggest that low grass cover and productivity in the drier portion of Kalahari could be attributed to low soil moisture whereas in the wet portion the low grass cover and productivity could be attributed to belowground competition from trees. The intermediate sites appear to provide optimal conditions for grass productivity, and this is reflected by the grass contributions to SOC.

2.4.3 Tree-grass competition for Nitrogen

Nitrogen is one of the factors limiting productivity in Kalahari, and plants rely on soil N fixed by cyanobacteria (Aranibar et al., 2004; Ries and Shugart, 2008). Dintwe et al. (2014) found that C:N of fine roots of *Mimosoideae* were not significantly lower (higher N) than of other species/families, which suggested that *Mimosoideae* were not fixing N_2. High surface temperature could be the reason many of these *Mimosoideae* species were not nodulating. Studies from East African savannas showed that the optimal temperature for N_2-fixing species to nodulate was about 35 °C, beyond which nodulation does not occur (Habish, 1970; Odee et al., 1995). The daily maximum temperature in Bokspits and Tshane, could easily reach 40 °C and results in the inhibition of nodulation. In South Africa savannas, Aranibar et al. (2003) showed that soil N content did not decreased with increasing fire frequency, despite the relative abundance and N_2 fixing woody legumes decreasing with fire frequency. Similarly, Cook (1994) estimated that the rate of N fixation by legumes in Australia was insufficient to replace the annual loss of N by fires. These findings suggested some factors other than legumes were responsible for balancing the soil N lost by fires. Observations in the Kalahari have indicated that biological soil crusts tend to colonize around shrubs and thorny plant species, probably because they are less disturbed compared to other plant types (Berkeley et al., 2005; Dougill and Thomas, 2004). This relationship may lead to symbiotic relationship, where BSC provided plants with N while plants provide the BSC with other types of nutrients and protection. This relationship may have led to the misconception that savanna legumes, particularly in Africa, fix N (Schmidt and Stewart, 2003; Sprent, 2009).

Our results show that the difference between foliar and soil $\delta^{15}N$ was an order of magnitude lower than the difference between foliar and atmospheric $\delta^{15}N$ (Table 4). Conversely, foliar $\delta^{15}N$ values were closer to soil $\delta^{15}N$ values than atmospheric values suggesting that plants in Kalahari obtain most of their N from the soil rather than through fixation. Aranibar et al. (2004) suggested that plants in the wetter portion of the Kalahari could be fixing nitrogen based on their low foliar $\delta^{15}N$ values. We have found that soil $\delta^{15}N$ values are also the lowest in Shakawe, our wettest site. It is possible that the low foliar $\delta^{15}N$ values found by Aranibar et al. (2004) in the wetter portion of the Kalahari do not necessarily suggest N-fixation but rather reflect the source of N. The relatively low soil $\delta^{15}N$ in Shakawe could be due to higher soil moisture, which facilitates fixation of atmospheric N by soil microbes. The rate of N fixation by microbes could be higher in the wetter portions of Kalahari, and lower in the drier portions.

It is likely that C_3 and C_4 in the drier parts of Kalahari have evolved under low soil N, and have developed adaptation mechanism to access the limited soil N. Priyadarshini et al. (2013) suggested that grasses, which usually exhibit N limitation, benefit from N redirected by trees. Furthermore, the structure of the Kalahari soils is characterized by low quantities of clay and humus colloids (Table 2), which have low cation exchange capacities, and high porosity and permeability, could potentially enhance N leaching and redirection leading to a relatively homogenous distribution of $\delta^{15}N$ in the soil, thus making N available to non N-fixing plants (Priyadarshini et al., 2013).

2.5 Conclusion

Trees in the Kalahari are likely not fixing atmospheric N_2, and depend on soil N, despite abundance of leguminous tree species. Grasses, on the other hand, could be benefitting from N redirected by trees.

Tree C contribution increased with an increase in MAP in Kalahari, whereas grass C contribution followed a non-linear relationship with MAP with the intermediate-precipitation sites having the highest C_4 contribution. Our results showed that C_3 plants (shrubs and trees) contribute more SOC at 10 cm and below 30 cm whereas grasses contribute more SOC in the intermediate layer (10 - 30 cm). These results suggest that grasses accumulate most of their root biomass in the 30 cm zone. Trees, on the other hand allocate their roots in the top 10 cm and below 30 cm zone. This tree-grass interaction results in trees to exploiting superficial soil moisture as well as deeper ground water, while grasses exploit water in an intermediate layer, though our results clearly show that all three layers are mixed. We, therefore, conclude that the co-existence of trees and grasses in the savannas is primarily maintained by a mixed three-layer root system, contrary to the commonly assumed separated two-layer root system suggested by Walter. Trees and shrubs dominate the surface layer through their lateral roots in the top layer, followed by grass roots dominating the middle layer and finally tree roots (vertical roots and tap roots) dominating the deeper soil layers.

We also observed a dominance of grass-derived C in the middle of the precipitation gradient observed here. We suggest that this is the natural consequence of our proposed three-layer belowground competition theory. In the northern, wettest portion of our 'dry' savanna transect, grass-derived C is low relative to tree-derived C. This results from trees accessing surface soil moisture and thereby reducing water availability for grasses, the roots of which are below the surficial woody roots. In the middle of the transect, lower overall precipitation reduces the growth of trees, as evidenced by the lower contribution of tree C to the SOC. This allows water to penetrate deeper into the soil to reach the intermediate-depth grass roots. In the dries portion of the transect, we suggest, both grass and woody productivity are severely limited by low soil moisture. Here, trees rely on water from rare, large precipitation events that replenishes the deeper portions of the soil profile. Grasses, on the other hand, are able to also use shallower rain events that penetrate only to 20-30 cm. Trees do allocate some roots to the surface layer in these drier areas, but exclusive use of deeper soil moisture allows survival during drought periods, which are longer and more frequent in the drier areas, favoring trees that utilize this strategy.

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Chapter 3: The contribution of biological soil crust to soil carbon fluxes in dryland ecosystems

Abstract

Although drylands cover about 40% of the land surface and are subject to the impact of climate change, there is insufficient understanding of dryland soil respiration. Dryland soils are characterized by the abundance of biological soil crusts (BSC), which can cover as much as 70% of the land surface. While BSC fix and sequester carbon (C) into the soil, soil respiration releases large quantities of C from the soil into the atmosphere, through heterotrophic and autotrophic respiration. Here, we conducted an experiment to estimate the contribution of BSC to C fluxes in a dryland ecosystem. We measured soil respiration and net carbon exchange (NCE) in a wet soil fully covered by BSC, and after the removal of the crust. We also measured Q_{10} before and after removal of the crusts in all the treatments. Q_{10} is a measure of the rate of biogeochemical process change, in this case - soil respiration, when temperature increases by 10°C. stable C and Nitrogen (N) isotopic signature of the BSC and associated soils. Our results showed that removal of the crust resulted in a 50% decrease in respiration, and 45% increase in NCE. We estimated BSC photosynthesis and respiration at 9.8 and 6.6 g CO_2 yr^{-1}. The C isotopic analysis showed that BSC fixed 57.6% and 42.4% of CO_2 from the atmosphere and soil air, respectively. We used simple and direct methods to separate BSC respiration from total soil respiration, as well as to distinguish the sources of CO_2 assimilated by BSC. We have also demonstrated that removal of BSC

resulted in increased Q_{10}, which in turn could accelerate soil CO_2 efflux. The Q_{10} in the crusted soils was 2.3 and 1.1 for soil respiration and NCE respectively. Given the extensive spatial distribution of BSC, their rates of CO_2 assimilation and temperature sensitivity, we concluded that BSC could play a significant role in mitigating the impact of climate change by assimilating a significant portion of atmospheric and soil respired CO_2. Based our results, we recommend implementation of proper land management practices that could allow establishment, restoration and developments of BSC in drylands.

3.1 Introduction

Soils store more than three times the amount of organic carbon in aboveground biomass and twice the amount in the atmosphere and vegetation biomass combined (Hibbard et al., 2005; Revelle and Suess, 1957; Schlesinger and Bernhardt, 2013a). Soil respiration represents the largest single pathway of CO_2 loss from the soil to the atmosphere (Box, 1978; Houghton and Woodwell, 1989; Trumbore, 2009). At global scale, soil respiration releases 75 Pg C yr^{-1} - 100 Pg C yr^{-1} (Bond-Lamberty and Thomson, 2010; IPCC, 2013; Raich and Schlesinger, 1992). For comparison, the rate of soil CO_2 efflux is an order of magnitude greater than the rate of fossil fuel combustions emissions (Mielnick and Dugas, 2000; Raich et al., 2002).

Soil respiration is a sum of autotrophic and heterotrophic respiration. Autotrophic refers to organisms that synthesize their own carbohydrates from CO_2 such as plants, whereas heterotrophic refers to organisms that depend on pre-formed organic matter for their energy and nutrition support (Büdel, 2005; Hibbard et al., 2005). With this definition, autotrophic soil respiration would include CO_2 efflux from plants roots and biological soil crusts (BSC), while heterotrophic respiration would include CO_2 efflux from everything else in the soil. Autotrophic respiration from plants roots is estimated to amount to about half of the plant gross primary productivity (Makhado and Scholes, 2012). The other component of autotrophic respiration, which comes from BSC is not well understood, and have received less attention despite the fact that BSC are a very common feature in dryland ecosystems, covering up to about 70% of the surface area (Evans and Johansen, 1999; Garcia-Pichel et al., 2003). The fact that drylands are extensive in size covering about 40% of the global land surface potentially make BSC a very important component of biogeochemical processes.

Biological soil crusts are pioneers of deserts soils, whereby they excrete amylase to stabilize soil surface and enhance soil capacity of resistance to aeolian and fluvial erosion (Belnap et al., 2016; Bu et al., 2015; Isichei, 1990; Okin et al., 2006). Belowground, BSC bind the soil or sand together by means of cyanobacterial polysaccharides as well as enmeshments by filaments, fungal hyphae and moss and lichen rhizines (root-like filaments) (Ward, 2016). The ratio of soil loss in soils with cyanobacteria crust compared to the same without crust was estimated at 1:22 (Isichei, 1990). In the Colorado Plateau, Belnap et al. (2013) observed that water ran off was lower in the BSC with the highest level of development (LOD) than in the crust with the lowest LOD. Similarly, as LOD increased, infiltration increased and the runoff decreased. Biological soil crusts also improve the nutrient status of the soil, increase seedling establishment and survival of some species (Belnap et al., 1994). Studies utilizing stable nitrogen (N) isotope have demonstrated that N fixed by cyanobacteria in crusts is available to and used by neighboring vascular plants (Mayland and McIntosh, 1966; Mayland et al., 1966).

Physiological activities and spatial distribution of BSC are regulated by environmental factors such as moisture availability, vegetation cover and disturbance (Belnap et al., 2016; Zhang et al., 2016). Regionally, soil texture control BSC establishment, while at local scale vegetation plays a significant role (Bu et al., 2015). For instance, BSC on sand surface grow and expand fastest than in other soil types, whereas BSC under the canopy survive most easily due to the favorable conditions produced by the vegetation (Kidron et al., 2002; Petrou and Milios, 2012).

Elbert et al. (2009) estimated BSC biomass in drylands to be ~17 Pg C, which translates to ~8.5 Pg C (assuming 50% C content). The global net primary productivity (NPP, photosynthesis minus respiration) for BSC is estimated at 3.9 Pg C yr^{-1}, which corresponds to ~6% of the NPP of terrestrial vegetation (~60 Pg C yr^{-1}) (Elbert et al., 2012; Sancho et al., 2016). For reference, NPP by BSC is of similar order of magnitude as the annual global carbon release due to biomass burning, which is at 8.3 Pg C yr^{-1} (IPCC, 2013). Regional studies have shown that BSC have NPP ranging between 22 g C m^{-2} yr^{-1} to 37 g C m^{-2} yr^{-1} (Evans and Lange, 2003; Garcia-Pichel et al., 2003). In the western Mojave Desert, USA, the NPP of BSC was estimated at 11.7 g C m^{-2} yr^{-1}, whereas in Mu Us and Gurbantunggute deserts in China, the NPP of BSC was estimate at 2 - 6 g C m^{-2} yr^{-1} (Brostoff et al., 2005; Feng et al., 2014; Su et al., 2013). Although there is uncertainty in the total contribution of BSC to the soil C budget, the existing estimates show that biological soil crusts play a major role in CO_2 fixation and soil C sequestration.

BSC are also important because they fix atmospheric nitrogen (N_2), thus improving soil fertility and enhancing ecosystem productivity, especially in regions where rainfall and anthropogenic inputs of N are low (Belnap, 1995, 2002). The rate of N fixation by BSC is about 40% (45 Tg yr^{-1}) of the global estimate of N fixation (107 Tg yr^{-1}) (Elbert et al., 2009; Elbert et al., 2012).

In drylands, the annual rate of N_2 fixation through BSC ranges between 0.1 to 10 g N m^{-2} yr^{-1} (Belnap, 2002), which translates to ~3 Pg N yr^{-1}, suggesting that N fixation by BSC maybe crucial for C sequestration by plants. Recent studies in some dryland ecosystems have shown little evidence of N_2 fixation by leguminous plants (Aranibar et al., 2003; Aranibar et al., 2004; Dintwe et al., 2014). In Southern African savannas, Aranibar et al. (2003) found negative correlation between fire frequency and abundance of N_2 fixing woody legumes, but found that soil N content was relatively consistent despite decreasing woody legume abundance as fire frequency increased. These findings suggested that some factors, other than N_2 fixation by plants were responsible for replenishing soil N. Similarly, Cook (1994) estimated that the rate of N_2 fixation by legumes in Australia was insufficient to replace the annual loss of N_2 by fires. In the Colorado Plateau, USA, Harper and Belnap (2001) reported a significant increase in N (and other bio-essential elements) content in BSC associated plants. These studies implicate BSC, at least partially, in closing the N budget of dryland soils.

The aim of this study was assess the contribution of BSC to soil C fluxes in a dryland ecosystem. To this end, we investigated diurnal respiration and net carbon exchange in soils with intact crust and after crust removal using automated soil respiration measurement system. Our research goal was to take the analyses beyond the simple measurements by combining soil efflux measurements with stable C and N to partition sources of CO_2 and N_2 fixed by BSC. We hypothesized that BSC fix CO_2 from both the soil and atmosphere, and therefore we intended to quantify the contribution of each carbon source. That is, how much CO_2 fixed by BSC was assimilated from the soil and from the atmosphere. Because BSC are photosynthetic, we also intended to estimate their net carbon contribution to the soil.

3.2 Materials and methods

3.2.1 Site description

The study was conducted at the Jornada Experimental Station in New Mexico, USA (Lat 32.618181, Lon -106.746316). Jornada is categorized as a shrubland ecosystem that has undergone significant conversion from grassland in the last century and a half (Buffington and Herbel, 1965; Gibbens et al., 1983; Gibbens and Beck, 1987). The mean annual precipitation (MAP) is about 230 mm and with more than 80% of precipitation coming in summer (Wainwright, 2006). The average maximum temperature in this area is 36°C. Soil organic carbon and total nitrogen content in Jornada is about 3.54 mg C g^{-1} and 0.38 mg N g^{-1}, respectively (Bird et al., 2002).

3.2.2 Field Measurements

3.2.2.1 Soil respiration

We selected two sites representing sand and clay soils. In each site we identified a 50 x 50 cm plot completely covered with biological soil crusts (BSC). Soils were watered for two days, at three hours intervals so that the system would stabilize and that bursts of CO_2 associated with wetting would be driven off (Cable and Huxman, 2004; Thomas and Hoon, 2010; Thomas et al., 2008). At the end of the first day of watering, we carefully inserted a 20-cm diameter soil collar and continued watering on the second day. The collar was inserted 24 hours before taking the measurement to allow the system to equilibrate. The first set of measurements was conducted on day three using a Li-COR Clear Long-Term Chamber (8100-104C) connected to Automated Soil Gas Flux System (Li-8100A, Li-COR, Lincoln, NE, USA). The clear chamber allows measurement of net carbon exchange (NCE), which is the difference between gross photosynthesis and ecosystem respiration (Equation 1a). We took the measurements with the BSC intact. On day four, we used the opaque Survey Chamber (Li-8100-103, 20 cm) to take measurements. Because the opaque chamber does not allow sunlight to go through, it measures total respiration (Equation 1b). At the end of the day, at night, we carefully removed the soil crust by inserting a flat spatula into the soil profile to a depth of 2 cm (Castle et al., 2011). The removed crust was air-dried and saved in a labeled bag for laboratory analysis. On day five we measured soil respiration in the crust-removed soil using the opaque chamber (Equation 1c), and finally, on day six, we used the clear chamber to take net carbon exchange measurements (Equation 1d). The

CO_2 flux measurements were taken between 7 am and 11 pm at 30 minutes intervals. The experimental setup is illustrated in Figure 1.

Once we commenced taking measurements, we watered the plots at night and early in the morning before sunrise. At the end of the experiment on day seven, we collected soils from the plots from 0 cm to 15 cm depth at 5 cm intervals. The soil samples were air-dried and saved in labeled bags for laboratory analysis.

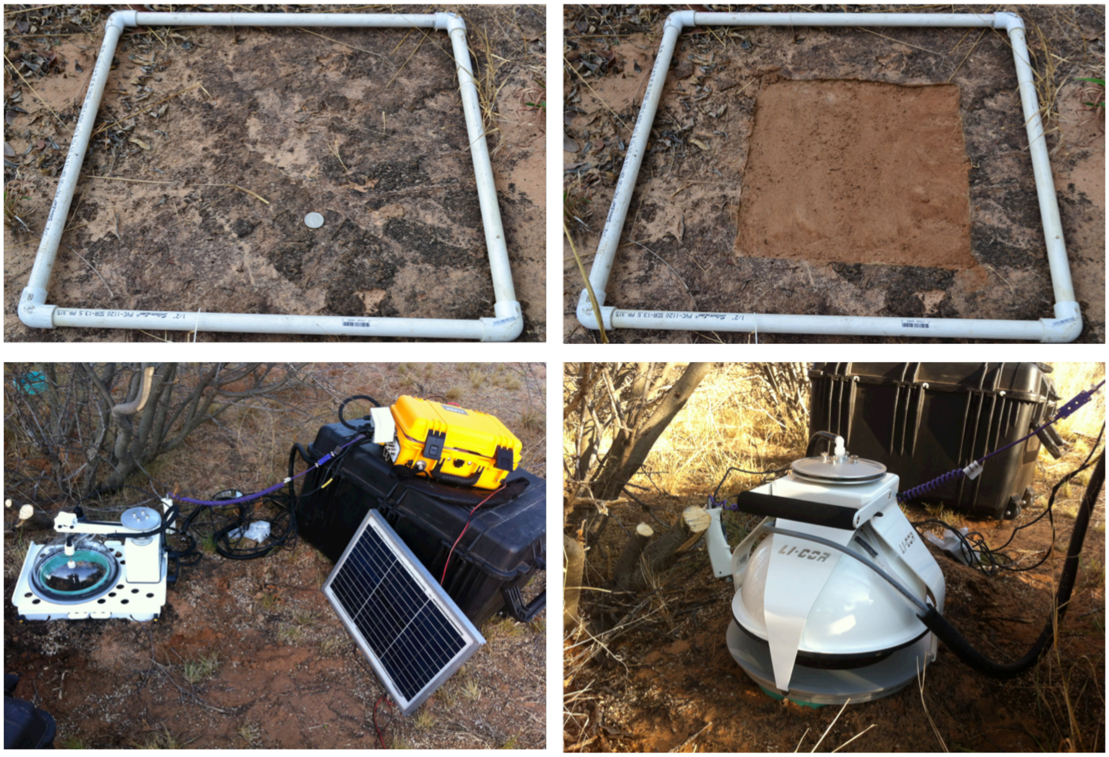

Figure 3-1. The experimental setup. The pictures on the top left and top right show the intact biological soil crust (BSC) and the scalped BSC, respectively. The bottom left picture shows the automated soil gas flux system (LI-8100A) and the clear chamber, whereas the bottom right picture shows the opaque chamber, placed on a soil collar.

Respiration and photosynthesis of the crust were estimated using the following equations,

$$\text{Respiration}_{crust} = \text{microbial}_{resp} + \text{roots}_{resp} + \text{BSC}_{resp} \qquad \text{(Equation 1a)}$$

$$\text{Respiration}_{nocrust} = \text{microbial}_{resp} + \text{roots}_{resp} \qquad \text{(Equation 1b)}$$

$$\text{NCE}_{crust} = \text{microbial}_{resp} + \text{roots}_{resp} + \text{BSC}_{\text{photo}} + \text{BSC}_{resp} \qquad \text{(Equation 1c)}$$

$$\text{NCE}_{nocrust} = \text{microbial}_{resp} + \text{roots}_{resp} \qquad \text{(Equation 1d)}$$

where *resp* and *photo* represent respiration and photosynthesis respectively.

To assess the effect of crust removal in C balance, for example respiration, we subtracted Equation 1b from Equation 1a. We subtracted the values pairwise, for example, we subtracted respiration$_{\text{crust}}$ value measured at 9 am from the respiration$_{\text{nocrust}}$ value measured at 9 am, and used the differences to compute the overall percentage difference.

3.2.2.2 Soil temperature and photosynthetic active radiation

We used Li-190 Quantum Sensor to measure photosynthetically active radiation (PAR, µmol of photons in m^{-2} s^{-1}). The volumetric soil moisture content was measured using Theta-Probe Type ML2x (Delta-T Devices Ltd, Cambridge, UK). This is a dimensionless parameter, expressed as a percentage (θ, %V) or a ratio (m^3 m^{-3}). The Li-190, Theta-Probe and soil thermometer we connected to the Li-8100A and recorded measurements at 30-minute intervals.

At the clay site, we did not measure CO_2 fluxes but collected BSC and associated soils from 0 to 15 cm depth at 5 cm intervals.

3.2.3 Laboratory analysis

3.2.3.1 Biological soil crust analysis

The soil layer attached to the underside of the air-dried biological soil crusts was carefully removed from the crust with a scalpel, and was treated as crust-associated soil. The crust-associated soils were sieved using a 2-mm standard sieve. About 10 g of subsamples of BSC and crust-associated soils were ground into a powder using a ball mill (Cianflone Scientific Instruments Corporation, Pittsburgh, PA, USA). A ~3-g subsample of the ground samples was weighed into a screw-cap vial along with 6 ml of 95% ethanol to extract chlorophyll, and added magnesium carbonate to avoid acidification (Castle et al., 2011; Lan et al., 2011). The solution was shaken immediately after adding magnesium carbonate. The samples were centrifuged for one hour at 3500 rpm (Thermo Fisher Scientific, Waltham, MA, USA). The supernatant was analyzed for chlorophyll content using GENESYS^{TM} 10S UV-Vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA), using 95% ethanol as a blank. The concentrations of total chlorophyll, chlorophyll a (chla), and chlorophyll b (chlb) were calculated with the following equations from Ritchie (2008):

$$\mathrm{Chla} = 0.0604\mathrm{E}_{632} - 4.5224E_{649} + 13.2969E_{665} - 1.7453E_{696} \qquad (2a)$$

$$\mathrm{Chlb} = -4.1982\mathrm{E}_{632} + 25.7205E_{649} - 7.4096E_{665} - 2.7418E_{696} \qquad (2b)$$

$$\mathrm{Total\ Chl} = 24.1209\mathrm{E}_{632} + 11.2884E_{649} + 3.7620E_{665} + 5.8338E_{696} \qquad (2c)$$

where E_{λ} is the absorbance at a given wavelength (λ), and the units of chlorophyll concentration in μg m^{-3} (g cm^{-3}).

3.2.3.2 Total organic carbon and nitrogen analysis

Total organic carbon (TOC) and total nitrogen (TN) content were analyzed in the BSC, crust-associated soils samples following the protocol outlined by Dintwe et al. (2014). A small portion of the soil and BSC sample was weighed and placed into 5x9 mm silver capsule (Costech Analytical, Valencia, CA, USA). The open silver capsules were fumigated in an atmosphere created by a beaker of concentrated HCL placed in a bell jar for 24 hours to remove carbonates (Harris et al., 2001). After HCl fumigation, the capsules were sealed and analyzed for soil organic carbon (SOC) and total nitrogen (TN) using an Elemental Combustion System (Costech Analytical, Valencia, CA, USA), calibrated using acetanilide ($C_6H_5NH(COCH_3)$) as a standard.

3.2.3.3 Stable carbon and nitrogen isotope analysis

The BSC and associated soils were analyzed for $\delta^{13}C$ and $\delta^{15}N$. The samples underwent the same treatment for TOC and TN analysis, except that the isotope ratios were measured using the Elemental Combustion System interfaced with continuous gas flow ConFlo IV (Thermo Scientific, Waltham, MA, USA) to gas isotope ratio mass spectrometer (Delta V Plus, San Jose, CA, USA). The isotope analysis was performed at the stable Isotope Ratio Mass Spectrometry (IRMS) facility at the University of California Irvine.

The isotope ratios were calculated using Equation 3, where R was the element measured, x was heavier isotope and y was the lighter isotope of the element measured (Amundson et al., 1998; Craig, 1953; Farquhar et al., 1989; Keeling et al., 2005; O'Leary, 1981, 1988; Wang et al., 2008).

$$\delta^{x}R\ ‰ = \left(\frac{({}^{x}R/{}^{y}R)_{sample}}{({}^{x}R/{}^{y}R)_{standard}-1}\right) * 10^{3} = \frac{\left(R_{sample}-R_{standard}\right)}{R_{standard}} * 10^{3} \qquad \text{Equation 3}$$

By convention the $\delta^{13}C$ and $\delta^{15}N$ were reported as parts per thousand (per mil) relative to that for Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 respectively (Craig, 1957; Mariotti, 1983; Werner and Brand, 2001). Reproducibility of these measurements was approximately ±0.2‰.

3.2.4 Statistical analysis

3.2.4.1 Soil respiration

Regression analysis was used to examine the relationship between CO_2 fluxes and microclimate variables. CO_2 efflux was observed to increase in the morning, reached maximum late in the afternoon and decreased in the evening (parabolic). Based on this observation, we fitted a quadratic function to assess diurnal CO_2 efflux (Equation 4).

$$R_s = \alpha x^2 + \gamma x + \theta \qquad \text{Equation 4}$$

where α, γ and θ are coefficients, and x is time of the day (hours). We also observed CO_2 efflux had an exponential relationship with soil temperature, so we fitted an exponential function between CO_2 fluxes and soil temperature (Equation 5), where R_s is CO_2 flux (g m^{-2} h^{-1}), T is the mean soil temperature (°C) at 0-10 cm depth, and β and κ are constants fitted with the least squares technique (Xu and Qi, 2001).

$$R_s = \beta e^{\kappa T} \qquad \text{Equation 5}$$

3.2.4.2 Temperature sensitivity

To assess soil temperature sensitivity, we calculated Q_{10}, a measure of the rate of soil respiration change when temperature increases by 10°C (Hoff and Lehfeldt, 1899). We used Equation 6, where k is the temperature coefficient derived from Equation 5 (Hashimoto, 2005; Tjoelker et al., 2001; Xu and Qi, 2001).

$$Q_{10} = e^{10k} \qquad \text{Equation 6}$$

In the cases where CO_2 efflux and temperature had linear relationship we calculated Q_{10} using Equation 7 (Curiel et al., 2004; Makhado and Scholes, 2012);

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2-T_1}\right)} \qquad \text{Equation 7}$$

where R_1 is the efflux measured at time T_1 and R_2 is the efflux measured at T_2.

3.3 Results

3.3.1 Total organic carbon, total nitrogen and isotopic signatures

The TOC and TN content in all the samples from the clay site were higher than in sandy site (Table 1). The clay soils had six times more TOC than sandy soils, whereas BSC from clay site had twice as much TOC as BSC from sandy soil. There was a positive relationship between TOC and TN in all the samples ($R^2 = 0.91$). TOC and TN content decreased with depth in both two sides.

The $\delta^{13}C$ in BSC from clay site was more enriched (less negative) compared to the crust from the sandy site, whereas the associated soils crust soils from the clay site were less enriched than soils from sandy site.

The $\delta^{15}N$ in the crust and associated soils from the sandy site were higher than isotopic signature of the respective samples from the clay site. The crust from the clay site had the lowest $\delta^{15}N$ than other samples.

Table 3-1. Organic Carbon and Total Nitrogen content and isotopic composition of BSC and associated soils from Jornada. The uncertainties are presented as standard errors. * Data not available

Site	Sample	Carbon (mg g^{-1})	Carbon (%)	$\delta^{13}C$ (‰)	Nitrogen (mg g^{-1})	$\delta^{15}N$ (‰)	Nitrogen (%)	C:N
Sandy	Crust	16.0 ± 4.6	1.6 ± 0.5	-14.5 ± 0.7	0.95 ± 0.33	1.6 ± 0.2	0.09 ± 0.03	16.9
	Soil from crust	7.5 ± 1.5	0.8 ± 0.2	-9.7 ± 0.6	0.33 ± 0.10	5.4 ± 0.1	0.03 ± 0.01	22.9
	0	7.3 ± 1.6	0.7 ± 0.2	*	0.28 ± 0.08	*	0.03 ± 0.01	26.2
	5	2.0 ± 0.6	0.2 ± 0.1	*	0.08 ± 0.02	*	0.01 ± 0.00	24.5
	10	2.4 ± 0.9	0.2 ± 0.1	*	0.10 ± 0.04	*	0.01 ± 0.00	24.0
	15	2.3 ± 0.9	0.2 ± 0.1	*	0.08 ± 0.02	*	0.01 ± 0.00	29.1
Clay	Crust	34.4 ± 0.0	3.4 ± 0.0	-12.1 ± 0.5	2.23 ± 0.00	0.8 ± 0.5	0.22 ± 0.00	15.4
	Soil from crust	26.0 ± 0.4	2.6 ± 0.0	-10.3 ± 0.5	1.52 ± 0.04	2.7 ± 0.3	0.15 ± 0.00	17.1
	0	25.2 ± 0.0	2.5 ± 0.0	*	0.96 ± 0.00	*	0.10 ± 0.00	26.3
	5	15.6 ± 4.2	1.6 ± 0.4	*	0.62 ± 0.35	*	0.06 ± 0.04	25.1
	10	15.9 ± 1.4	1.6 ± 0.1	*	0.57 ± 0.03	*	0.06 ± 0.00	27.9

3.3.1.1 Chlorophyll content

The chlorophyll-a content in the BSC from the sandy site was higher than the chlorophyll-a content of the crust from the clay site (Table 2). There was no chlorophyll-a detected in the crust-associated soils. Furthermore, there was no chlorophyll-b in all the samples.

Table 3-2. Chlorophyll-a content in BSC and associated soils from Jornada. The uncertainties are presented as standard errors.

Site	Sample	Chlorophyll a ($mg\ g^{-1}$ BSC)	Carbon	
			($mg\ g^{-1}$ soil)	(%)
Sandy	Crust	0.02 ± 0.01	16.0 ± 4.7	1.6 ± 0.5
	Soil from crust	0.00 ± 0.00	7.5 ± 1.5	0.8 ± 0.2
Clay	Crust	0.01 ± 0.00	34.4 ± 0.0	3.4 ± 0.0
	Soil from crust	0.00 ± 0.00	26.0 ± 0.4	2.6 ± 0.0

3.3.1.2 Soil respiration

During the day, respiration decreased after removal of the BSC (Figure 2). Respiration was higher than NCE in soils with BSC. Net carbon exchange increased after removal of the crust. Respiration was significantly higher than NCE in soils with BSC (p-value = 0.01, n = 44).

There was no significant difference between soil respiration and NCE after the removal of the crust (p-value = 0.69, n = 44).

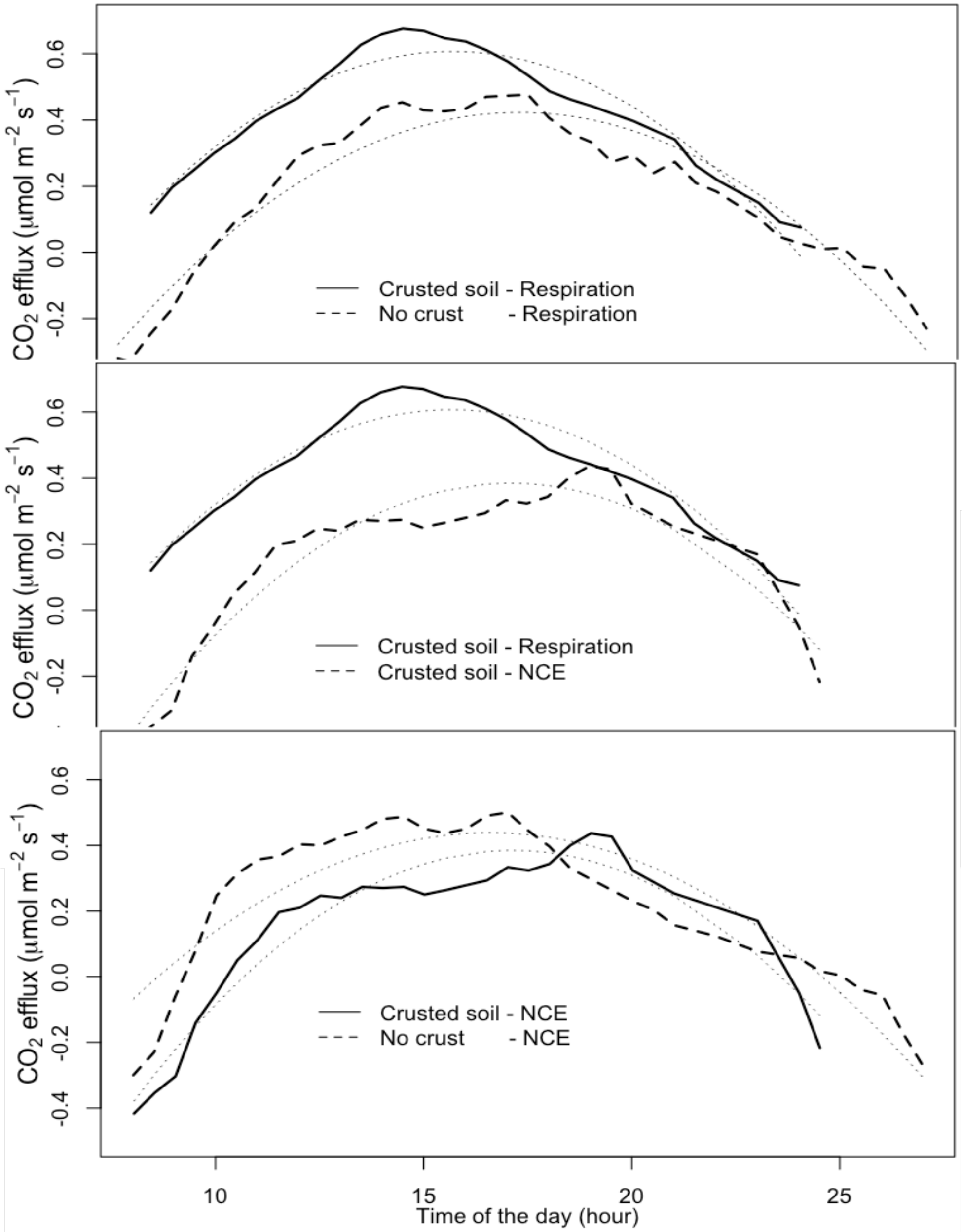

Figure 3-2. The effect of biological soil crust on CO_2 efflux in Jornada LTER. NCE is Net carbon exchange. The thin dotted lines were fitted using a quadratic function.

During the night there was no significant difference in CO_2 efflux between the treatments (p-values > 0.20, n = 24). The mean maximum respiration and NCE occurred late in the afternoon, at about 1800 hours (Table 3).

Table 3-3. The effect of biological soil crusts to CO_2 fluxes in Jornada Experimental Range

Treatment	Mean flux (µmol CO_2 m^{-2} s^{-1})	Max flux (µmol CO_2 m^{-2} s^{-1})	Approximate time at max efflux (Hour)	Total daily flux (µmol CO_2 m^{-2} d^{-1})
Soil with crust - Respiration	0.47 ± 0.19	0.69	1700 ± 1	15080.7
Soil with crust - Net C Exchange	0.14 ± 0.24	0.39	1800 ± 1	4462.4
Soil no crust - Respiration	0.24 ± 0.26	0.55	1800 ± 1	7908.5
Soil no crust - Net C Exchange	0.32 ± 0.24	0.53	1800 ± 1	10250.0

3.3.1.3 Temperature sensitivity

There was an exponential relationship between soil CO_2 efflux and the soil temperature in all the treatments, except NCE in soils with crust where the relationship was linear (Figure 3). The Q_{10} for soils with crust was lower than in the soils with no crust. The Q_{10} in respiration was higher than in associated NCE treatment.

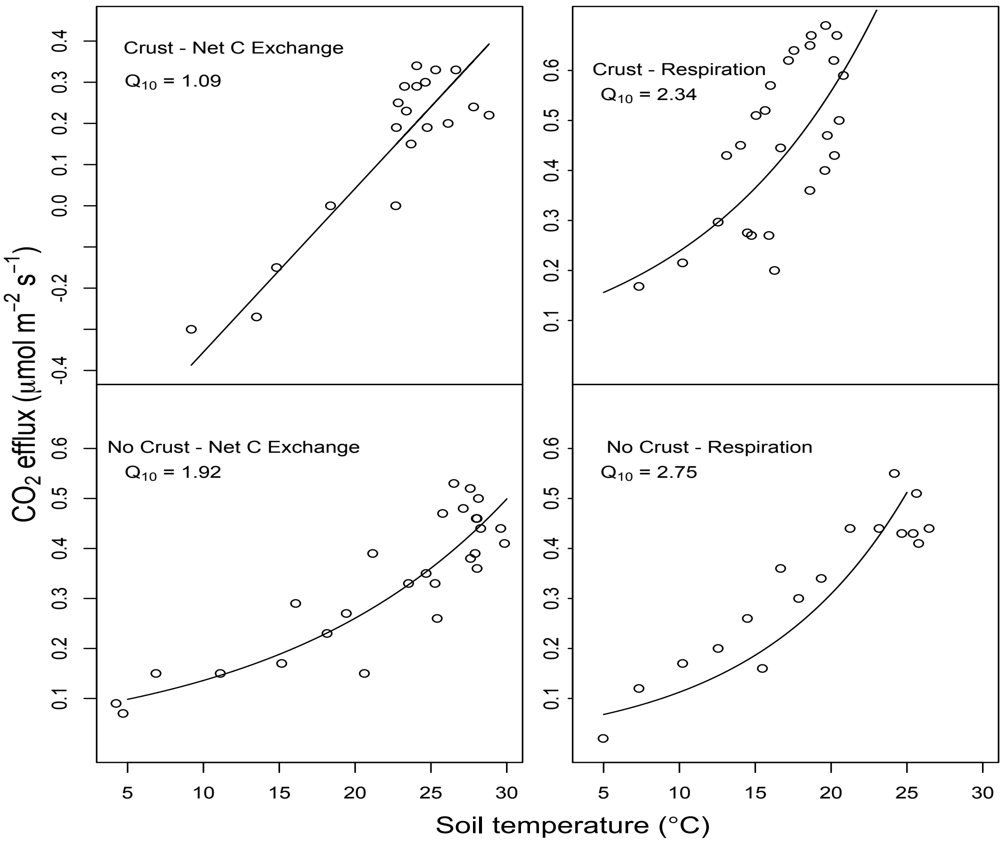

Figure 3-3. The relationship between CO_2 efflux and soil temperature. Soil respiration and NCE rate increased in response to the removal of BSC, resulting in higher Q_{10}

Similarly, there was an exponential relationship between soil temperature and BSC photosynthesis and respiration (Figure 4). The temperature sensitivity for photosynthesis was almost twice that of respiration.

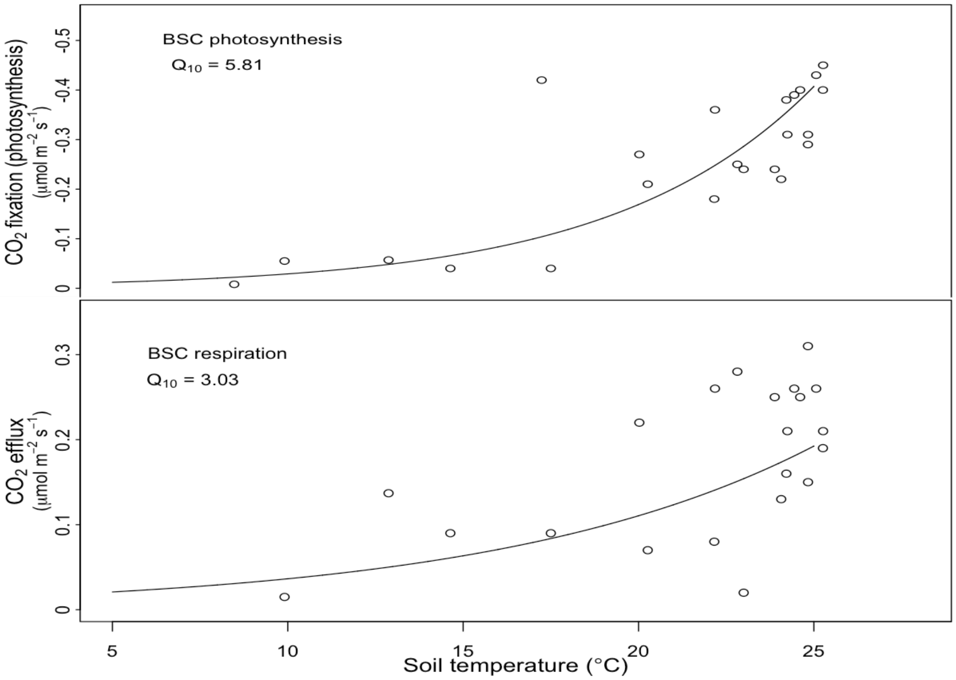

Figure 3-4. The relationship between soil temperature and BSC photosynthesis and respiration.

3.4 Discussion

3.4.1 Nitrogen fixation

We used $\delta^{15}N$ values to investigate N-fixation and N input of the BSC in the sand and clay soils. We assumed that the $\delta^{15}N$ of the crust reflected the $\delta^{15}N$ of the source and no isotopic discrimination occurs during N uptake (Craine et al., 2015; Handley and Raven, 1992; Hobbie et al., 1999). By definition, the $\delta^{15}N$ of the atmospheric N_2 is 0‰, whereas that of the soil is usually greater than 0‰. Therefore, $\delta^{15}N$ of N-fixing crust should be very close to 0‰ (±2‰), slightly modified by diffusion fractionation and isotope effect associated with N fixation (Shearer et al., 1983; Virginia et al., 1989). Non N-fixing crusts should have $\delta^{15}N$ greater than >2‰. Similarly, if BSC are the main source of soil N, then the $\delta^{15}N$ of the soil should be closer to that of the crust. The $\delta^{15}N$ of the crusts from the two sites was less than 2‰, indicating that the crusts were fixing atmospheric CO_2. Although the $\delta^{15}N$ of the crusts were lower than 2‰, the $\delta^{15}N$ in the crusts from sandy soils was double those in the crusts from clay soils (Table 1), suggesting that the two crusts had different rates of N_2 fixation, possibly due to variations in microbial species composition, denitrification rates, differences in soil moisture, or other biophysical factors. A similar pattern was observed in the crust-associated soils, where $\delta^{15}N$ in sandy soils were twice as high as in clay soils. The reason for high $\delta^{15}N$ in sandy soils could be that there was high soil microbial activity, which discriminated in favor of the lighter N isotope resulting in enrichment of ^{15}N (Blackmer and Bremner, 1977; Connin et al., 2001; Delwiche and Steyn, 1970). Fractionation during decomposition produces inorganic N that has a lower $\delta^{15}N$ than the bulk soil, causing the remaining soil N to become gradually enriched in $\delta^{15}N$ (higher $\delta^{15}N$) (Evans and Belnap, 1999; Pardo and Nadelhoffer, 2010; Piccolo et al., 1994). The low total nitrogen (TN) content in the sandy soil also provides evidence that there could be other activities responsible for the depletion of the soil N. The other reason why the clay site had higher TN content could be due to the soil texture. Usually, clay particles contain much higher organic material than sandy soils. The organic material particles are negatively charged, therefore they electrostatically adsorb positively charged essential nutrient ions (Belnap and Harper, 1995; Lange, 1974; Lange, 1976).

3.4.2 Photosynthetic pathway in BSC

The BSC from our study site had an average $\delta^{13}C$ of -13‰, indicating that they were using C_4 photosynthetic pathway. Except for succulent desert plants, organisms that use C_3 photosynthetic pathway are associated with $\delta^{13}C$ ranging between -35% and -20‰, whereas those that use C_4 photosynthetic pathway are associated with $\delta^{13}C$ ranging between -14‰ and -9‰ (Ehleringer and Cerling, 2001; Ehleringer and Rundel, 1989; Evans and Belnap, 1999; Farquhar et al., 1989). Further, the $\delta^{13}C$ results suggested that the crusts in Jornada were likely dominated by cyanobacteria. The average $\delta^{13}C$ in cyanobacterial biomass has been estimated at -14‰ (Máguas et al., 1995; Palmqvist, 1993).

C_4 species are thought to have evolved under drier and warmer climatic conditions, when the atmospheric CO_2 concentration was much lower than in the current atmosphere (Cerling et al., 1993; Ehleringer et al., 1991). Therefore, we do not speculate cyanobacteria-dominated crust to respond, or benefit from climate change because they are already adapted to arid conditions and low atmospheric CO_2 concentration. In the Nevada Desert Free-Air Carbon Enrichment (FACE) facility, Billings et al. (2003) showed that BSC productivity and N-fixation rates were not affected by CO_2 enrichment. Several studies had shown that C_4 photosynthesis becomes saturated at concentrations above the current atmospheric CO_2 levels, whereas C_3 photosynthesis does not (Ehleringer et al., 1991; Farquhar et al., 1989). Therefore, if changes in species composition or biomass density take in the BSC, the changes could be attributed to climate change-related factors such as intensive land use and soil erosion.

3.4.3 Chlorophyll content

Chlorophyll content in the crusts from the sandy site was 0.02±0.01, whereas crusts from the clay site were 0.01±0.00, mg per gram, indicating that chlorophyll content in the two crusts was significantly different. Although difference in chlorophyll between the two crusts could be attributed to sampling strategy (e.g. soil v.s crust ratio), we minimized the bias by maintain consistency in our sampling method in the two sites, and during laboratory analysis of chlorophyll content. Based on visual assessment of vegetation cover in the study area, we found that the sandy site had more vegetation cover than the clay site. Therefore, these results could mean that the relatively higher chlorophyll content in the sandy site might be a result of shrubs protecting the crust. For instance, recent studies had indicated that BSC on sandy surface grow and expand fastest than in other soil types, and that BSC under the canopy survive most easily due to the favorable conditions produced by the vegetation (Kidron et al., 2002; Petrou and Milios, 2012). Conversely, the low chlorophyll content in the clay site reflected lack of vegetation cover and protection, which resulted in the crust exposed to physical disturbances such as aeolian and fluvial disturbance.

The BSC in the sandy site had higher chlorophyll content than the crusts in the clay site. However, C content in the soil profile was higher in clay soil compare to the than in sandy site. This pattern suggested that much more of the C in the sandy soils was in cyanobacterial biomass compared to the clay soils, which could either have C in other types of organisms, or simply result from stabilization of organic C in the soil. Therefore, it is important to interpret chlorophyll content with caution, particularly when it is used as a proxy measure for biomass abundance in cyanobacteria and C cycling (Belnap et al., 2013).

3.4.4 Soil respiration

Respiration from crust-removed soil was 0.1 g CO_2 m^{-2} h^{-1}, when calculated using the maximum CO_2 efflux (Table 3). Although this value is of the same order of magnitude with values reported from other studies, our value is about three-fold lower than other values reported. For instance, Wang et al. (2007b) reported 0.23 to 0.74 g CO_2 m^{-2} h^{-1} efflux in dry soils in the Kalahari, and that the values increased 10-fold after wetting. Other studies in the Kalahari reported soil respiration between 1.5 to 5.9 g CO_2 m^{-2} h^{-1} (Thomas and Hoon, 2010; Thomas et al., 2011). Fan et al. (2015) estimated soil respiration in South Africa's savanna ecosystem to range between 0.27 and 0.15 g CO_2 m^{-2} h^{-1}. In the Brazilian Cerrados soil respiration during wet season was estimated between 0.22 and 0.33 g CO_2 m^{-2} h^{-1} whereas, dry season estimates were 2 g CO_2 m^{-2} h^{-1} (Hill and Hanan, 2010; Rocha et al., 2002). In Australian savannas Chen et al. (2002) estimated soil respiration to range between 0.19 to 0.57 g CO_2 m^{-2} h^{-1} during the wet season and 1.2 to 3.6 g CO_2 m^{-2} h^{-1} during the dry season. The low CO_2 efflux values in our site could be attributed to soil and vegetation types, microbial abundance and climatic conditions. For instance, Makhado and Scholes (2012) showed that soil respiration differed significantly between more clayed soil and sandier soil. The soil respiration they reported was 0.540 and 0.484 g CO_2 m^{-2} h^{-1} (p-value = 0.028) for clayed and sandy soils, respectively. They further speculated the respiration differences to be a result of differences in microbial composition.

In the Chihuahuan Desert, southwestern USA, Parker et al. (1984) reported that litter plays an important role in determining soil moisture and microbial composition, which ultimately influence soil respiration.

3.4.5 Carbon exchange

Biological soil crusts have been reported to have a considerable photosynthetic potential, and represent an important carbon sink (Feng et al., 2014; Thomas et al., 2008). To assess the contribution of BSC to soil carbon dynamics, we calculated net crust fixation using data in Table 3, with the following equations:

$$\mathrm{Rs}_{crust} = \mathrm{Rs}_1 - \mathrm{Rs}_0 \qquad \text{(Equation 8a)}$$

$$\mathrm{Ps}_{crust} = \mathrm{NCE}_1 - \mathrm{Rs}_1 \qquad \text{(Equation 8b)}$$

$$\mathrm{Fix}_{crust} = \mathrm{Ps}_{crust} + \mathrm{Rs}_{crust} \qquad \text{(Equation 8c)}$$

where Rs_{crust}, Ps_{crust} and Fix_{crust} are crust respiration, photosynthesis and net fixation respectively. The subscripts 1 and 0 denote crust and no crust cover in the soil, respectively. For example, to mean net crust fixation values in Table 4 were calculated as follow:

Crust respiration = 0.47 – 0.24 = 0.22 μg CO_2 m^{-2} s^{-1}

Crust Photosynthesis = 0.14 – 0.47 = - 0.33 μg CO_2 m^{-2} s^{-1}

Net Crust fixation = -0.33 + 0.22 = -0.11 μg m^{-2} CO_2 s^{-1}

Table 3-4. The contribution of biological soil crusts to CO_2 fluxes in Jornada Experimental Range. Assumed 21 days of rainy days per year, with 9 hours of sunshine.

Treatment	Mean flux (µmol CO_2 m^{-2} s^{-1})	Max flux (µmol CO_2 m^{-2} s^{-1})	Approximate time at max efflux (Hour)	Yearly fluxes (g CO_2 m^{-2} yr^{-1})
Crust respiration	0.22 ± 0.10	0.39	1500 ± 1	6.6
Crust photosynthesis	-0.33 ± 0.12	-061	1500 ± 1	9.8
Net crust fixation	-0.11 ± 0.09	-0.24	1600 ± 1	3.2

We calculated net primary productivity (NPP_{crust}) of the crust, in accordance with the method of Brostoff et al. (2005):

$$NPP_{crust} = (Fix_{crust})(\%\ cover_{crust})(rainy\ days\ yr^{-1})(365\ days\ yr^{-1})$$

(Equation 9)

where (Fix_{crust}) is the daily CO_2 fixation (Equation 8c), $\%\ cover_{crust}$ is the proportion of land surface covered by the crust. $Rainy\ days\ yr^{-1}$is the mean total number of rainy days per year with > 1 mm of rainfall. Our calculations showed that the annual net CO_2 fixation by biological soil crust in the sandy soils was 3.2 g CO_2 m^{-2} yr^{-1}, which translated to NPP of 0.9 g C m^{-2} yr^{-1} (Table 4). Our NPP value fell within the 0.4 – 2.3 g C m^{-2} yr^{-1} in cyanobacterially dominated crusts (Evans and Lange, 2001). In the Mu Us Desert, China, Feng et al. (2014) reported NPP by BSC at 3.46 to 6.05 g C m^{-2} yr^{-1}, whereas Brostoff et al. (2005) reported 11.7 g C m^{-2} yr^{-1} in Mojave Desert, USA. For comparison, the NPP of shrubs (C_3) and grasses (C_4) plants in Jornada has been estimated at 125 g C m^{-2} yr^{-1} and 200 g C m^{-2} yr^{-1}, respectively (Huenneke et al., 2002). Although the NPP of the crusts seem low compared to NPP of vascular plants, it is important to point out that the extensive spatial distribution of the crusts make then an important source of soil C. From conservation and land management point of view, our results incidate that allowing establishment of BSC could increase soil C sequestration. Studies have indicated that soil C input from BSC increases as the level of development increases (Belnap et al., 1994; Belnap et al., 2013; Su et al., 2012).

To compare respiration of crust-removed soil with BSC respiration, we calculated the fluxes using the Brostoff's method. We only calculated heterotrophic respiration for rainy days only, because BSC are active only when they have been wetted. Our estimates indicated that the annual respiration was 2.0 and 6.6 g C m^{-2} yr^{-1}, for crust-removed soil and BSC respiration, respectively. Although the BSC respiration estimates are three-fold greater than respiration of crust-removed soil, BSC respiration is offset by C fixation by the crust, resulting in net carbon gain. Heterotrophic respiration, in many cases, is not affected by plant input and could results in either net C loss or gain.

The NPP and respiration of the BSC in our study site were an order of magnitude lower than the values reported for Mu Us, China, Mojave, USA and the Kalahari deserts (Feng et al., 2014; Thomas and Hoon, 2010). One of the reasons why our NPP value was lower could be due to the differences in species composition of the crust. In our study area the $\delta^{13}C$ suggested that the dominant species were cyanobacteria, whereas the dominant species in study conducted by Brostoff et al. (2005) were green algal lichens. With reported $\delta^{13}C$ values ranging between -36‰ and -14‰, it is not clear whether lichens use C_3 or C_4 photosynthesis, (Beazley et al., 2002; Lange et al., 1988; Máguas et al., 1995). Some studies have indicated that lichens use C_3 photosynthesis, other studies suggested C_4 photosynthesis, while some suggested that lichens use intermediate C_3-C_4 photosynthesis (Flores et al., 2009; Snelgar and Green, 1981; Teeri, 1981). Therefore, it is difficult to compare our results with that of Brostoff et al. (2005) because they did not report $\delta^{13}C$ of their samples.

We also used extremes of 21 rainy days yr^{-1} and 9 hours of sunshine, whereas other studies did not take into account the duration of sunshine during a 24 hour period of the day (e.g. Feng et al., 2014). That is, they did not consider the duration of sunshine, which translated in to 24 hour of photosynthesis per day. It is also possible that the high CO_2 fluxes reflected the high soil C content in other soils compared to our soil C content. Higher soil C content might translate in to higher respiration rates during rainfall pulses (Thomas and Hoon, 2010), making more CO available to the crust for photosynthesis. The other reason why other studies reported relatively high respiration values was that they maximally watered the soil crusts and immediately measured CO_2 fluxes (Feng et al., 2014). Studies from many parts of the world have shown that wetting BSC causes an immediate increase in CO_2 efflux over the first hour after wetting, with the peak rates remaining high for about two days, a process called 'Birch effect' (Birch, 1964; Bowling et al., 2011; Fan et al., 2015; Thomas and

Hoon, 2010; Wang et al., 2007b). The sources of the respired CO_2 during wetting events are not fully understood, though it is speculated that some of the CO_2 resulted from microbial attack during the breaking up of organic matter aggregates due wetting. During wetting, C from extracellular polymetric substances could also provide a source of readily available energy to heterotrophic soil microbes (Mager, 2008). It is also possible that as the wetting front moves down the soil profile, water displaces CO_2-rich soil air (Brady and Weil, 2007; Tan, 2011), releasing some of the soil CO_2, thus making it available to the crusts in to the atmosphere.

Furthermore, CO_2 fluxes differ from other studies because of the different methods in the experimental setup. Whereas we treated the crust-removed plot as a control, other studies compared CO_2 fluxes from crusted soils to non-crusted soils (e.g. Castillo-Monroy et al., 2011; Thomas, 2012; Thomas et al., 2011). Adjacent plots do not necessarily have similar functional properties; in particular the belowground root distribution could significantly differ between plots thus biasing results. Therefore using adjacent plots (one with crust and the other with no crust) as control introduces considerable uncertainty to the comparisons. The fact that the two plots have different BSC cover, perhaps suggest that they undergo different biogeochemical or disturbance processes; therefore direct comparison between CO_2 fluxes does not necessarily reflect the actual difference. With our method it was possible disentangle BSC respiration from root and mycorrhizal respiration, whereas with the other method it is almost impossible to disentangle BSC respiration from root respiration. Here, we propose the use of our method of removing the crust and treat the crust-removed plot as a control, because removing the crust reduces uncertainty that could result from landscape heterogeneity.

3.4.6 Carbon cycling

Respiration was higher than NCE in the crusted soils, indicating that the presence of sunlight stimulated BSC to fix CO_2 that was respired from the soil (Figure 2). Similarly, NCE in crusted soils was lower than in crust-removed soils. Our results indicated that removal of the crust resulted in the respired CO_2 escaping into the atmosphere. If the biological crusts were fixing atmospheric CO_2 exclusively, then the removal of the crusts would have no impact in NCE. Furthermore, during the day, there was no significant difference between NCE and respiration in crust-removed soils (p-value = 0.69, $R^2 = 0.80$, n = 44). This result indicated that after the removal of the BSC there was no CO_2 assimilation, further highlighting that BSC fixed some of the soil respired CO_2.

To quantify the contribution of the soil and atmosphere to CO_2 assimilation by the crusts we used stable C isotopic analysis. Here, we assumed the $\delta^{13}C$ of the atmosphere to be -8.2‰ (Keeling et al., 2005). Because we did not measure $\delta^{13}C$ of the respired soil CO_2, we estimated it indirectly in accordance to the method of Bowling et al. (2008), which assumed that root respired CO_2 was 2.5‰ higher than foliar $\delta^{13}C$. In our study area, $\delta^{13}C$ of the dominant species, *Prosopis glandulosa*, was reported to be -25.7‰ (Bai et al., 2008; Boutton et al., 1999; Boutton et al., 1998). Based on Bowling's method, we estimated the root respired CO_2 at -23.2‰. Using two-endmember mass balance ratio, we calculated that in the sandy site, 54.8% and 45.2% of the assimilated was derived from the atmosphere and the soil, respectively. In the clay site, 60.3% and 39.7% of the assimilated CO_2 was derived from the atmosphere and the soil, respectively. Our results provided quantitative evidence that BSC were fixing CO_2 from the soil and the atmosphere, and taking up relatively more CO_2 from the atmosphere. Although the soil CO_2 is usually higher than the atmosphere (Brady and Weil, 2007; Tan, 2011), we speculated that BSC would have easier access to atmospheric CO_2 because chlorophyll are located on the upper side of the crust.

Because soil respiration is a sum of autotrophic and heterotrophic respiration, the removal of one component would cause a decrease in soil respiration. Therefore, we expected respiration from the crusted soils to be greater than in crust-removed soil. However, during the night, there was no significant difference between respiration from the soils with the crust and crust-removed soils (p-value = 0.20). Our results suggested that BSC were not active at night, or that they carried out minimal respiration, which did not alter the overall soil respiration.

3.4.7 Temperature sensitivity

To assess the effect of temperature in CO_2 in crusted and crust-removed soils we calculated Q_{10}, a measure of rate of change of a chemical reaction when temperature increases by 10°C (Hoff and Lehfeldt, 1899). The Q_{10} for soil respiration in crust-removed soil (heterotrophic respiration) was 2.75, and was consistent with the Q_{10} values from South African savannas, which ranged between 1.1 and 3.1 (Makhado and Scholes, 2012; Thomas and Hoon, 2010; Thomas et al., 2011). However, the experiments in southern Africa did not involve removal of the crust, rather the authors selected soils patches with no soil crust. At global scale the Q_{10} for soil respiration was estimated at 1.4 – 2.0 (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015; Zhou et al., 2009). It is important to point out that the global Q_{10} for soil respiration is the average of all the ecosystems such as forests and drylands, and affected by an array of environmental factors. For instance, Thomas and Hoon (2010) reported Q_{10} of 12.6 in heavily wetted soils, a value which is not feasible from biological point of view.

Our results indicated that the presence of BSC reduced Q_{10} for respiration and NCE. Conversely, the removal of the crust led to an increase in Q_{10} for respiration and NCE. Our results are consistent with observations from China, where Q_{10} increased after crust disturbance (Feng et al., 2013). However, removal of the crust in NCE resulted in 76% increase in Q_{10}, which was much higher than the 17% increase in the respiration experiment. The difference in Q_{10} changes could be attributed to morphological and functional processes of bare soil and BSC. It is possible that the resulting bare soil after the crust removal received higher solar radiation, which accelerated microbial activity, resulting in more CO_2 efflux as soil temperature increases. In the presence of the crust, it is likely that much of the heat from solar radiation does not reach the soil. Therefore, as solar radiation increases during the day, only BSC respond to temperature change. To test this hypothesis, we calculated Q_{10} for BSC respiration and found it to be 3.0, which is closer to that of crusted soils (Q_{10} = 2.3). Our results indicated that BSC act as a buffer, trapping a significant portion of solar radiation, which would otherwise be absorbed by the soil.

Although BSC respond to the ambient temperature, it is likely that they have adaptation mechanisms that enable them to regulate their biogeochemical processes such as respiration. One of the mechanisms could be photosynthesis, which involves the utilization of solar energy in fixation of CO_2. We calculated Q_{10} for BSC photosynthesis and found it to be 5.8. These results suggested that BSC photosynthetic functionality crust was more sensitive to temperature than the respiration functionality.

3.4.8 Climate change and BSC carbon fluxes

Global climate models and regional models have predicted that drylands will become warmer and drier due to climate change (IPCC 2013, Hartmann et al., 2013; Knapp et al., 2008; Shongwe et al., 2009). The predicted climate change could results in drylands being a carbon source, particularly as belowground carbon stocks respond to changes (Dintwe et al., 2014). The effect of climate warming could stimulate microbial metabolism and results in immediate increase in microbial respiration (Dijkstra et al., 2011). However, BSC could offset some of the potential impacts of climate change by assimilation of soil CO_2 and by lowering the overall Q_{10} for soil respiration, compared to places with no crusts.

Changes in vegetation structure due to intensive land use could increase BSC abundance. Berkeley et al. (2005) reported that bush encroachment enhanced the establishment of BSC, which in turn, improve soil fertility by fixing nitrogen, thus promoting further bush encroachment. The positive feedback mechanism between bush encroachment and establishment of BSC could result in increased CO_2 fixation, and potentially render drylands net C sink or zero net C balance. In addition to assimilating a considerable amount of CO_2, bush encroachment species and BSC help reduce soil temperature, thus decreasing soil respiration and NCE Q_{10}. This process could potentially mitigate the rate of soil C loss to the atmosphere.

3.5 Conclusion

Here, for the first time, we used a simple and direct method to separate BSC respiration from total soil respiration, as well as to distinguish the sources of CO_2 assimilated by soil BSC. We have estimated the rate of photosynthesis and NPP of BSC. We have also demonstrated that removal of BSC and increasing soil temperature resulted in an increase in Q_{10}, for respiration and NCE with pronounced effects in NCE.

In the context of climate change, our results suggested that proper land management, which promotes establishment and development of the biological crust, could mitigate the consequences of soil CO_2 loss. Furthermore, our results suggested that the global soil respiration rates in drylands are likely overestimated, and that the estimated feedbacks between soil CO_2 efflux and climate change could be lower than predicted. Our conclusion is consistent with other studies, where the impact of climate change on soil respiration was predicted to be lower than current estimates (Bradford et al., 2008).

For future analysis, we propose the integration of different methodologies such as stable isotope analysis, eddy covariance fluxes, and remote sensing to argument CO_2 field measurements. This approach could help determine and quantify the contribution of the different CO_2 sources. Lastly, we propose that researchers pay more attention to NCE, because it is a critical parameter for understanding the carbon balance of the ecosystem.

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Chapter 4 : Fire-induced albedo change and surface radiative forcing in Sub-Saharan Africa savanna ecosystems: implications for the energy balance

Abstract

Surface albedo is a critical parameter that controls surface energy balance. In dryland ecosystem, fires play a significant role decreasing surface albedo, resulting in positive radiative forcing. In this study, we investigate the long-term effect of fire on surface albedo. We devised a method to calculate short, medium and long-term effect of fire-induced radiative forcing and their relative effects on energy balance. We used MODerate-resolution Imaging Spectroradimeter (MODIS) data in our analysis, covering different vegetation classes in Sub-Saharan Africa (SSA). Our analysis indicated that mean fire-induced albedo change in SSA was -0.013, -0.020 and -0.021 for savannas, shrubland and grasslands respectively. At regional scale, mean fire-induced albedo change in savannas was -0.012 and -0.013 for Northern Sub-Saharan Africa (NSSA) and Southern Hemisphere Africa (SHA), respectively, whereas albedo change in grasslands was -0.019 and -0.022 for NSSA and SHA, respectively. In savannas post-fire albedo took about 48 days to reach a minimum value, while in grasslands albedo change took about 24 and 16 days to reach minimum values in NSSA and SHA, respectively. In savannas and grassland post-fire enhanced vegetation index (EVI) took 16 and 24 days, respectively, to reach minimum values. The EVI recovery time in savannas was 56 and 64 days in NSSA and SHA, respectively, whereas in grasslands the EVI recovery time was > 200 and 80 days in NSSA

and SHA, respectively. The mean fire-induced radiative forcing in burn areas in Sub-Saharan Africa (SSA) was 2.96 W m^{-2}, which exerted mean continental and global radiative forcing of 0.14 and 0.032 W m^{-2}, respectively. We showed that the impact of fire in surface albedo has long-lasting effects, and varies with vegetation type. The long-term effects of fire-induced albedo change and associated radiative forcing were an order of magnitude greater than the short-term effects, suggesting that fires exerted a far more radiative forcing than previously thought. These findings provide crucial information, particularly to climate and land-atmosphere studies. We concluded by recommending the use of medium- and long-term method when assessing the impact of fire on surface energy balance.

4.1 Introduction

For millions of years, fires have been an integral part of the Earth's biogeochemical processes and influenced land-atmosphere interactions (Belcher et al., 2010; Glasspool et al., 2004; Pausas and Keeley, 2009). At local scale, fires play a critical role in influencing natural selection and plant evolution, a process that contributed to evolution and expansion of flammable ecosystems (Bond and Keeley, 2005). Conversely, fire spread is facilitated by plant species that have evolved to withstand burning (Liu. et al., 2010). Fires consume large quantities of biomass and release CO_2 and smoke (black carbon) into the atmosphere, and deposit ash and charcoal onto the ground surface (Jin and Roy, 2005; Smith et al., 2005). The ash and charcoal deposition causes darkening of the ground surface, which reduces surface albedo especially at infrared wavelengths (Roy et al., 2005; Xue et al., 2004). Albedo, defined as the ratio of the reflected solar radiation to the incoming solar radiation (Ångström, 1925), is the key component controlling surface energy balance over land thereby driving local climate and ecosystem functions (Dickinson, 1983). Surface albedo is important because it affects the Earth's radiative energy balance by regulating how much incoming solar radiation is absorbed or reflected by the surface, a process called radiative forcing (IPCC, 2013; Pinty et al., 2000; Wendt et al., 2007; Xue et al., 2004). Positive radiative forcing results in increased energy absorption and promotes warming, while negative radiative forcing results in decreased energy absorption and leads to cooling.

Fire-induced albedo change and associated radiative forcing have started to attract the attention of ecologists, climatologists and policy makers (Bowman et al., 2009; De Sales et al., 2015; Gatebe et al., 2014; IPCC, 2013; López-Saldaña et al., 2014; Myhre et al., 2005). Recent studies show that in boreal forest, post-fire albedo increases and results in negative radiative forcing (Flannigan et al., 2009; Huang et al., 2014; Jin et al., 2012; Lyons et al., 2008; Oris et al., 2013; Randerson et al., 2006). However, in dryland ecosystems such as savannas and grasslands, post-fire albedo decrease and cause positive radiative forcing (Gatebe et al., 2014; Jin and Roy, 2005; López-Saldaña et al., 2014). In North American boreal forest the radiative forcing exerted by fire-induced albedo change ranges between -4.5 W m^{-2} and -1.3 W m^{-2} (Jin et al., 2012; Lyons et al., 2008), whereas in African and Australian savannas it has been reported to be between 0.1 W m^{-2} and 0.5 W m^{-2} (Gatebe et al., 2014; Jin and Roy, 2005; Myhre et al., 2005). Although at local and regional scales boreal fires exert negative radiative forcing, the overall global impact could be positive radiative forcing due to the high CO_2 emissions (Hao and Liu, 1994; Tansey et al., 2004). Despite the relatively low radiative forcing in savanna fires, their global contribution is important because savannas contribute more than 80% of global fires, have high fire frequency, and are relatively evenly distributed between the northern and southern hemispheres (van der Werf et al., 2010).

Fires do not only affect surface albedo, they have far reaching consequences on land-atmosphere interactions. Combustion of biomass releases CO_2, black carbon (BC), CO and other greenhouse gases in to the atmosphere. The radiative forcing of BC biomass burning is estimated at 0.2 W m^{-2}, and exerts 0.04 W m^{-2} on snow (Myhre et al., 2013). Global emissions of CO_2 due to fires are estimated to be about 2.6 Pg C yr^{-1}, and that 0.5 Pg C yr^{-1} of the emissions is associated with anthropogenic deforestation, while additional flux of 1.2 Pg C yr^{-1} is released indirectly as a result of decomposition of vegetation killed by fire but not combusted (van Der Werf et al., 2003; van der Werf et al., 2010). The combustion by-products have radiative forcing that could affect the overall energy balance of the globe. For example, Bowman et al. (2009) estimated that global CO_2 emissions from deforestation fires alone contribute up to 19% of the total increased radiative forcing since preindustrial times. Savanna and grassland fires contribute a total of 44% of CO_2 emissions, followed by deforestation and woodland fires with 20% and 16%, respectively (van der Werf et al., 2010). CO_2 has radiative forcing of 1.68 W m^{-2}, and growth rate of 0.27 W m^{-2} per decade (Myhre et al., 2013). Furthermore, CO_2 has climate sensitivity of 1.5°C W^{-1} m^2 to 6.2°C (Royer et al., 2007). Climate sensitivity is the estimate of how much the Earth's climate will warm in response to a radiative forcing (IPCC AR4, 2007). In the case of CO_2, climate sensitivity refers to global warming in response to doubling of CO_2 concentration in the atmosphere. Black carbon released by wildfires can absorb a million times more energy than CO_2, and is estimated to have climate sensitivity of 0.6 °C W^{-1} m^2 (Chung and Seinfeld, 2005). Additionally, Chung and Seinfeld (2005) predicted that direct radiative forcing of anthropogenic BC could lead to a decrease in precipitation, particularly in 0° – 20°S regions of the world. In comparison, other long-lived greenhouse gases such as N_2O, CH_4 and Halocarbons have global radiative forcing of 0.48, 0.16 and 0.34 W m^{-2}, respectively (IPCC AR4, 2007).

The ever-increasing world population exerts pressure on the available land resources, resulting in rapid land use change such as conversion of forests into rangelands and croplands, particularly in the Amazon Basin (Bustamante and Ferreira, 2010). The main tool used in large-scale land conversion is fire, because fire can quickly and effectively reduce biomass of newly cleared forests to nutrient-rich ash that can fertilize crops (Cochrane, 2009; Miranda et al., 2009). The released CO_2 by biomass burning, which is not returned to the terrestrial system when forests are replaced by rangelands and croplands, combined fire-induced albedo change, results in the overall positive radiative forcing (Arneth et al., 2010; Bowman et al., 2009; Cochrane, 2009; Flannigan et al., 2005; Miranda et al., 2009). The total net anthropogenic activities exert global radiative forcing of about 1.5 W m^{-2} (IPCC, 2013).

General circulation models show that fire-prone ecosystems are warming rapidly as a result of climate change (IPCC 2013, Hartmann et al., 2013; Knapp et al., 2008; Randerson et al., 2006; Shongwe et al., 2009). Fires are likely to respond to climate change, because they are regulated by precipitation (fuel load) and temperature (dry fuel load). The projected increase in air temperature and decrease in precipitation is likely to increase fire potential, frequency, intensity as well as the length of the fire season particularly in the United States, South America, Africa and Australia (Liu. et al., 2010; Pechony and Shindell, 2010). The interaction and feedback between fire activity and climate change is of significant importance because fire-prone ecosystems are extensive, covering 40% of the Earth's land surface, and responsible for more than 85% of the global fires (Bond et al., 2005; Chapin et al., 2011; Hao and Liu, 1994; Rundel et al., 2016; Tansey et al., 2004).

In light of the projected increase in fire frequency and intensity, resulting of human-induced climate change and land use change, it is imperative to comprehensively assess and quantify fire-induced albedo change, and the associated surface shortwave radiative forcing (SSRF). In this study, we calculated SSRF taking into account the long-term fire-induced albedo change and duration of albedo recovery. To the best of our knowledge, all previous studies have assessed 'instantaneous' fire-induced albedo change to calculate SSRF (Gatebe et al., 2014; Jin and Roy, 2005; Lyons et al., 2008). We argue that 'instantaneous' fire-induced albedo change and associated SSRF do not reflect the full impact of fire, thus underestimating the impact of fire on energy balance. Here, we devised methods to calculate short-, medium- and long-term albedo changes, and the associated SSRF fire-prone ecosystems.

We conducted our study in Africa, because it is the single largest continental source of burning biomass, with its fires responsible for about 50% of the total amount of vegetation burned globally each year (Cahoon et al., 1992; Cooke et al., 1996; D'Odorico et al., 2007b; Flannigan et al., 2009; Hao and Liu, 1994; Riaño et al., 2007; Ribeiro et al., 2008; Roberts et al., 2009; Scholes et al., 1996; van der Werf et al., 2006; Werf et al., 2004). Africa has the highest rates of fires with peak biomass combustion as high as 6 million tons of fuel per day in the southern hemisphere and 9 million tons in the northern hemisphere (Roberts et al., 2009). The landscape of Africa makes it an ideal place to study fire and its associated impact on climate change. The north-south and east-west geographical orientation of Africa's southern and northern hemispheres, respectively provide an environment conducive to study the relationship between fire-induced albedo and environmental factors such as precipitation, vegetation structure and land use type.

4.2 Materials and methods

4.2.1 Study area

The study was conducted in Sub-Saharan Africa (SSA) savannas and grasslands (Fig. 1). Africa has the largest area of savannas, covering more than 50% (18 million km^2) of the continent's land surface (Smit, 2004). The southern hemisphere of Africa (SHA) has the largest continuous stretch of savannas that cover an area of ~14 million km^2 of land surface, whereas northern sub-Saharan Africa (NSSA), that is, Africa north of the equator and south of the Sahara, covers about 3 million km^2 of land surface (Grace et al., 2006; Scholes and Archer, 1997; Smit, 2004).

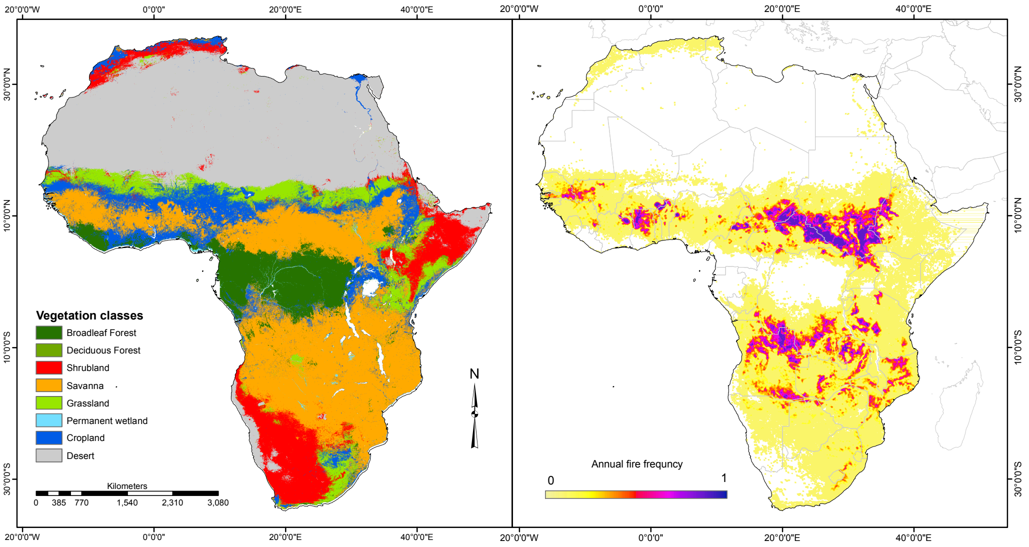

Figure 4-1. The map on the left shows the vegetation classes in Africa, following the International Geospehere-Biosphere Programme land cover classification. The map on the right shows fire distribution and frequency in Africa.

4.2.2 Brief description of data set used

Moderate Resolution Imaging Spectroradiometer (MODIS) burn product (MCD45A1), shortwave black sky albedo (MCD43A3), BRDF Albedo Quality (MDC43A2), Enhanced Vegetation Index (MOD13A1) and vegetation classes (MCD12Q1) were use for this analysis, covering the period 2000-2015 were acquired from NASA's Earth Observing System Data and Information System (http://reverb.echo.nasa.gov). All the MODIS products used in this analysis had a 500 m spatial resolution. The MODIS burned area product, MCD45A1, provides an day of the year when pixels burn. The product is generated using an algorithm that takes advantage of the spectral, temporal and structural changes on the land surface caused by deposits of charcoal and ash, removal of vegetation and changes in vegetation structure (Roy et al., 2008; Roy et al., 1999). The MODIS albedo product (MCD43A3) is generated through an algorithm that applied semi-empirical kernel-driven bidirectional reflectance (BRDF) model using multi-date, multispectral and atmospherically corrected surface reflectance data to generate 16-day combined product, with 8-day overlap (Schaaf et al., 2002). Enhanced Vegetation Index (EVI; MOD13A1) is a 16-day product designed to enhance the vegetation reflected signal from measured spectral responses by combining more than two wavelengths in the regions 0.6-0.7 m and 0.7-1.1 m (Huete, 2012). EVI has improved sensitivity over high- and low- biomass regions through a de-coupling of the canopy and soil backgrounds and atmospheric effects. For vegetation classes, we used *International Geosphere-Biosphere Program* (*IGBP*) vegetation classes retrieved from the MCD12Q1 yearly MODIS land cover product (Friedl et al., 2010).

In addition, the monthly downward shortwave radiation flux (DSWRF) and precipitation data at 0.25° and 0.5° spatial resolution respectively from 2000-2014 were used in this analysis (Liu et al., 2012; Rodell et al., 2004). The DSWRF data was obtained from Global Land Data Assimilation System (http://disc.sci.gsfc.nasa.gov) while precipitation data was Tropical Rainfall Measuring Mission (https://pmm.nasa.gov). We also used the WorldClim digital elevation model (DEM) at 30 arc-seconds, resampled to 500-m resolution, was used in our analysis (Hijmans et al., 2005).

4.2.3 Image processing- Albedo, EVI and burn products

The monthly burn products were composited into yearly products. In the case where a pixel had more than one fire occurrence in a year, the last burn date was retained. The resulting output was a 15-band stacked burn product, each band corresponding to the years 2001 through 2015, sequentially. To obtain a single land-cover classification for the entire area, we selected the most common International Geosphere-Biospehre Programme (IGBP) vegetation class from the MOD12Q2 product over all years for each pixel.

A database of fire was produced by identifying all fires in 500-m pixels across Africa for the period 2000-2015 from the MOD45A1 data. For each fire pixel (i.e. a recorded fire in a particular year for a particular pixel), we extracted the albedo, EVI, DSWRF and precipitation from a period beginning three months before the fire and continuing until nine months after the fire. This is the record of the fire in the year of the burn (YB). In addition, for each fire pixel we extracted albedo, DSWRF, and EVI for the full year beginning 15 months before the fire (the year before burn, YBB) and the full year beginning nine months after the fire (the year after burn, YAB). This was done only for fires from 2001-2014 because MODIS data is only available from February, 2000 onward.

For our analysis, we wish to compare the behavior of pixels that burned against the control case without fire. An inherent difficulty of this approach rests in the fact that an unburned pixel may have been burnable, but may have lacked only conditions for ignition, in which case it is a good representation of the 'control' case. However, some pixels may not be burnable even in the presence of ignition because of the state of the vegetation or other considerations. There is no approach using remote sensing data to differentiate clearly between these two cases. We reason that a pixel in which fire does occur must, at least some of the time, exhibit conditions that make it burnable, as opposed to a neighboring pixel that may never be burnable. Thus, we conclude a safe comparison between burned and unburned pixels is a comparison of a burned pixel, in the year it burns, against itself, in years it doesn't burn (YBB and YAB). Thus, provided that no fire occurs in the antecedent or subsequent year, the average of the YBB and YAB timeseries for fire pixels are used as controls for each fire pixel timeseries. This average is considered the control and was calculated for all fire pixels for which it could be calculated (that is, for fire pixels in which the YBB isn't before the beginning of the MODIS record, and fire pixels for which fire did not also occur in the year before and/or after).

4.2.4 Fire-induced albedo (and EVI) change

We calculated fire-induced albedo change for each pixel using YB (year of burn) and control datasets. We calculated three types of albedo change. In the fist approach, we calculated short-term albedo change (ΔA_1) using YB as outlined in equation 1.

$$\Delta A_1 = a_{f\_t1} - a_{f\_t0} \qquad \text{Equation 1}$$

where $a_{f_t1}$is the next albedo value after time of burn, and a_{f_t0} is the value of albedo at the time of burn.

We calculated another short-term albedo change (ΔA_2) using YB and YAB datasets as outlined in equation 2.

$$\Delta A_2 = a_{f\_t1} - a_{c\_t1} \qquad \text{Equation 2}$$

where a_{c_t1} is the value of albedo in the control dataset.

To calculate maximum albedo change (ΔA_{max}) we identified and located the lowest albedo value after fire occurrence (a_{f_tmin}) in the YB dataset, and located the associated value in the control dataset (a_{c_tmin}). We calculated the difference between the two values as shown in equation 3.

$$\Delta A_{max} = a_{f\_tmin} - a_{c\_tmin} \qquad \text{Equation 3}$$

This approach allowed us to calculate the impact of fire on albedo using burn and no-burn data taking the date of burn into account. For example, if a_{f_tmin} occurred in October 31st, then a_{c_tmin} would also be on the 31st October.

Furthermore, we calculated albedo recovery time (R_{time}). Albedo was considered recovered when a_{burn} reached 95% $a_{control}$. To calculate recovery time we subtracted burn date from the date when albedo was deemed recovered.

$$R_{time} = date_{recovered} - date_{burn} \qquad \text{Equation 4}$$

2.5 Surface shortwave radiative forcing due to the impact of fire

Surface shortwave radiative forcing (SSRF) due to only fire was calculated by multiplying albedo change by associated surface incoming solar radiation ($I_{burn}^{\downarrow}$). We calculated $SSRF_1$ and $SSRF_2$ using ΔA_1 and ΔA_2 respectively, using equation 5.

$$SSRF_1 = -(I_{burn}^{\downarrow} * \Delta A_1) \qquad \text{Equation 5}$$

We also calculated medium-term SSRF ($SSRF_{tmin}$) and long-term SSRF ($SSRF_{t90}$). The $SSRF_{tmin}$ was calculated by averaging all the SSRF values between time of burn and when albedo reached minimum, equation 6.

$$SSRF_{med} = -\frac{1}{N}\sum_{i=0}^{t_{min}} \mathrm{I}_{ti}(a_{f\_ti} - a_{c\_ti})$$

Equation 6

where *i* is time after burn. The same approach was used calculate long-term SSRF ($SSRF_{long}$), where *i* is time when albedo was deemed recovered (t_{90}).

4.3 Results

4.3.1 Fire regime and environmental variables

Our analysis indicated that more than 90% of the fires occurred in the dry season, in the two regions. In NSSA the dry season occurred November to March, whereas in SHA the dry season occurred in May to October. Most fires occurred in areas receiving between 300 mm and 1500 mm MAP, with peaks fires occurring at 800 – 1200 mm MAP in both NSSA and SHA. About 22% and 12% of savannas burn annually in the NSSA and SHA respectively (Table 1). In grasslands, 2% and 5% burn annually in NSSA and SHA respectively. At continental scale, savannas and grasslands contribute about 9.9% and 0.5% to total burn area, respectively.

Table 4-1. Annual fire regime in Africa ecosystems, over a 15 years period (2001 – 2015)

Region	IGBP Vegetation class	Vegetation class area (x 10^6 km^2)	(%) Area total land surface	Burn area km^2 year^{-1} (x 10^3)	Average Annual Ecosystem burn (%)	Contribution to regional burn area (%)	% burn to total land surface
North Sub-Saharan Africa (NSSA)	Savanna	3.3	13.0	746.9	22.4	85.2	2.9
	Grassland	2.4	9.6	48.6	2.0	5.6	0.2
	Shrubland	2.1	8.4	5.8	0.3	0.7	0.0
	Cropland	16.3	63.5	74. 7	0.5	8.6	0.3
South Hemisphere Africa (SHA)	Savanna	5.6	58.1	678.2	12.0	87.7	7.0
	Grassland	0.7	6.7	32.9	5.0	5.8	0.3
	Shrubland	1.5	15.3	14.6	1.0	2.8	0.2
	Cropland	0.8	8.4	18.4	2.3	3.4	0.2
Sub-Saharan Africa (SSA)	Savanna	9.0	25.3	1425.0	15.9	87.7	9.9
	Grassland	3.1	8.8	81.5	2.6	5.0	0.5
	Shrubland	3.6	10.3	20.3	0.6	1.3	0.2
	Cropland	17.2	48.4	93.1	0.5	5.9	0.5

4.3.2 Fire-induced albedo

In all cases ΔA was negative. Grasslands had the largest ΔA_1 ('instantaneous' albedo change) than other ecosystems, with SHA experiencing the largest ΔA_1 (Table 2). In each region, savannas had the smallest ΔA_1. Shrublands had the largest ΔA_2 and ΔA_{max} than other ecosystems in NSSA and SHA. At continental scale, grasslands experienced the largest ΔA_{max} followed by shrublands, croplands and savannas respectively (Table 2). In NSSA grasslands had the largest ΔA_{max} whereas in SHA shrublands had the largest ΔA_{max}.

Table 4-2. Fire induced albedo change. The short-term 1 was calculated using burn albedo while

			Albedo change (unitless)		
Region	IGBP Vegetation Type	Mean annual burn area (x 10^3 km^2)	Short-term 1 ($\alpha_{f\_t1} - \alpha_{f\_t0}$)	Short-term 2 ($\alpha_{f\_t1} - \alpha_{c\_t1}$)	Maximum change ($\alpha_{f\_tmin} - \alpha_{c\_tmin}$)
NSSA	Savanna	746.9	-0.012 ± 0.011	-0.015 ± 0.019	-0.023 ± 0.017
	Shrubland	48.6	-0.017 ± 0.016	-0.033 ± 0.030	-0.045 ± 0.040
	Grassland	5.8	-0.019 ± 0.017	-0.040 ± 0.039	-0.055 ± 0.059
	Cropland	74. 7	-0.013 ± 0.012	-0.021 ± 0.025	-0.030 ± 0.028
SHA	Savanna	678.2	-0.013 ± 0.011	-0.018 ± 0.018	-0.025 ± 0.014
	Shrubland	32.9	-0.021 ± 0.014	-0.050 ± 0.025	-0.050 ± 0.023
	Grassland	14.6	-0.022 ± 0.015	-0.036 ± 0.024	-0.040 ± 0.022
	Cropland	18.4	-0.016 ± 0.016	-0.025 ± 0.026	-0.025 ± 0.024
SSA	Savanna	1425.0	-0.013 ± 0.011	-0.017 ± 0.018	-0.024 ± 0.016
	Shrubland	20.3	-0.020 ± 0.015	-0.047 ± 0.027	-0.048 ± 0.028
	Grassland	81.5	-0.021 ± 0.016	-0.038 ± 0.034	-0.049 ± 0.048
	Cropland	93.1	-0.014 ± 0.013	-0.021 ± 0.026	-0.029 ± 0.027

short-term2 and maximum change were calculated using burn and control albedo.

4.3.3 Pre and post-fire albedo and EVI pattern

In NSSA, the savanna burn albedo (YB) values started higher than control values (Figure 2). After fire occurrence, burn-albedo values dropped below the control values, until after seven weeks when they started to go up again. In SHA the burn-albedo values started lower than control values, increased steadily and reached the same values as the control just before the fire occurrence. After fire occurrence, burn-albedo values dropped below the control values, and started to recover after seven weeks. The burn-albedo values in NSSA grassland were always lower than the control and decreased after fire occurrence. In SHA grassland the burn-albedo values were higher than control but decreased after the burn.

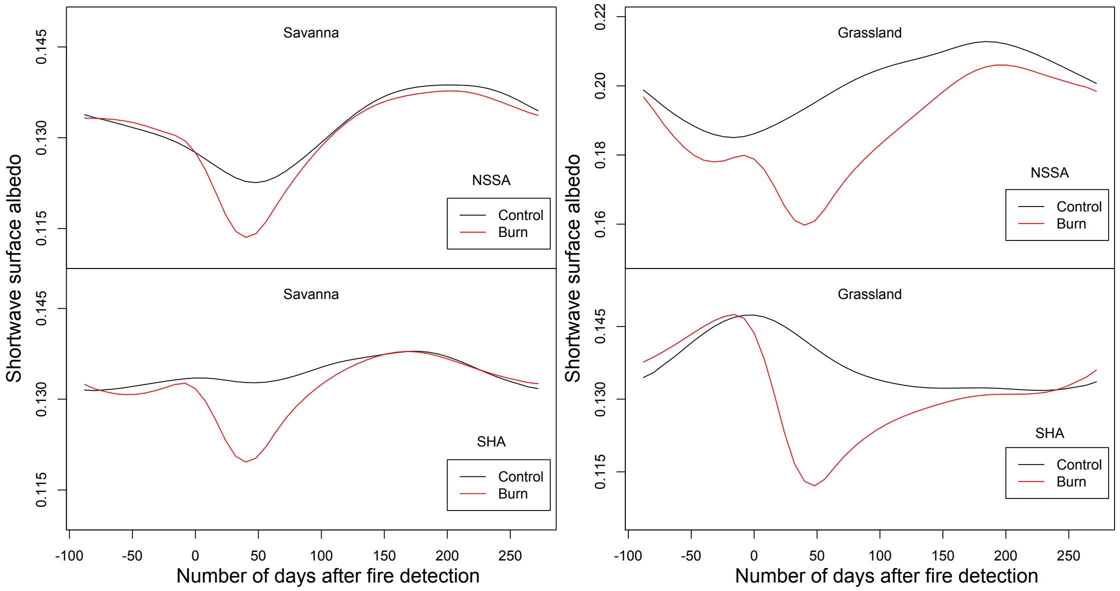

Figure 4-2. The effect of fire on albedo in savannas and grasslands in NSSA and SHA. In NHA the burn-albedo for grasslands was always lower than control albedo in the years when there was fire, possibly indicating accumulation of biomass of fresh/green annual grasses In SHA, the burn-albedo for grasslands was always higher than control, possibly indicating accumulation of dry biomass of perennial grasses.

Savannas took longer time, compared to other vegetation classes, for post-fire albedo to reach the lowest values, while grasslands took the shortest time (Table 3). In the savannas recovery took the shortest time, while in shrublands and grasslands it took the longest (Table 3).

Table 4-3. Median number of days from the date of burn per treatment. T_1 represents the number of days after burn and the next observation, while t_{min} and t_{90} represent the number of days it takes for albedo and EVI change to reach maximum and 90% recovery, respectively.

Treatment	Region	Median number of days per observation					
		Short-term		Maximum change (t_{min})		Recovery (t_{90})	
		t_1 (1)	t_1 (2)	Albedo	EVI	Albedo	EVI
NSSA	Savanna	8 ± 0	8 ± 0	48 ± 60	16 ± 26	128 ± 22	56 ± 21
	Shrubland	8 ± 0	8 ± 0	32 ± 63	32 ± 27	> 240	> 200
	Grassland	8 ± 0	8 ± 0	24 ± 70	24 ± 27	>200	> 200
	Cropland	8 ± 0	8 ± 0	40 ± 74	16 ± 26	184 ± 24	80 ± 19
SHA	Savanna	8 ± 0	8 ± 0	48 ± 52	16 ± 39	128 ± 23	64 ± 27
	Shrubland	8 ± 0	8 ± 0	16 ± 40	16 ± 40	>248	> 200
	Grassland	8 ± 0	8 ± 0	16 ± 60	24 ± 37	> 240	80 ± 17
	Cropland	8 ± 0	8 ± 0	40 ± 79	32 ± 36	200 ± 19	120 ± 36

The burn-EVI and the control values in the savannas started the same until fire occurrence when burn-EVI values dropped (Figure 3). After the drop, the EVI values remained constant for about two weeks and then started to go up again four weeks, until they reached the control values. In the grasslands, burn-EVI values started higher than the control, with the NSSA showing a considerable difference (Figure 3). The burn-EVI values in grasslands remained constant for about two weeks after burn, and then started to recover four weeks after the fire. In SHA grasslands the burn-EVI reached control values upon recovery, whereas in NSSA burn-EVI values never reached control values.

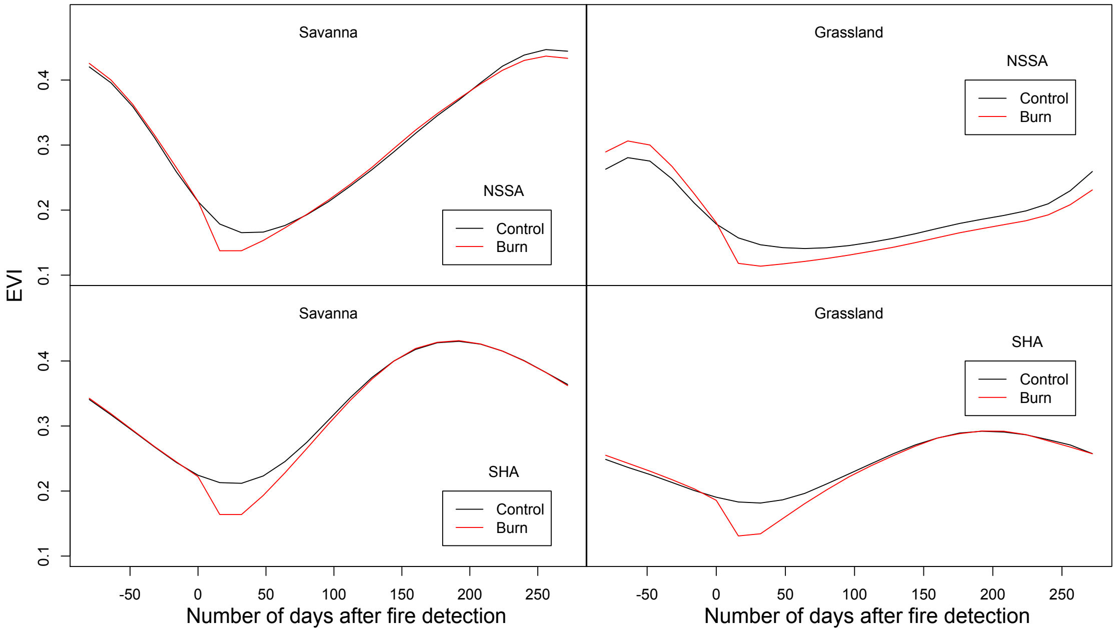

Figure 4-3. The effect of fire on EVI in savannas and grasslands in NSSA and SHA. EVI decreased immediately after fire. In NHA grasslands never recovered from the impact of fire within one year period

The EVI in savannas took about 16 days to reach minimum value after burn, while grasslands took about 24 days (Table 3). Post-fire EVI recovery was faster in savannas than in other vegetation classes.

4.3.4 Radiative forcing due to fire-induced albedo change

In all cases radiative forcing was positive. The short-term-1 (SSRF1) exerted by fire-induced albedo change was greatest in grasslands and least in savannas in NSSA and SHA (Table 4). In NSSA, SSRF2 was greatest in grasslands whereas in SHA it was greatest in shrublands. Similarly, maximum radiative forcing (SSRF-max), medium-term and long-term SSRF were greatest in grasslands and shrublands in NSSA and SHA respectively.

Table 4-4. Surface shortwave radiative forcing exerted due to fires. *I* and *N* represent the incident surface incoming solar radiation (W m^{-2}) and the number of samples per observation, respectively

Region	IGBP Vegetation Type	Mean annual burn area (x 10^3 km^2)	Shortwave Surface Radiating Forcing (W m^{-2})				
			Short-term (SSRF1)	Short-term (SSRF2)	SSRF-max	Medium-term	Long-term
			$I(\alpha_{f\_t1} - \alpha_{f\_t0})$	$I(\alpha_{f\_t1} - \alpha_{ct1})$	$I(\alpha_{f\_tmin} - \alpha_{c\_tmin})$	$1/N\sum_{i=0}^{tmin} I_{ti}(a_{f\_ti}-a_{c\_ti})$	$1/N\sum_{i=0}^{t90} I_{ti}(a_{f\_ti}-a_{c\_ti})$
NSSA	Savanna	746.9	2.62 ± 2.20	2.66 ± 2.30	4.70 ± 3.01	2.53 ± 2.09	2.45 ± 1.69
	Shrubland	48.6	3.70 ± 3.42	5.89 ± 4.42	10.24 ± 8.79	5.38 ± 3.96	4.41 ± 3.11
	Grassland	5.8	4.43 ± 3.55	7.23 ± 5.88	13.03 ± 13.58	6.64 ± 5.19	5.46 ± 3.91
	Cropland	74. 7	2.95 ± 2.58	3.81 ± 3.58	6.66 ± 6.24	3.59 ± 3.18	3.23 ± 2.43
SHA	Savanna	678.2	2.96 ± 2.28	3.31 ± 2.35	5.62 ± 3.04	3.13 ± 2.07	2.94 ± 1.59
	Shrubland	32.9	4.65 ± 2.93	8.11 ± 3.53	10.85 ± 5.14	7.04 ± 3.06	5.17 ± 2.22
	Grassland	14.6	5.00 ± 3.05	5.97 ± 3.34	8.75 ± 4.54	5.40 ± 2.91	4.32 ± 2.14
	Cropland	18.4	3.81 ± 3.27	4.14 ± 3.60	5.74 ± 5.42	3.83 ± 3.11	3.42 ± 2.30
SSA	Savanna	1425.0	2.83 ± 2.26	3.07 ± 2.35	5.29 ± 3.05	2.91 ± 2.09	2.76 ± 1.64
	Shrubland	20.3	4.46 ± 3.06	7.66 ± 3.83	10.73 ± 6.07	6.70 ± 3.33	5.02 ± 2.45
	Grassland	81.5	4.66 ± 3.37	6.72 ± 5.04	11.27 ± 11.03	6.13 ± 4.44	5.00 ± 3.35
	Cropland	93.1	3.09 ± 2.72	3.88 ± 3.59	6.46 ± 6.08	3.64 ± 3.17	3.27 ± 2.41

4.3.5 Implication of medium and long-term SSRF on energy balance

Because the impact of fire on surface albedo occurred continuously over a long time (Figure 2), we calculated the relative effect of each of the SSRFs. For short-term relative effect $R_{s1}$and R_{s2}, we divided the SSR1 and SSR1, respectively, by the number of days it took for albedo to recover (t_{90}) (Table 3). For medium-term relative effect R_{med}, we multiplied $SSRF_{med}$ by number of days it took for albedo to reach minimum, and divided by t_{90}, as shown in equation 7.

$$R_{med} = \frac{1}{N} \sum_{i=0}^{t_{min}} \frac{t_{min}}{t_{90}} \mathrm{I}_{ti} (a_{f\_ti} - a_{c\_ti})$$

Equation 7

Because the long-term SSRF happened at t_{90}, it was treated as relative long-term effect (R_{long}). This approach resulted in normalized relative SSRFs, and enabled for direct comparison between the SSRFs.

The radiative forcing effect increased with time in all the ecosystems (Table 5). For example, in NSSA savannas, the relative SSRF effect was 0.16, 0.16, 0.93 and 2.45 W m^{-2} for R_{s1}, R_{s2}, R_{med} and R_{long} respectively.

Table 4-5. Relative effect of fire-induced surface shortwave radiative forcing. *I* and *N* represent the incident surface incoming solar radiation (W m^{-2}) and the number of samples per observation, respectively

Region	IGBP Vegetation Type	Mean annual burn area (x 10^3 km^2)	Relative effect of fire-induced Shortwave Surface Radiating Forcing (W m^{-2})				
			Short-term (SSRF1)	Short-term (SSRF2)	Maximum (SSRF)	Medium-term	Long-term
			$\mathrm{I}[\mathrm{a}_{\mathrm{f\_t0}}\text{-}\mathrm{a}_{\mathrm{f\_t0}}]/\mathrm{t}_{90}$	$1/t_{90}[\mathrm{a}_{\mathrm{f\_t1}}\text{-}\mathrm{a}_{\mathrm{f\_t1}}]$	$\mathrm{t}_{\mathrm{min}}/\mathrm{t}_{90}[\mathrm{a}_{\mathrm{f\_t1}}\text{-}\mathrm{a}_{\mathrm{f\_t1}}]$	$1/\mathrm{N}\sum_{\mathrm{i=0}}^{\mathrm{tmin}}\frac{t_{min}}{t_{90}}\mathrm{I}_{\mathrm{ti}}(\mathrm{a}_{\mathrm{f\_ti}}\text{-}\mathrm{a}_{\mathrm{c\_ti}})$	$1/\mathrm{N}\sum_{\mathrm{i=0}}^{\mathrm{t90}}\mathrm{I}_{\mathrm{ti}}(\mathrm{a}_{\mathrm{f\_ti}}\text{-}\mathrm{a}_{\mathrm{c\_ti}})$
NSSA	Savanna	746.9	0.16 ± 0.14	0.16 ± 0.14	1.73 ± 1.11	0.93 ± 0.77	2.45 ± 1.69
	Shrubland	48.6	0.12 ± 0.11	0.20 ± 0.15	1.37 ± 1.17	0.72 ± 0.53	4.41 ± 3.11
	Grassland	5.8	0.18 ± 0.14	0.29 ± 0.24	1.56 ± 1.63	0.8 ± 0.62	5.46 ± 3.91
	Cropland	74. 7	0.13 ± 0.11	0.17 ± 0.16	1.48 ± 1.39	0.8 ± 0.71	3.23 ± 2.43
SHA	Savanna	678.2	0.18 ± 0.14	0.20 ± 0.14	2.08 ± 1.12	1.16 ± 0.76	2.94 ± 1.59
	Shrubland	32.9	0.15 ± 0.10	0.27 ± 0.12	0.72 ± 0.34	0.47 ± 0.20	5.17 ± 2.22
	Grassland	14.6	0.16 ± 0.10	0.19 ± 0.11	0.56 ± 0.29	0.35 ± 0.19	4.32 ± 2.14
	Cropland	18.4	0.15 ± 0.13	0.17 ± 0.14	1.15 ± 1.08	0.77 ± 0.62	3.42 ± 2.30
SSA	Savanna	1425.0	0.17 ± 0.14	0.19 ± 0.14	1.95 ± 1.13	1.07 ± 0.77	2.76 ± 1.64
	Shrubland	20.3	0.15 ± 0.10	0.26 ± 0.13	1.07 ± 0.61	0.67 ± 0.33	5.02 ± 2.45
	Grassland	81.5	0.17 ± 0.12	0.24 ± 0.18	1.00 ± 0.98	0.55 ± 0.40	5.00 ± 3.35
	Cropland	93.1	0.13 ± 0.11	0.16 ± 0.15	1.36 ± 1.28	0.77 ± 0.67	3.27 ± 2.41

To determine the mean regional SSRF1 we multiplied this forcing by the proportion of the total burn area to the total regional land area, which gave mean regional SSRF1 of 0.09 W m^{-2} (Table 6). Performing similar analysis for SHA and SSA we found mean regional SSRF1 of 0.24 and 0.14 W m^{-2} for SHA and SSA, respectively. Performing the same analysis using

SSRF2, we calculated mean regional SSRF2 to be 0.01, 0.28 and 0.15 W m^{-2} for NSSA, SHA and SSA, respectively.

At continental scale, the weighted mean relative effect was 0.17, 0.19, 1.02 and 2.93 W m^{-2} for R_{s1}, R_{s2}, R_{med} and R_{long} respectively (Table 6). At regional scale SHA experienced the highest weighted relative SSRF effect than relative effects NSSA in all the treatments. In this analysis, we found that R_{long} and R_{med} effects were an order of magnitude greater than R_{s1}, R_{s2}, with the long-term showing greatest effects.

Table 4-6 The weighted mean of SSRF and the relative effect of SSRF in burn area, and the mean regional radiative forcing. The contribution of vegetation type to burn area were used as weights. The mean regional (and continental) radiative forcing were calculated by multiplying proportion of burn by SSRF.

Region	Weighted mean	Short-term (SSRF1)	Short-term (SSRF2)	Maximum SSRF	Medium-term SSRF	Long-term SSRF
NSSA	SSRF in burn area	2.76 ± 2.32	3.04 ± 2.62	5.37 ± 3.92	2.87 ± 2.37	2.7 ± 1.89
SHA		3.15 ± 2.38	3.63 ± 2.48	5.95 ± 3.27	3.39 ± 2.18	3.10 ± 1.66
SSA		2.96 ± 2.35	3.36 ± 2.58	5.73 ± 3.67	3.16 ± 2.29	2.93 ± 1.78
NSSA	Regional / continental SSRF	0.09 ± 0.08	0.10 ± 0.09	0.18 ± 0.13	0.10 ± 0.08	0.09 ± 0.06
SHA		0.24 ± 0.18	0.28 ± 0.19	0.46 ± 0.25	0.26 ± 0.17	0.24 ± 0.13
SSA		0.14 ± 0.11	0.15 ± 0.12	0.26 ± 0.17	0.14 ± 0.1	0.13 ± 0.08
NSSA	Relative effect of SSRF	0.16 ± 0.13	0.17 ± 0.15	1.70 ± 1.16	0.91 ± 0.75	2.70 ± 1.89
SHA		0.18 ± 0.14	0.20 ± 0.14	1.92 ± 1.05	1.08 ± 0.71	3.10 ± 1.66
SSA		0.17 ± 0.14	0.19 ± 0.15	1.86 ± 1.12	1.02 ± 0.74	2.93 ± 1.78

We further calculated the global radiative forcing exerted by fires in Africa. Assuming the global land surface area of 150 x 10^6 km^2 (Coble, 1987), we calculated that the annual burn area in Africa was 1.6 x 10^6 km^2, and constituted 1.1% of the global land surface area. Multiplying the SSRF1 for SSA by 1.1% we found that fires in Africa exerted a global radiative forcing of 0.032 W m^{-2}. Similarly, we used SSRF2 for SSA and calculated that fires in Africa exerted global radiative forcing of 0.036 W m^{-2}.

4.4 Discussion

4.4.1 Fire-induced albedo change and vegetation structure

In NSSA savannas burn-albedo values started slightly higher than the control values, whereas in SHA savannas the burn-albedo values started slower lower than the control values (Figure 2). However, the difference between the burn-albedo and control albedo values was not statistically different. The difference between albedo patterns in NSSA and SHA savannas could be attributed to vegetation structure and composition (Figure 1). In NSSA the dominant tree species are deciduous acacias, which lose their leaves during the dry season, whereas in SHA there is a great variety in vegetation composition ranging from deciduous acacias in the south to broadleaf–evergreen trees in the north (Caylor et al., 2003; Scholes et al., 2002).

In NSSA the post-fire short-term shortwave albedo (ΔA_1) decreased by 0.012 and 0.019 in savannas and grasslands respectively, whereas in SHA it decreased by 0.013 and 0.022 in savannas and grassland respectively (Table 2). Our results are consistent with results from northern Australia where albedo decrease was higher in grassland than woodland savannas (Jin and Roy, 2005). One of the reasons why grasslands experienced a much greater decrease in albedo could be due to the amount of fuel load and the type of the fires. Grasslands tend to form a continuous carpet, which facilitates the spread and increase fire intensity (Romero-Ruiz et al., 2010). In savannas, the discontinuous grass carpet reduces fire spread and intensity. Grasses usually experience a complete combustion whereas shrubs and trees partially burn. van Altena et al. (2012) showed that there was a positive correlation between species flammability and fire severity in a landscape. Similarly, Amraoui et al. (2010) suggested that vegetation type in Sub-Saharan Africa regulated fire activity. Biomass combustion resulted in grasslands covered by continuous black-gray residues whereas in savannas the surface was be covered by discontinuous black-grey residue and bare soil patches. As a result, we conclude that vegetation and land cover type play important role in influencing post-fire albedo pattern.

4.4.2 Post-fire albedo and EVI recovery

We observed that post-fire albedo continued to decrease for couple of weeks before then recovery (Figure 2). We expected albedo to drop abruptly in the first week (8 days) and to remain constant for a few weeks before recovery. The reason why post-fire albedo continued to drop could be that the residues were not translocated to another place by aeolian or hydrological process, but rather they remain on the same place. De Sales et al. (2015) suggested that in NSSA post-fire albedo would decrease abruptly, and then increase beyond the control values as a result of exposing bare soil due to vegetation deterioration and ash being translocated to other places. However, our results showed that post-fire albedo did not increase beyond control values. The fact that albedo recovery did not exceed control values suggests that albedo recovery was a function of vegetation recovery, and was not influenced by bare soil patches. For bare soil patches to be fully exposed there has to be strong winds or substantial runoff post fire, but our precipitation results did not show any anomalous high rainfall events following fire events. Furthermore, we do not expect fire-prone ecosystems to have large inter-canopy spaces; otherwise fire would not spread.

Here, it is important to make a distinction between post-fire albedo recovery and albedo increase due to bright bare soil patches. Albedo recovery happens when burn-albedo values increase and stabilize upon reaching control values (Figure 2), whereas in the case where albedo increases due to soil background effect, the values exceed the control albedo values. In light of this, we suggest that post-fire albedo continued to decrease because charcoal, ash and other residues were not translocated to other places, but rather the residues covered bare soil patches between plant canopies.

Post-fire EVI recovered faster than albedo in NSSA and SHA regardless of vegetation type (Table 3). This pattern indicated that vegetation recovery was pre-requisite for albedo recovery (Pinty et al., 2000; Tsuyuzaki et al., 2009). As vegetation recovered, the contribution of the soil surface, charcoal and ash decreased and the overall albedo converged to values reflecting vegetation radiative properties. Post-fire EVI in grasslands took longer to recover compared to savannas, which possibly reflected combustion intensities in the two ecosystems. Grasslands tend to experience surface fires, which are more intense and severe than those in savannas (Bowman et al., 2009; Viegas, 2002). Similar observations were made in Northern Australia where severe and intense fires resulted in longer recovery time, whereas less intense fires resulted in shorter vegetation (EVI) and albedo recovery time (Beringer et al., 2003).

4.4.3 Fire-induced surface shortwave radiative forcing

The concept of radiative forcing has been widely used to evaluate and compare the strength of the various factors affecting the Earth's radiation balance, and how they influence climate change (Myhre et al., 2013). In this study, we have presented four different methods of calculating radiative forcing.

Our results where we used the conventional method (Equation 5) indicate that grasslands had the highest SSRF1 than other ecosystems whereas savannas had the lowest SSRF1. Similar results were in northern Australia where SSRF1 in savannas was lower than in grasslands Jin and Roy (2005). However, more than 80% of the burn area occurred in savanna ecosystems, therefore radiative forcing from savannas play an important role in regional to continental scale, because of their spatial and extensive distribution. In NSSA the SSRF1 in burn area was 2.96 W m^{-2}. For comparison, Myhre et al. (2005) reported that biomass burning exerted SSRF1 of 0.10 W m^{-2} in the African continent. While Myhre et al. (2005) reported a local mean maximum SSRF of 8.0 W m^{-2} due to biomass burning, our results indicated a maximum of 5.8 W m^{-2} radiative forcing in burn areas in the Africa. In Australia, *Jin and Roy* [2005] calculated the regional and continental SSRF1 to be 1.18 and 0.52 W m^{-2} for northern Australia and continental Australia, respectively, which are higher than the values reported for Africa.

The SSRF2 results, where we calculated the difference between burn-albedo and control, were about 30% greater than SSRF1 results. Because burn and albedo data was the same for SSRF1 and SSRF2 dataset, the difference in the results could be attributed only to the difference between control data and albedo data at the time of burn. That is, control albedo tends to go up after the date of the fire (given the annual cycle) whereas the burn goes down, resulting in the overall difference increases. In the SSRF1, the control data represent albedo values eight (8) days before burn, whereas in SSRF2 the control data reflect albedo values in the absence of fire. We also found that maximum SSRF, which occurred when burn-albedo reached minimum value, was at least 80% greater than SRRF1 and SSRF2 in all the ecosystems. Our results suggest that the conventional method (SSRF1) underestimates the effect of fire on surface energy balance, and they highlight the importance of considering temporal variability when assessing radiative forcing exerted by fires.

4.4.4 Implication of medium and long-term SSRF on energy balance

We used short-term SSRF and calculated that fires in Africa exerted a continental radiative forcing of 0.14 and 0.15 W m^{-2} for SSRF1 and SSRF2, respectively, while at global scale African fires exerted radiative forcing of 0.032 and 0.036 W m^{-2} for SSRF1 and SSRF2, respectively. However, our global estimates are higher than the global mean raditive forcing of 0.028 W m^{-2} reported by López-Saldaña et al. (2014). The reason why global mean radiative forcing was low could be attributed to the negative radiative forcing exerted by boreal forest fires.

Furthermore, the medium- and long-term relative effects of fire-induced albedo change on radiative forcing were an order of magnitude greater than short-term effects (Figure 4).

Using these ratios we estimated that the mean global radiative forcing exerted by fires in Africa could be an order of magnitude greater than short-term estimates.

4.4.5 Disparity and discrepancy in estimating fire-induced albedo change

Currently, there is an inconsistency of results for fire-induced albedo change, between studies. For example, Gatebe et al. (2014) estimated albedo change in NSSA savannas to be -0.0022, which was an order of magnitude lower than our results. Similarly, Myhre et al. (2005) reported 0.1 W m-2 radiative forcing over the African continent, order of magnitude lower than our calculated value. The discrepancy could largely be attributed to the methods of assessment used in the studies. Gatebe et al. (2014) used unburned neighboring pixels as control, whereas in our study we compared a pixel to itself (Equations 2 & 3). Although the approach of comparing two neighboring pixels is commonly used (e.g. Gatebe et al., 2014; Huang et al., 2014; Lyons et al., 2008; Myhre et al., 2005; Samain et al., 2008), it does not take into account heterogeneity of vegetation classes. That is, it assumes homogenous vegetation cover. Neighboring pixels do not necessarily represent a similar biome, and the fact that the adjacent pixel did not burn could be an indication that the vegetation types and prevailing environmental conditions in the two pixels were different. When we used the neighboring pixels method, the burn and control curves did not line up in the pre-burn period, indicating that they were not a good proxy. Myhre et al. (2005) used the approach of neighboring pixels and concluded that fire-induced albedo change in the African was insignificant and less important in regional and global energy balance. Our method (Equation 2 & 3) also took into account temporal variation between burn and control data. To the best of our knowledge, all previous studies did not take into account the temporal variation between burn and control datasets. We have shown that calculating fire-induced albedo change using the conventional method (Equation 1) results in much lower values compared to Equation 2. We went a step further, and calculated maximum albedo change (Equation 3), and the results were more than twice higher than results obtained using the neighbor method. These three sets of results clearly show that calculating fire-induced albedo change using the conventional approach underestimates the impact of fire, which in many cases has lead to the conclusion that fire-induced albedo change was insignificant and less important to energy balance (Myhre et al., 2005) than our results suggest.

4.5 Conclusion

Because our results showed that fire had long lasting effects of surface albedo (Figure 2), we derived a method to calculate the relative effect of surface shortwave radiative forcing at different time scales (Equation 7). Our results show that the relative effect of SSRF increased with time (Table 5). The long-term relative effect was an order of magnitude greater that short-term relative effect, conforming to our hypothesis that short-term albedo change underestimates the overall radiative forcing of fire. Here, for the first time we have shown that the conventional method of assessing fire-induced albedo change and associated radiative forcing underestimates the impact of fire in regional and global energy balance.

For future assessment of SSRF, we recommend taking into account the effect of fire-produced aerosols and greenhouse gases as well as issue of translocation of combustion residues by wind, as this could help understand and address the global energy balance. A better understanding of these processes could help improve climate model projections, particularly on the issue of climate change and land-atmosphere feedbacks.

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Chapter 5: Using the Century model and CMIP5 climate projections to assess soil organic carbon in savannas

Abstract

Climate models indicate that climate change is likely to affect carbon (C) cycling in the savannas, but the magnitude and direction of change are not fully understood. In this study, we used the Century model analyze how net primary productivity (NPP), soil respiration and soil C sequestration would respond to an increase in atmospheric CO_2 and soil temperature. We also assessed the coupled effects of precipitation and temperature on C dynamics under future climatic conditions, as well as the decoupled effects of each of the climate variables under three IPCC climate scenarios; historical, Representative Concentration Pathway 2.6 (RCP2.6) and RCP8.5. An increase in soil temperature results in loss of soil organic C (SOC), whereas doubling atmospheric CO_2 concentration causes an increase in SOC. The increase in air temperature causes soil respiration to increase, while it causes NPP to decrease. A decrease in precipitation causes both soil respiration and NPP to decrease. We calculated that the total SOC in Kalahari – Botswana, under IPCC historical climate scenario, is 0.3 Pg C in the top 20 cm, and estimated the rate of SOC loss at 0.34×10^{12} g C yr^{-1} and 0.63×10^{12} g C yr^{-1} under RCP2.6 and RCP8.5, respectively. We further estimated the total SOC in the top meter at 0.9 Pg C, and the rate of SOC loss at 1.1×10^{12} g C

yr^{-1} and 2.0 x 10^{12} g C yr^{-1} under RCP2.6 and RCP8.5, respectively. Our results indicate that drier sites are more vulnerable to climate change that wetter sites.

5.1 Introduction

Soils are an important part of the biosphere, and fundamental resource of life on Earth. Globally, soils contain about 1500 Pg of organic carbon (SOC) (1 Pg = 10^{15} g) in the top meter, and additional 900 Pg of inorganic C (SIC), compared to 600 and 730 Pg C in vegetation biomass and the atmosphere, respectively (Batjes, 1996; Eswaran et al., 1993; Kirschbaum, 2000; Lal, 2008; Schimel, 1995; Schlesinger and Bernhardt, 2013b). The SOC pool consists of highly active humus and relatively inert charcoal. It comprises a mixture of, i) plant and animal residues at various stages of decomposition, ii) substances synthesized microbiologically and/or chemically from the breakdown products, and iii) of the bodies of live and dead micro-organisms (Schnitzer, 1991). The SIC pool is made of elemental C and carbonate minerals such as calcite, dolomite and gypsum, and primary carbonates derived from the weathering of parent material (Lal, 2008). The importance of SOC sequestration is based on the assumption that enlargement of SOC reduces the concentration of atmospheric CO_2 (Ringius, 2002). Conversely, loss of SOC could rapidly increase atmospheric CO_2 and results in detrimental effects in biogeochemical process (Townsend et al., 1997). While soil, vegetation and atmosphere C pools are largely driven by climate, SOC sequestration is mainly controlled by a balance between C in plant residues returned to soil and that released into the atmosphere (Blanco-Canqui and Lal, 2004; Trumbore, 2009). At pedon and local scales, factors such as vegetation productivity and microbial activity control SOC sequestration, while at landscape to regional scales precipitation and temperature control soil C dynamics (White II et al., 2009).

Savannas are an important component of dryland ecosystems, and contain 15% of global SOC (Dintwe et al., 2014; Glenn et al., 1993; Grace et al., 2006; Jobbágy and Jackson, 2000; White II et al., 2009). However, SOC stock in the savannas is facing potential changes from anthropogenic-driven climate change. Global climate models predict that savannas will experience a decrease in mean annual precipitation (MAP) and an increase in mean annual temperature (MAT) by the end of the 21st century (IPCC 2013, Hartmann et al., 2013; Knapp et al., 2008; Shongwe et al., 2009). Further, the International Energy Agency reference scenario projected that CO_2 emissions into the atmosphere would increase by more than 60% between 2004 and 2030, a process that could accelerate there rate climate change (World Energy Outlook 2004, pg. 30). Because precipitation and temperature are the principal factors regulating SOC dynamics, any slight changes in these two factors could have significant impact in soil C sequestration, which could cause savannas to become a C sink or source (Lal, 2003, 2008).

Although it is well established that there is a strong link between climate change and C cycling in savannas (Lal, 2001), there is still lack of information on the magnitude and direction of the overall soil C balance. For instance, in southern African savannas, Dintwe et al. (2014) predicted that a decrease in precipitation would cause 14% loss in SOC by the end of the century. Cao et al. (2001) used CEVSA biogeochemical model to simulate SOC dynamics in African savannas in response to climate change. They concluded that plant production and SOC stocks would decrease, but the increasing atmospheric CO_2 might reverse the effect of climate change and lead to net C gain in vegetation and soils. Still in African savannas, Zeng and Neelin (2000) used the QTCM model and suggested that a decrease in precipitation could increase vegetation productivity, and ultimately SOC sequestration. With these contradictory analyses, it is clear that more work need to be done in order to assess and understand the potential impacts of climate change in SOC balance in savanna ecosystems (Bombelli et al., 2009; Ciais et al., 2011; Colwell et al., 2008). Because of their vast extent, drylands are considered to have great potential for SOC sequestration, a process that could mitigate or exacerbate the impacts of global climate change (Lal, 2001; Lal, 2003). Furthermore, the relatively stable savanna soils, compared to other ecosystems, and their current low SOC content could enhance their capacity to sequester and store carbon over a very long period of time (Lal, 2008).

A significant challenge to any fundamental understanding of SOC dynamics has been the lack of a suitable framework for investigating SOC at regional scales across meaningful climatic gradients without effects arising from differences in soil texture, elevation and other geophysical variables. In this study, we used the Century model to simulate SOC under future climatic conditions in the Kalahari savannas of southern Africa. With its homogenous soils, flat relief and strong north-south precipitation gradient, the Kalahari provides an ideal environment to study the impact of climate change on SOC dynamics. Because the structure of the Kalahari allows a space-for-time substitution (Dintwe et al., 2014), we selected the Kalahari as a representative of other drylands. Several studies have been conducted in the Kalahari to assess SOC content, below- and aboveground biomass, rooting pattern, soil respiration, fire regime as well as nutrients cycling (Bhattachan et al., 2012b; Dintwe et al., 2014; Makhado and Scholes, 2012; Meyer et al., 2013; O'Donnell et al., 2015; Okin et al., 2008; Thomas and Hoon, 2010; Thomas et al., 2011; Wang et al., 2012; Wang et al., 2009). However, very few studies have assessed the potential impacts of climate change in SOC dynamics in the Kalahari.

Our goal was assess the coupled effects MAP, MAT, soil temperature and atmospheric CO_2 in SOC dynamics. Several studies have suggested that terrestrial ecosystems are responding to climate change, particularly to changes in precipitation, temperature and atmospheric CO_2 (Drake et al., 1997; Hall et al., 2005), predominantly through the response of plants and soil microbes. Here, we used the Century model to assess temperature dependence of decomposition rates and the rate of C accumulation through the process of primary production.

5.2 Method and materials

5.2.1 Study sites

Soil organic carbon was simulated using Century model in the Kalahari savannas of southern Africa. The Kalahari Transect (KT) is one of the International Geosphere-Biosphere Program (IGBP) large scale terrestrial transects aimed at studying the effects of changes in climate, land use and vegetation dynamics (Koch et al., 1995). The Kalahari Basin is characterized by deep and homogenous sand that covers an area of ~2.5 million km^2

between latitudes 12 – 29 °S and longitude 14 – 28 °E (Thomas and Shaw, 1991a). The soils in the KT are slightly acidic, ~90% sand, have low organic C and total nitrogen (TN) content (Dintwe et al., 2014; Wang et al., 2007b). The Kalahari falls within a steep north-south precipitation gradient, with south being the driest and north being the wettest (Batisani and Yarnal, 2010; Nicholson and Entekhabi, 1987; Tyson and Crimp, 1998). The vegetation structure in the KT is firmly tied to mean annual precipitation, MAP (Caylor and Shugart, 2006; Caylor et al., 2003). In the north the vegetation is dominated by woody broad-leaf C_3 plants and perennial C_4 grasses, while in the south the dominant species are annual C_4 grasses with sparse fine-leaf woody C_3 species (Bhattachan et al., 2012a; Leistner, 1967; Meyer et al., 2013; Ringrose et al., 2003). The lack of relief, steep moisture gradient and sandy soils make the Kalahari an ideal environment to assess the effects of climate change (particularly precipitation and temperature) on carbon cycling with minimal background effects from abiotic and geophysical features like soil texture and relief.

We selected four study sites along the Kalahari north-south precipitation gradient to perform the analysis (Figure 1). These are the sites where we have previously assessed soil C content, below- and aboveground biomass, rooting pattern as well as nutrients cycling (Bhattachan et al., 2012b; Dintwe et al., 2014; Meyer et al., 2013; O'Donnell et al., 2015; Okin et al., 2008; Wang et al., 2012; Wang et al., 2009).

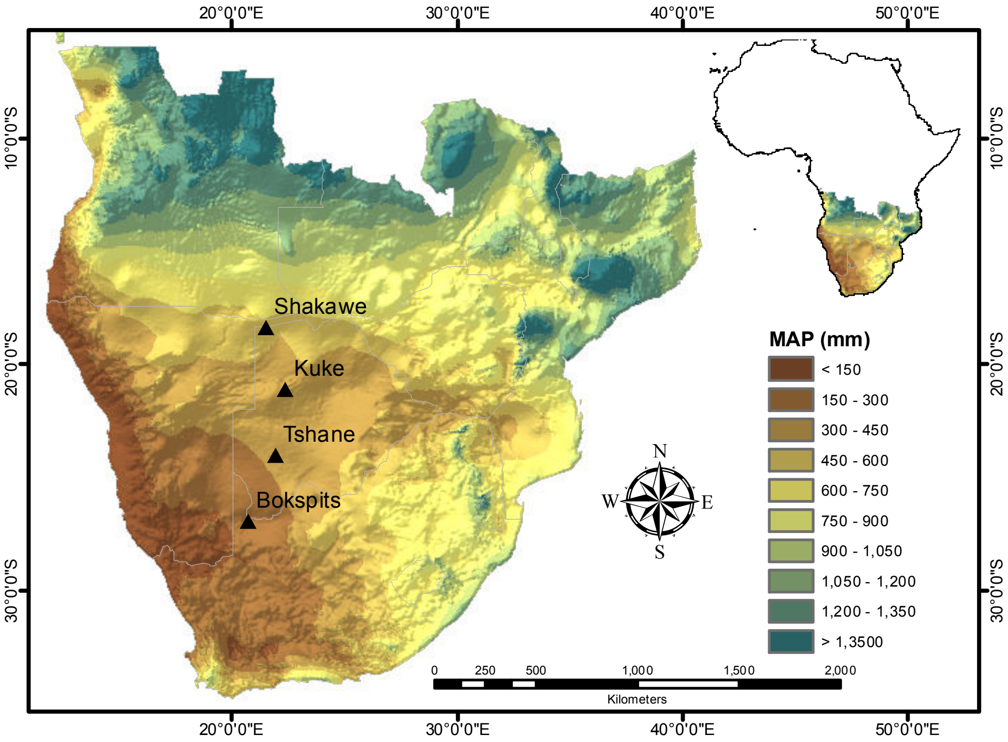

Figure 5-1. The study sites in the Kalahari precipitation gradient. The southern portion receives the lowest mean annual precipitation (MAP), whereas the northern portion receives the highest MAP.

5.2.2 Field measurement

The protocols for collecting soil samples in the four study sites, analyzing SOC, and the total nitrogen (TN) have been reported by Dintwe et al. (2014).

5.2.2.1 Model parameterization and execution

The Century model uses a combined mechanistic and regression approach to simulate terrestrial C, N, P and S fluxes (Parton et al., 2010; Parton et al., 1994). It requires monthly precipitation, minimum and maximum temperature, initial C content and soil physical properties. We computed mean monthly precipitation and temperature for each site using ensemble-mean monthly data output from all the Coupled Model Intercomparison Project Phase 5 (CMIP5) models (Meehl et al., 2000) (Figure 2). The ensemble-mean CMIP5 data is available in two time frames: historical and future projections. Historical data covers the time period from 1850 through 2005, whereas future projections covered from 2006 through 2300, though we ran our simulations only through 2200. In cases where a CMIP5 model had more than one run per simulation, we only used the first run. For future climatic conditions, we used both RCP2.6 and RCP8.5 climate scenarios.

To parameterize the Century model, we used dry deciduous C_3 trees and annual C_4 grasses to represent the vegetation composition in the Kalahari (Bird et al., 2004; Setshogo and Venter, 2003; Weare and Yalala, 1971). Soil texture data was obtained from Bhattachan et al. (2012b), while bulk density and pH were derived from (Wang et al., 2007b) (Table 1). Because there was no readily available data on soil C pools (active, slow and passive) to parameterize Century model, we used an indirect method to estimate the initial SOC pools; we ran Century stochastically, using historical CMIP5 results to characterize climate variables, and simulated the SOC pools for 6000 years, until all pools were at equilibrium simulation (Carvalho Leite et al., 2004). The simulated SOC pool values were then used as input and parameter variables for additional runs.

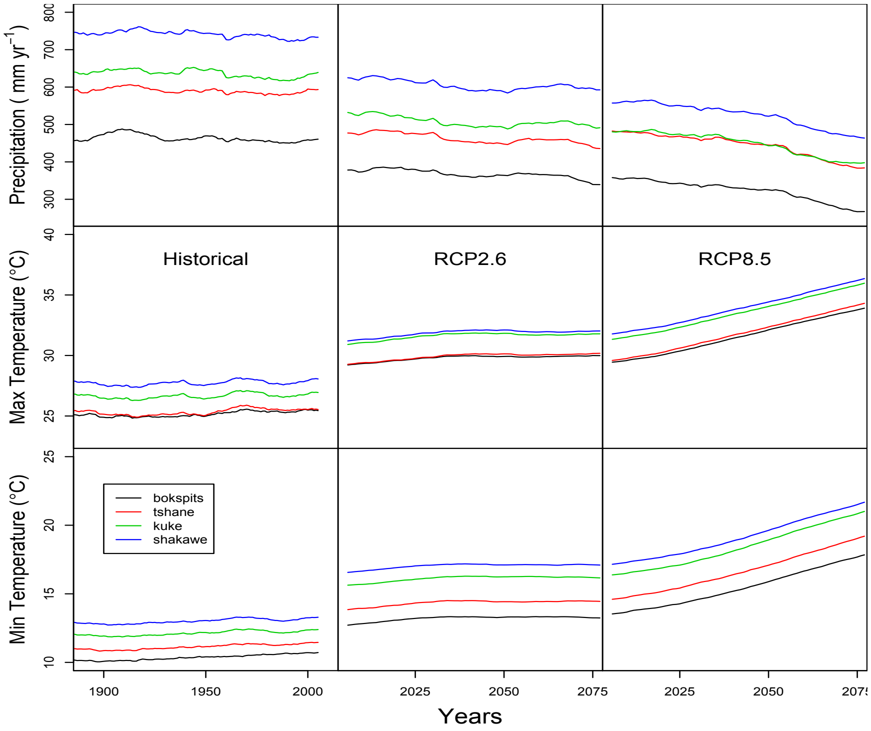

Figure 5-2. The CMIP5 climate data used in the simulations

In each site, we ran simulations using historical climate to assess the effects of double CO_2, soil temperature increase and the combined effects of the two variables in SOC. To assess the response of SOC to soil temperature, we arbitrarily increased the soil temperature by 2°C. All the changes were set to happen in 2025.

Table 5-1. Model parameterization. The initial carbon pools and lignin were obtained by running the model stochastically for 3000 years, and used the output as initial parameters. For initial tree and grass, we used C_3 and C_4 plants respectively.

Site	Geographical location		Texture	Bulk Density	Soil pH
	Latitude	Logitude	(%sand, %silt, %clay)	(g cm^{-3})	
Bokspits	-26.8442	20.6983	96.1, 3.1, 0.8	1.43	5.50
Tshane	-21.0169	21.8689	95.0, 4.1, 0.9	1.44	6.23
Kuke	-20.9767	22.4800	96.0, 1.0, 3.0	1.45	6.14
Shakawe	-18.3642	21.8419	95.0, 4.0, 1.0	1.49	5.02

We further assessed the effects of precipitation and ambient temperature change in SOC under RCP2.6 and RCP8.5 scenarios (Representative Concentration Pathway, RCP). For instance, to assess the effect of precipitation, we started the simulation in 4000 BC, using historical precipitation and temperature, and running stochastically in order to reach equilibrium. In 1850, the model switched from running stochastically to using the actual historical weather data through the 2005. In 2006, the model switched from historical precipitation to future precipitation, and simulated stochastically through 2200. We double CO_2 and increased the soil temperature in 2025. Under RCP2.6 and RCP8.5 scenarios, soil warming at 1 m depth is predicted to almost keep pace with ambient temperature, with about 10 less warming in soil than air, globally (Phillips et al., 2014). Other studies predict that soil temperature will increase by up to about 5-6°C at the end of the 21st century, depending on the emission scenario (Frazer, 2009; Phillips et al., 2014). We therefore, increased the soil temperature by 10% of the air temperature in each RCP climate scenario.

We assessed the combined effects of precipitation and temperature using the above-described algorithm, except that in 2006 the model used future precipitation and temperature.

Because Century simulates SOC to a depth of 20 cm, we calculated total SOC content at 20 cm using field observed values, which enabled to make direct comparison between field data and simulated values (Kelly et al., 1997). To this end, we integrated the SOC curves provided in Dintwe et al. (2014)from 0-20 cm. For each site we selected initial trees and grasses such that at equilibrium, under historical climate conditions, Century yielded SOC values similar to the adjusted field values (Kelly et al., 1997).

5.3 Results and Discussion

5.3.1 Ensemble mean of historical and future climate scenario

Bokspits, the driest site, has the lowest historical mean annual precipitation (MAP), whereas Shakawe (wettest) has the highest MAP (Table 2). Similarly, under RCP2.6 and RCP8.5 scenarios, the MAP increases from Bokspits, Tshane, Kuke through Shakawe, respectively. In all the sites, historical MAP is higher than RCP2.6 precipitation, which in turn is higher than in RCP8.5 scenario.

Table 5-2. Mean annual precipitation, minimum temperature and maximum temperature derived from CMIP5 projections. The data was used to parameterize the model.

Site	CMIP5 climate scenario	Precipitation (mm year^{-1})	Minimum Temperature °C	Maximum Temperature °C
Bokspits	Historical (1850 – 2005)	463.2 ± 9.9	10.4 ± 0.2	25.2 ± 0.2
Tshane		590.1 ± 7.1	11.1 ± 0.2	25.4 ± 0.3
Kuke		636.4 ± 10.1	12.1 ± 0.2	26.7 ± 0.2
Shakawe		741.3 ± 9.0	13.0 ± 0.2	27.7 ± 0.2
Bokspits	RCP2.6 (2006 – 2300)	367.8 ± 11.3	13.2 ± 0.2	29.8 ± 0.2
Tshane		462.8 ± 13.3	14.3 ± 0.2	29.9 ± 0.3
Kuke		507.6 ± 13.3	16.1 ± 0.2	31.6 ± 0.3
Shakawe		605.4 ± 12.9	17.0 ± 0.2	31.8 ± 0.3
Bokspits	RCP8.5 (2006 – 2300)	323.3 ± 27.3	15.4 ± 1.3	31.5 ± 1.4
Tshane		444.5 ± 30.7	16.6 ± 1.4	31.8 ± 1.4
Kuke		448.8 ± 30.9	18.4 ± 1.4	33.5 ± 1.4
Shakawe		525.0 ± 32.0	19.1 ± 1.4	33.9 ± 1.4

In all the sites, the historical mean air temperature is the lowest, followed by RCP2.6 and finally RCP8.5 (Table 2). Bokspits has the lowest mean temperatures, whereas Shakawe has the highest mean temperatures under all climate scenarios. The mean minimum temperature and maximum temperature increase with an increase in MAP (Table 2).

5.3.2 Simulated C fluxes using historical climate scenario

5.3.2.1 Soil organic carbon

Bokspits, the driest site, has the lowest SOC content whereas Shakawe has the highest (Table 3). The net primary production (NPP) is highest in Shakawe, followed by Tshane and Kuke, respectively. Bokspits has the lowest NPP of 80.5 g C m^{-2}. Although Thane has lower MAP than Kuke, field measurements show that Tshane has more SOC that Kuke. Therefore, we parameterized the model such that the output results match field measurements.

Table 5-3. Soil Organic carbon, Net Primary Production and soil respiration estimated using CMIP5 historical climate data.

Site	Adjusted Field Observation (0-20 cm) (g C m^{-2})	Modeled SOC (g C m^{-2})	Net Primary Production (g C m^{-2} $year^{-1}$)	Soil Respiration (g C m^{-2} $year^{-1}$)
Bokspits	336.0	361.0 ± 0.3	80.7 ± 0.1	48.0 ± 0.1
Tshane	601.2	607.2 ± 0.2	209.1 ± 0.3	119.5 ± 0.1
Kuke	467.3	472.7 ± 0.1	177.5 ± 0.7	101.1 ± 0.3
Shakawe	649.7	653.5 ± 0.2	251.3 ± 0.3	140.1 ± 0.2

Similarly, simulated soil respiration is highest in Shakawe, followed by Tshane and Kuke, respectively. Soil respiration and NPP are three-fold lower than values in Shakawe, whereas MAP in Bokspits is twice lower than in Shakawe.

5.3.2.2 Soil respiration

Our simulated soil respiration is of the same order of magnitude with field measurements reported by Wang et al. (2007b). They reported 0.23 to 0.74 g CO_2 m^{-2} h^{-1} efflux in dry soils in the Kalahari, and that the fluxes increased 10-fold after wetting. For comparison, we converted hourly fluxes to yearly fluxes, and also converted from CO_2 to C. We assume that respiration takes place during the day (12 hours) when the temperatures are warm. The converted values from Wang et al. (2007b) are 275 to 884 g C m^{-2} yr^{-1}. Similarly, our simulated values are of the same order of magnitude with those reported by Fan et al. (2015), where they estimated soil respiration in South Africa's savanna ecosystem to range between 179 and 323 g CO_2 m^{-2} h^{-1}. We further calculated that other studies in the Kalahari reported much higher soil respiration, ranging between 1791 and 7048 g C m^{-2} yr^{-1} (Thomas and Hoon, 2010; Thomas et al., 2011).

In the Brazilian Cerrados soil respiration during wet season was estimated between 263 and 394 g C m^{-2} yr^{-1} whereas, dry season it was estimated at 2390 g C m^{-2} yr^{-1} (Hill and Hanan, 2010; Rocha et al., 2002). In Australian savannas, Chen et al. (2002) estimated soil respiration to range between 227 to 681 g C m^{-2} yr^{-1} during the wet season and 1433 to 4300 g C m^{-2} yr^{-1} during the dry season. The difference in soil respiration between sites is likely due to precipitation, which in turn, regulates soil C input and decomposition. In the Brazilian Cerrados, the MAP ranges between 600 and 2200 mm, whereas in Australian savannas MAP ranges from 500 to 1200 mm (Bustamante and Ferreira, 2010; Hutley et al., 2011). The SOC in the Cerrados and Australia savannas is estimated at 25700 g C m^{-2} and 15100 g C m^{-2}, respectively (Castro and A, 1995; Chen et al., 2003). In the Kalahari-

Botswana, the driest and wettest sites have 1397 g C m^{-2} and 1982 g C m^{-2}, respectively, with MAP between 200 and 540 (Dintwe et al., 2014).

5.3.2.3 Net primary productivity

The NPP increases with MAP, and are consistent with results from other studies, where there is a positive correlation between vegetation cover and precipitation in tropical grasslands and savannas (Hall et al., 1995). These results suggest a water limitation on productivity (Caylor et al., 2004; Caylor et al., 2003; Sankaran et al., 2005; Scanlon et al., 2002). Similarly, soil respiration and SOC increased with increase in precipitation, highlighting the importance of precipitation in biogeochemical processes such as decomposition, except for Kuke.

Our simulated NPP values range between 80.7 g C m^{-2} yr^{-1} at the driest site and 251 g C m^{-2} yr^{-1} at the wettest site. These results are consistent wit those of Woodward and Lomas (2004), who used the Sheffield Dynamic Global Vegetation Model (SDCVM) to simulate NPP along the Kalahari precipitation gradient. Their results showed that NPP increased with precipitation, with 245 g C m^{-2} yr^{-1} and 409 g C m^{-2} yr^{-1} at the driest and wettest site, respectively. Their driest site was Tshane, while their wettest site was Mongu (878 mm yr^{-1}). Caylor and Shugart (2004) in comparison, simulated NPP in Tshane and Pandamatenga (~698 mm), and estimated NPP to be 710 g C m^{-2} yr^{-1} and 1280 g C m^{-2} yr^{-1}, respectively, approximately three times what Century predicted.

5.3.3 The effect of CO_2 and soil temperature on SOC pools

5.3.3.1 Increased soil temperature

Increasing soil temperature by 2°C results in a net loss in SOC in all the sites (Table 4). The two driest sites lose about 8% of the SOC, whereas the two wettest sites lose about 6% SOC. Similarly, the combined effect of increased soil temperature and doubled atmospheric CO_2 results in a decrease in soil C in all the sites, with the two driest sites each losing about 7% SOC.

However, the effect of temperature increase is more pronounced than the combined effect of temperature and doubled CO_2. One of the reasons why SOC decreased when soil temperature increases is that plants experience high evapotranspiration, and counteract it by reducing stomatal conductance. Closing of the stomata leads to low rates of CO_2 fixation, which in turn results in low NPP and soil C sequestration.

Table 5-4. Modeling the effects CO_2 and soil temperature on SOC using CMIP5 historical climate data. The CO_2 and soil temperature changed in year 2025.

Site	Adjusted Field Observation (0 – 20 cm) (g C m^{-2})	Soil Organic Carbon (g C m^{-2})				
		1971 - 2005	2100 – 2150			
		Historical climatic condition	Historical CO_2 & Soil Temperature	Soil Temperature (+2°C)	Double CO_2	Double CO_2 Soil (+2°C)
Bokspits	336.0	361.0 ± 0.3	361.4 ± 0.2	332.9 ± 1.6	365.1 ± 0.1	336.6 ± 1.5
Tshane	601.2	607.2 ± 0.2	607.5 ± 0.4	561.8 ± 1.6	610.6 ± 0.2	565.1 ± 1.4
Kuke	467.3	472.7 ± 0.1	472.9 ± 0.3	445.6 ± 1.0	481.1 ± 0.4	452.0 ± 0.6
Shakawe	649.7	653.5 ± 0.2	653.9 ± 0.1	617.2 ± 2.7	656.7 ± 0.1	614.6 ± 1.5

5.3.3.2 Doubled CO2

Doubling atmospheric CO_2 results in an increase in SOC in all the sites, with Kuke experiencing the highest increase of 2% (Table 4). Ojima et al. (1993) used Century model to simulate SOC in savannas, and found that doubled CO_2 increased NPP, resulting in higher soil C sequestration and SOC content. Several studies suggested that elevated CO_2 reduces stomatal conductance and transpiration, and improves water use efficiency (WUE) (Bazzaz, 1990; Drake et al., 1997; Woodward and Bazzaz, 1988). Water use efficiency, defined as the amount of water lost during the fixation of CO_2 in photosynthesis (Lambers et al., 2008), differs between fine- and broad leaved trees. In the Kalahari, thin-leafed C_3 shrubs are the dominant species in the driest site, whereas broad-leafed C_3 trees are the dominant species in the wettest site. It is possible that the C_3 plants in the dry sites of the Kalahari experience high evapotranspiration, and in response, reduce their stomatal conductance to minimize water loss. Several studies have shown that when exposed to elevated CO_2, plants, particularly C_3 responded by closing stomata (Ainsworth and Rogers, 2007; Dawson et al., 2002; Diefendorf et al., 2010; Farquhar and Richards, 1984; Farquhar et al., 1989; Friend and Cox, 1995). The grasses, which are mainly C_4 plants, do not respond significantly to an increase in atmospheric CO_2 because they evolved under low atmospheric CO_2 conditions, and are adapted to low CO_2 conditions (Cerling et al., 1997; Cerling et al., 1993; Ehleringer et al., 1997; Quade and Cerling, 1995; Ward, 2005).

Although reducing stomatal conductance improves WUE, it causes the plants to undergo C starvation and results in low NPP. However, as atmospheric CO_2 increases, plants respond by fixation more CO_2 without increasing stomatal aperture. Considering the physiological functions of C_3 and C_4 plants in the Kalahari, we concluded that SOC increases when atmospheric CO_2 increases because C_3 plants respond to the elevated CO_2, by fixing more CO_2 than they do at low CO_2 concentrations.

In the context of climate change, our results show that C_3 plants will benefit from elevated atmospheric CO_2, but the increase in soil temperature will counteract the effects of elevated CO_2. Because C_4 plants do not respond significantly to elevated CO_2, and are adapted to warm condition, overall vegetation (C_3 and C_4) response will be a slight increase in NPP, and soil C sequestration under increased soil temperature and atmospheric CO_2 concentration.

5.3.4 The effect of precipitation and temperature on SOC pools

In all our results we find that temperature and precipitation have equal impact on SOC stocks. This is consistent with field measurements, where it was reported that variations of precipitation and temperature are closely related throughout physical and biogeochemical processes (Wu et al., 2013).

In the RCP2.6 scenario, our results show that temperature and precipitation each causes SOC to decrease by about 5%, with a combined effect of 10% loss in SOC (Table 5). Ojima et al. (1993) used Century to simulate SOC in semi-arid ecosystems under climate change scenario, and found that SOC decreased by up to 14%. However, we cannot directly compare our results with theirs because they did not specify which climate scenario they used. They also did not simulate the effect of doubled CO_2, which we included in our simulations. In our opinion, doubled CO_2 should be included in the simulations because the current climate change is primarily a consequence of elevated atmospheric CO_2 (IPCC, 2013).

Our results in the RCP8.5 indicate that temperature and precipitation each results in 7% decrease in SOC. The highest loss in SOC occurs in the two extreme sites, the wettest and the driest sites. The combined effect of temperature and precipitation results in 18% loss in SOC, with the driest site experiencing the highest C loss of 22%.

Table 5-5. Modeling the effects of precipitation and temperature on SOC under Historical, RCP2.6 and RCP8.5 climate scenarios

Site	Soil Organic carbon (g C m^{-2})						
	1971-2005	2100-2150					
	Historical climate condition	Historical Precipitation		Historical Temperature		RCP2.6 Climate scenario	RCP8.5 Climate scenario
		RCP2.6 Temperature	RCP8.5 Temperature	RCP2.6 Precipitation	RCP8.5 Precipitation		
Bokspits	361.0 ± 0.3	340.5 ± 1.5	328.3 ± 1.9	351.7 ± 1.8	349.4 ± 2.7	313.6 ± 2.8	279.5 ± 3.3
Tshane	607.4 ± 0.3	578.1 ± 3.1	563.0 ± 4.3	544.1 ± 1.6	513.5 ± 1.9	538.6 ± 4.4	499.2 ± 5.0
Kuke	472.9 ± 0.3	460.7 ± 2.7	453.4 ± 3.4	445.0 ± 1.8	437.5 ± 2.4	439.7 ± 4.9	398.0 ± 4.6
Shakawe	653.8 ± 0.2	607.9 ± 2.0	602.6 ± 3.2	623.4 ± 2.8	632.5 ± 4.9	594.9 ± 5.3	548.0 ± 7.5

We found that the effect of temperature on SOC is more pronounced in the two extreme sites than in the intermediates sites in all the climate scenarios. Conversely, the effect of precipitation is more pronounced in the intermediate sites than in the extreme sites, in all the climate scenarios. To investigate the driving factors behind these patterns we assessed the effect of temperature and precipitation on soil respiration and NPP of C_3 and C_4 plants.

5.3.5 The effect of precipitation and temperature on soil respiration and NPP

Ensemble-average future temperature increases cause an increase in soil respiration and NPP for both C_3 and C_4 plants, whereas ensemble-average future precipitation decreases result in a decrease in soil respiration and NPP (Table 6). The combined future temperature and precipitation causes soil respiration and NPP to decrease. The RCP8.5 climate scenario has more effect that the RCP2.6 scenario.

5.3.5.1 Soil respiration

Simulations using a combination of historical precipitation and future temperature result in an increase in soil respiration in all the sites, in RCP2.6 and RCP8.5 scenarios (Table 6). Kuke experiences the highest average increase of 7%, whereas Shakawe has the lowest increase 4%.

Simulating SOC using a combination of historical temperature and future precipitation, our results show a decrease in soil respiration in all the sites (Table 6). The two intermediates sites experience the highest decrease in soil respiration; 14% and 10% in Tshane and Kuke, respectively, while Bokspits experiences a 6% decrease. The decreases in all the sites are more pronounced in RCP8.5 scenario. These results are consistent with results from other studies, where an increase in air temperature causes an increase in soil respiration (Curiel et al., 2004; Hashimoto, 2005; Thomas et al., 2011; Zhou et al., 2009). The reason why soil respiration decreases under drier conditions (low precipitation) could be that the soils become too dry, thus inhibit soil microbes to carry out their physiological activities effectively. Our hypothesis is supported by the results from combined effect of air temperature and precipitation, in which there is overall decrease in soil respiration. The magnitude, at which soil respiration decreases in response to the combined effect of temperature and precipitation, is high in the driest site and low in the wettest site, 16% and 9%, respectively under RCP2.6 emission scenario.

Table 5-6. Modeling the effects of precipitation and temperature on C dynamics under Historical, RCP2.6 and RCP8.5 climate scenarios

Site	Output	Carbon dynamics (g C m^{-2} year^{-1})						
		1971-2005	2100 - 2150					
		Historical climate condition	Historical Precipitation		Historical Temperature		RCP2.6 Climate scenario	RCP8.5 Climate scenario
			RCP2.6 Temperature	RCP8.5 Temperature	RCP2.6 Precipitation	RCP8.5 Precipitation		
Bokspits	Grass-NPP	42.8 ± 0.1	43.9 ± 0.0	44.2 ± 0.0	39.3 ± 0.3	37.5 ± 0.5	35.9 ± 0.3	30.1 ± 0.5
	Tree-NPP	37.9 ± 0.1	39.4 ± 0.1	39.7 ± 0.1	34.9 ± 0.5	33.3 ± 0.9	31.9 ± 0.5	28.8 ± 0.8
	Total-NPP	80.7 ± 0.1	83.3 ± 0.1	83.9 ± 0.1	74.2 ± 0.7	70.8 ± 1.2	66.9 ± 0.7	56.0 ± 1.0
	Respiration	48.0 ± 0.1	50.4 ± 0.0	50.9 ± 0.1	45.1 ± 0.4	43.4 ± 0.7	41.2 ± 0.4	34.8 ± 0.6
Tshane	Grass-NPP	102.8 ± 0.2	104.8 ± 0.1	105.9 ± 0.1	86.5 ± 1.3	83.7 ± 1.5	85.5 ± 1.3	79.7 ± 1.5
	Tree-NPP	106.3 ± 0.3	111.8 ± 0.1	112.9 ± 0.1	89.6 ± 2.2	86.6 ± 2.5	76.1 ± 2.1	71.1 ± 2.4
	Total-NPP	209.1 ± 0.3	216.6 ± 0.1	218.8 ± 0.1	176.1 ± 3	170.3 ± 3.4	173.7 ± 2.9	159.6 ± 3.3
	Respiration	119.5 ± 0.1	125.4 ± 0.2	127.1 ± 0.2	102.5 ± 1.6	99.3 ± 1.8	102.2 ± 1.5	94.2 ± 1.7
Kuke	Grass-NPP	89.9 ± 0.3	92.3 ± 0.2	92.9 ± 0.2	79.1 ± 0.9	74.3 ± 1.2	77.5 ± 0.9	65.4 ± 1.2
	Tree-NPP	87.6 ± 0.5	92.8 ± 0.3	93.5 ± 0.4	78.5 ± 1.5	73.1 ± 1.9	71.1 ± 1.5	62.6 ± 1.9
	Total-NPP	177.5 ± 0.7	185.1 ± 0.4	186.4 ± 0.5	157.6 ± 2	147.4 ± 2.6	153.5 ± 2	128.0 ± 2.5
	Respiration	101.1 ± 0.3	107.3 ± 0.1	108.4 ± 0.2	91.5 ± 1.1	86.1 ± 1.5	90.1 ± 1.0	75.7 ± 1.4
Shakawe	Grass-NPP	123.9 ± 0.2	125.7 ± 0.1	126.4 ± 0.1	112.6 ± 0.9	106.4 ± 1.4	109.2 ± 0.9	91.3 ± 1.3
	Tree-NPP	127.4 ± 0.3	131.4 ± 0.2	132.1 ± 0.2	116.8 ± 1.5	109.9 ± 2.3	109.4 ± 1.5	88.7 ± 2.2
	Total-NPP	251.3 ± 0.3	257.1 ± 0.2	258.5 ± 0.3	229.4 ± 2.0	216.3 ± 3.1	220.9 ± 2.0	180.0 ± 2.8
	Respiration	140.1 ± 0.2	144.6 ± 0.1	145.9 ± 0.1	129.9 ± 1.1	123.6 ± 1.6	126.3 ± 1.0	104.6 ± 1.5

5.3.5.2 NPP for C3 and C4 plant species

A combination of future temperature increases and historical precipitation causes NPP of C_3 and C_4 to increase, whereas a combination of future precipitation and historical temperature causes NPP to decrease (Table 6). The effect of temperature in NPP is twice as high in C_3 plants as in C_4 plants, consistent with the physiology of these different plants (Bazzaz, 1990; Caylor and Shugart, 2004; Ehleringer et al., 1997). Although the effect of precipitation in NPP of C_4 plants has the same magnitude as in C_3 plants, the effect is more pronounced in C_4 plants. The combined effect of temperature and precipitation results in a decrease in NPP in C_3 and C_4 plants. Similarly, the combined effect of temperature and precipitation is more pronounced in C_3 plants than in C_4 plants, except in the driest site (Bokspits) where NPP of C_4 was much lower than in C_3 plants. In average, NPP of C_3 and C_4 decreases by 14% and 19%, respectively, under RCP2.6 climate scenario. Under RCP8.5, NPP decreases by 26% and 29% in C_3 and C_4 plants, respectively.

Our results indicate that C_3 plants are more sensitive to climate change, particularly temperature, than C_4 plants. From ecological point of view, these results are of significant importance. For instance, Hély et al. (2006) used LPJ-GUESS ecological model and suggests that deciduous vegetation (C_3 plants) in Africa is sensitive to small changes in both the amount and seasonality of precipitation. Monserud et al. (1993) used BUYKO model and predicted vegetation composition change in the tropics and subtropics as a results of climate change, and that the magnitude of change would be determined by the magnitude of precipitation and temperature change. Because C_3 plants are the dominant plant type in the Kalahari, and stay alive throughout the year, as opposed to C_4 annual grasses, climate change will have significant impact in C fluxes in the Kalahari, and drylands in general. Modification of vegetation composition could results in alterations in NPP, and could also alter soil respiration because different plants have different physiological processes. For example, invasion of drylands by bush encroachment species could soil fertility by increasing soil total nitrogen (TN), and enhance microbial activity. Recent studies in the Kalahari reported invasion of non-native plants species such as *Prosopis spp* and expansion of native shrubs such as *Acacia spp* (Moleele et al., 2002; Muzila et al., 2011; Wiegand et al., 2005). Prosopis spp are commonly deep-rooted, evergreen, nitrogen-fixing plants (Archer, 1995; Simmons et al., 2008), whereas *Acacia spp* are commonly shallow rooted, dry deciduous plants, some of which are though to fix nitrogen (Brockwell et al., 2005; Githae et al., 2013; Raddad et al., 2005).

Bush encroachment species have also been reported to promote establishment of biological soil crust (BSC) by protecting them under canopy (Berkeley et al., 2005; Thomas and Dougill, 2007). The establishment of nitrogen-fixing BSC under bush canopies could enhance the competitive advantage of bush encroachment species and lead to further encroachment (Dougill and Thomas, 2004), which would alter SOC dynamics.

Changes in vegetation composition could also alter fire regime, a process that would ultimately alter C fluxes. Fire, when the burn, they convert biomass in to charcoal, ash, CO_2 and other products. The ash, which is usually deposited locally act a fertilizer and can promote further growth of fire prone species, resulting in a highly modified landscape.

5.3.6 Implication of climate change in the total soil C pools in the Kalahari

To evaluate the potential impact of climate change in SOC pools in the Kalahari, we assumed MAP as an indicator for SOC content in the sub-region. Our analysis shows that CMIP5 historical precipitation and simulated SOC (20 cm) have parabolic relationship:

$$SOC(g\ m^{-2}) = -1.5 \bullet\ 10^{-3}x^2 + 2.7x - 564 \qquad \text{(Equation 1)}$$

We also find that field adjusted SOC and the respective MAP have parabolic relationship:

$$SOC(g\ m^{-2}) = -7.6 \bullet\ 10^{-3}x^2 + 5.6x - 400 \qquad \text{(Equation 2)}$$

where x is mean annual precipitation.

Using Equation 1 to estimate SOC, we calculated the Kalahari – Botswana (i.e. the area inside Botswana underlain by Kalahari Sands) contains about 0.3 Pg C in the top 20 cm. When we used adjusted field measurements, Equation 2, our results indicate that Kalahari-Botswana contains 0.2 Pg C in the top 20 cm. The reason why the total simulated SOC is higher than adjusted SOC is because CMIP5 precipitation is at least 200 mm higher than field measured precipitation. At 20 cm depth, we calculated that historical SOC would decrease to 0.27 Pg C and 0.24 Pg C, under RCP2.6 and RCP8.5 respectively, by the end of the century. This translates to a loss of 0.34 x 10^{12} g C yr^{-1} and 0.63 x 10^{12} g C yr^{-1} under RCP2.6 and RCP8.5, respectively.

Dintwe et al. (2014) reported that Kalahari-Botswana contains 0.9 Pg C in the top one meter. We used this estimate to assess the magnitude of SOC loss due to climate change, assuming uniform warming throughout the soil profile. Recent studies have shown that soil warming at 1 m depth is almost equivalent to warming at 1 cm depth, indicating vulnerability of deep soil carbon pools (Phillips et al., 2014). Because our analysis indicated that SOC would decrease by 10.1% and 18.0% under RCP2.6 and RCP8.5, respectively, we calculated that SOC content would decrease to 0.81 Pg C and 0.73 Pg C, under RCP2.6 and RCP8.5 respectively (Figure 3), resulting in a net loss of 0.09 Pg C and 0.17 Pg C to the atmosphere over the next 85 years. This translated to an average of 1.1 x 10^{12} g C yr^{-1} and 2.0 x 10^{12} g C yr^{-1} loss under RCP2.6 and RCP8.5, respectively. In comparison, global emission of C due to fires is estimated at 2.6 Pg C yr^{-1}, with 0.5 Pg C yr^{-1} of the emission is associated with anthropogenic deforestation (van Der Werf et al., 2003; van der Werf et al., 2010). Although our SOC losses are three orders of magnitude lower than global C emission due to fires, it is important to point out that our results represent a small area of 530000 km^2. The Kalahari savannas cover about 2 million km^2, while global savannas cover 16 million km^2 (Scholes and Archer, 1997; Scholes and Hall, 1996; Thomas and Shaw, 1993). Therefore, at global scale, climate change is likely to cause soils in the savannas to release more C into the atmosphere than C emissions from fires.

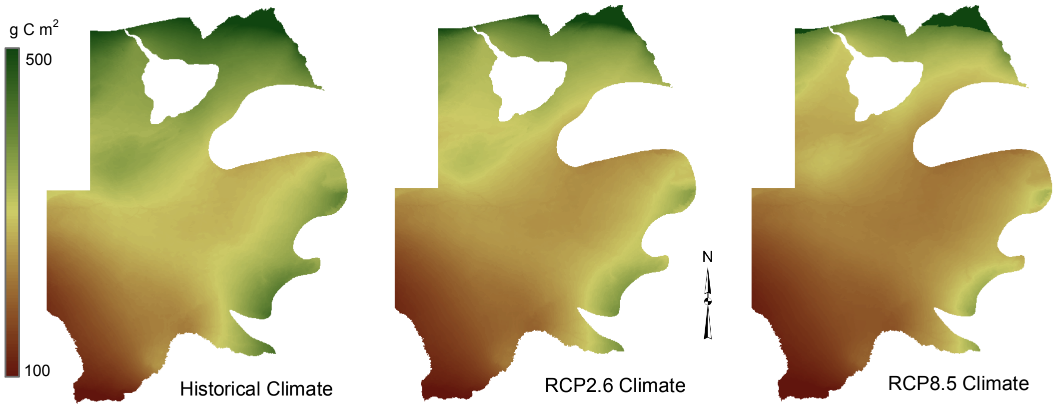

Figure 5-3. The impact of climate change on soil organic carbon in the Kalahari – Botswana. Under RCP2.6 and RCP8.5 climate scenarios, the SOC content would decrease by 10.1% and 18.0%, respectively.

Our current results are consistent with our previous work where we estimated that soils in the Kalahari could lose up to about 7% and 14% SOC under RCP4.5 and RCP8.5 climate scenario. Similarly, Hoffman and Vogel (2008) suggested that a 10% decrease in MAP could have severe consequences in biogeochemical processes in African savanna ecosystems, particularly the driest sites.

Despite these estimates, there is still lot of climate change-related questions that need to be addressed. For example, how would fire regime and herbivory respond to climate change, and affect the overall C balance. Another important component is the anthropogenic activity such as land use change and land use pressure. With the growing human population, and the predicted drier-warm climate, land use is likely to become more intense thus affecting C balance.

5.4 Conclusion

We have demonstrated, through model simulation, how C fluxes in the Kalahari would be affected by climate change. An increase in atmospheric CO_2 would enhance plant productivity, particularly C_3 plants. However, soil temperature increase would counteract the effects of CO_2 by enhancing soil C loss through microbial respiration.

We have also shown that temperature and precipitation each have equal contribution to maintaining SOC stocks, and that C fluxes respond to the overall sum of the effect of temperature and precipitation change. Therefore, the impact of climate change would be more severe under RCP8.5 than under RCP2.6 climate scenario.

The Kalahari is likely to become C source as climate becomes warmer and drier. We estimated that the soils in the Kalahari would lose about 10% and 18% SOC in the top one meter under RCP2.6 and RCP8.5, respectively.

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Chapter 6: Discussion and Conclusion

6.1 Climate change in drylands

Drylands are drought-prone biomes in which precipitation is less than the potential evapotranspiration for the whole year, or for the most part of it (D'Odorico and Porporato, 2006; Glenn et al., 1993; Lal, 2003). They include grasslands, shrublands, savannas, Mediterranean and deserts. Drylands support more than 2 billion (35%) of the world population, of which 90% live in developing countries (D’Odorico et al., 2013; MEA, 2005).

Dryland ecosystems are vulnerable to climate change, and would be affected by directional changes in climate and land use (Nicholson, 2001; Nicholson and Kim, 1997). More than 70% of global climate models (GCM) predict that mean annual precipitation (MAP) in drylands, particularly savannas, will decrease by about 10 - 25% and 15 - 45% under Representative Concentration Pathway 2.6 (RCP2.6) and RCP8.5 climate scenarios, respectively, by 2100 while mean annual temperature (MAT) will increase by about 1.5 - 3 °C and >4 °C under RCP2.6 and RCP8.5 climate scenarios, respectively (IPCC 2013, Hartmann et al., 2013; Knapp et al., 2008; Shongwe et al., 2009).

6.2 Savanna structure

Biogeochemical processes in drylands are not well understood particularly in the savannas. The lack of understanding makes it difficult to assess potential impacts of climate change. Savannas, as representative of drylands, have complex structure and functions. In this analysis, we have shown, for the first time, that belowground interaction is more complex that previously thought. We showed that the commonly perceived two layer root model, in which there is no competition for water between trees and grasses, does not explain why removal of trees results in grasses expanding, and vice versa. In light of results from stable carbon analysis, and results from other studies, we concluded that belowground interaction in savannas follow a three layer root pattern in which trees occupy the top 10 cm, followed by grasses to 30 cm depth and finally deep rooted trees below 30 cm. Our three layer model suggests that there is competition for water between trees and grasses, which explains why removal of one plant type cause an increase in the other plant type. Also our three-layer root model explains why hydraulic lift in trees (Yu and D'Odorico, 2015), benefits grasses.

While there is quest to understand savanna function, climate change adds another complexity to savanna question. Vegetation-climate models predict changes in vegetation structure and composition in savannas towards the end of the 21st century (Hély et al., 2006; Monserud et al., 1993; Tietjen et al., 2010). The magnitude of change would be determined by the magnitude of precipitation and temperature change. For instance, the Kalahari is experiencing invasion of non-native *Prosopis spp* and expansion of native shrubs such as *Acacia spp* (Moleele et al., 2002; Muzila et al., 2011; Wiegand et al., 2005). Prosopis spp are commonly deep-rooted, evergreen, nitrogen-fixing plants (Archer, 1995; Simmons et al., 2008), whereas *Acacia spp* are commonly shallow rooted, dry deciduous plants, with some thought to fix nitrogen (Brockwell et al., 2005; Githae et al., 2013; Raddad et al., 2005). The invasion and expansion of deep-rooted, nitrogen fixation plants and shallow-rooted plants could significantly alter biogeochemical processes, and possibly exclude or considerably reduce grasses in the system.

Changes in vegetation composition and structure have potential alter net primary productivity (NPP), soil respiration, fire regime and ultimately soil C sequestration. Hély et al. (2006) showed that deciduous C_3 plants in Africa are sensitive to small changes in both the amount and seasonality of precipitation. C_3 plants are the dominant plant type in the savannas, and stay alive throughout the year, compared to C_4 annual grasses; therefore, any slight change in the climate would affect their physiology, and in turn alter soil C sequestration.

Simulating C fluxes in the Kalahari savannas using the Century model, we found that NPP was negatively affected by future precipitation decreases and temperature increases. However, our simulations show that C_4 grasses were more affected by climate change than C_3 plants. The reason why C_3 plants were less affected than C_3 plants is that the simulations were carried out under doubled atmospheric CO_2 concentrations. Trees tend to benefit from elevated CO_2, a process that counteracts the combined effect of precipitation and temperature. Grasses, on the other hand, attain saturated photosynthesis under doubled CO_2, and as a result they do not benefit elevated CO_2. These intertwined relationship between C_3 plants, C_4 plants and climate variables such as precipitation, temperature and CO_2 result in C_3 plants gaining competitive advantage over C_4 plants. The ultimate outcome is reduction in grass cover, changes in belowground interactions such as rooting pattern and soil C sequestration. As climate change continues to take toll, rooting pattern and competition for water are likely to be primary determinants of tree-grass co-existence.

6.3 Soil respiration

Soil respiration in savannas, and drylands in general, is more complicated that previously thought because it involves the contribution from biological soil crusts (BSC), which are photosynthetic. The presence of BSC is influenced by soil disturbance and the presence of shrubs. For example, in the Kalahari, the development of BSC is enhanced by bush encroachment species such as Acacia spp (Berkeley et al., 2005; Dougill and Thomas, 2004; Thomas and Dougill, 2007). Bush encroachment species (C_3) benefit from the nitrogen fixed by BSC and also benefit from elevated CO_2. The relationship between bush encroachment species and BSC creates a positive feedback, which enhances further encroachment and thicketization of shrubs. Improved soil fertility, due to N-fixation by BSC, and elevated CO_2 give bush encroachment species a competitive advantage over grasses (C_4), and could alter soil respiration significantly. For instance, reduction or exclusion of grasses results in expansion of shrubs and BSC, and causes an increase in soil autotrophic respiration.

6.4 Fire regime

Changes in vegetation structure and composition do not only affect soil C sequestration, they affect fire regime. Climate models show that fire frequency would increase in response to climate change because of increases in extreme weather events such as lighting, windstorm and droughts (Shongwe et al., 2009). In our analysis, we have demonstrated that fire-induced albedo change has far-reaching effects, and that the radiative forcing due to albedo change is an order of magnitude greater than previously reported. In light of our new findings, and considering the predicted increases in fire frequency and extreme weather events, we concluded that the contribution of fires to global radiative forcing would increase significantly towards the end of the century.

6.5 Anthropogenic activity

Smith (2010) recognizes population demography, the growing demand of natural resources and services by humans and climate change as three of the four global forces shaping the future of our world, The World in 2050.

Savannas are home to about 30% of the human population, whose livelihoods depend on the rangeland resources and small-scale farming (Solbrig et al., 1991). With increasing human population and decreasing land resources, savannas are likely to face intensive land use pressure and experience significant changes in C dynamics. Furthermore, land use change such as conversion of woodlands and savannas into croplands, particularly in the Amazon Basin (Bustamante and Ferreira, 2010), will also influence C fluxes. The main tool used in large-scale land conversion is fire, because fire can quickly and effectively reduce biomass of newly cleared vegetation to nutrient-rich ash that can fertilize crops (Cochrane, 2009; Miranda et al., 2009). The other problem is that the released CO_2 by biomass burning is not returned to the terrestrial system, but emitted in to the atmosphere.

Savannas also support large numbers of herbivores of all kinds ranging from invertebrates to large vertebrates such as buffalos and elephants, providing breeding grounds for them.

Recently, many countries had joint forces and established Transfrontier parks in many savanna ecosystems these magnificent wildlife and landscapes. Transfrontier Parks (or Peace Parks) are a recent concept in nature conversation based on the principle of ecosystems not recognizing national borders (van Amerom & Büscher 2005). However, the implemented fire management strategies aim at excluding fires from the ecosystem and replacing the role of fire with herbivory. Fires and herbivory co-existed for millions of years through temporal niche separation. Fires rapidly combust dry biomass, whereas herbivory slowly combust standing biomass through respiration (Goldammer and Ronde, 2004). The recent developments whereby natural fires are excluded from the ecosystem would have significant impacts in vegetation dynamics, and ultimately C sequestration as climate becomes warmer and drier. It is important to take into account the broader array of anthropogenic activities when assessing potential impacts of climate change in C dynamics in savannas. The anthropogenic activities range from small-scale subsistence farming, such as slash-burn, through large-scale projects such as Transfrontier Parks. While small-scale projects could be assessed in situ, large-scale projects could be assessed through remote sensing technique and modeling, e.g. Century.

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