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IMPACT OF FIRE HISTORY ON CARBON STORAGE AND VEGETATION STRUCTURE IN THE SAVANNA ECOSYSTEM OF MOLE NATIONAL PARK IN THE NORTHERN REGION OF GHANA

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ABSTRACT

As a management tool to balance the existence of trees and herbaceous vegetation, many protected areas in savannas are undergoing a trend of burning. Management to reduce late dry season fires and focus on low intensity fires that usually occurs in early part of the dry season could substantially help increase aboveground and belowground carbon stocks and maintain the savanna vegetation structure. This study investigated the impact of fire history on vegetation structure and carbon stocks in the 4,800km^2 Mole National Park, Ghana.

Based on satellite imagery data obtained from NASA's Moderate Resolution Imaging Spectroradiometer and interviews of local people and park officials, burnt and unburnt areas in the park were identified. The area was classified into 28 study sites belonging to four fire histories based on time since last burn (2000-2016) and seasonality of burning (e. g. early and late dry season burning). Data was collected in late June and early July, 2016. The woody vegetation biomass was greatest in unburnt plots and lower in other fire histories, while herbaceous vegetation biomass was the highest in burnt areas and lowest in unburnt areas. Total ecosystem carbon stocks in unburnt area were significantly higher than recent late season burn sites and old late season burn sites but not recent early season burn sites. Belowground (0-17cm depth soil) carbon stocks contained in unburnt study sites was greater than carbon stocks in recent late season burn areas though the difference was only significant at depth 12-17cm. Study areas that were burnt later in the dry season contained less carbon stocks than areas burnt early in the dry season.

In conclusion, late dry season fires reduce vegetation structure, ecosystem carbon stocks and biomass, although soil carbon stocks seem to recover within four years. It is therefore suggested that, for effective management of the savanna ecosystem, early dry season fires with low intensity should be encouraged to prevent late dry season fire.

DECLARATION

I hereby declare that, except for references to other peoples' work, which have been duly cited, this dissertation is the result of an original research work and that this thesis has neither in whole nor in part been presented elsewhere for another degree.

DEDICATION

I dedicated this thesis to my dear husband Mr. Stephen Adofo and my lovely children, Esther Krang Adofo and Micheal Opoku Adofo for their support and encouragement. I am this far today because of your support.

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First, I give thanks to God for His protection and for bringing me this far. I express my deepest gratitude to my supervisors, Prof. Bente Jessen Graae and Associate Prof. James D. M. Speed for their insightful comments, advice and corrections, your support made this thesis a success. Furthermore, I would like to thank Dr. Stuart Smith for his time and endless willingness to give directions and correction on my drafts, I am grateful. I also express my profound gratitude to Newton Seidu of Mole National Park and Eric Asamoah of Ayikoo travel and tours for their support during data collection. My entire master program was achievable with support from the Norwegian State Educational Loan Fund (Lånekassen), I say a big thank you.

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INTRODUCTION

Savanna, covering approximately one-fifth of the global land surface area (Sankaran et al., 2005) is one of the largest vegetation types and home to about 20% of the world's population (Mistry & Beradi, 2014; Parr et al., 2014; van Wilgen, 2009). The savanna biome occurs in large areas of Africa (65%), Australia (60%) and South America (40%), and to a smaller extent in India and Southeast Asia (Huntley, 1982; Scholes & Hall, 1996). Savanna is known to be one of the most important biomes on the earth due to their immense geographical extent, the productivity of ecosystem services and high biodiversity (Moore et al., 2016). Savannas are estimated to account for 25% of the total gross primary production (GPP) and 20% global net primary production (NPP) making them potentially important ecosystem sinks of carbon on the earth (Beer et al., 2010). Approximately 5.8Pg of biomass and 30% of global carbon stocks are accounted for by savannas, hence their potential to significantly influence the global carbon cycle (Lal, 2002; Zuppinger-Dingley et al., 2011). The vegetation of savanna is characterized by a continuous grass stratum and discontinuous trees and shrubs of different heights and densities (Mistry & Beradi, 2014). The cover of woody plants has reflective impact on the rate of transpiration and production, nutrient cycling and carbon storage (Breshears & Barnes, 1999; Higgins et al., 2007).

Plant available moisture, nutrients, fire and herbivory (disturbance regimes) are the four key environmental variables recognized to be controlling the vegetation structure and biomass of savannas (Mistry & Beradi, 2014; Sankaran et al., 2008). Sankaran et al. (2005) documented that above 650 mm mean annual precipitation, water availability is sufficient to support a closed woody vegetation. Therefore, above this limit, disturbances (fire and herbivory) play an important role in balancing the existence of woody and herbaceous vegetation in savannas.

Biomass burning is a central process that prevents the savanna ecosystem from attaining their resource determined potential (Bond et al., 2003; Higgins et al., 2000) by directly consuming the herbaceous layer, causing top-kill of trees and preventing the establishment of new seedlings. Fire shapes the savanna biome by influencing the woody vegetation biomass, plant community composition and structure (Smit et al., 2010). Savannas are the most wide-ranging C_4 grassy vegetation and are therefore expected to be very productive and have the likelihood to support woodland if disturbances are properly managed (Beringer et al., 2015; Bond et al., 2005). Fire modifies understory community composition and maintains the diversity in herbaceous plants (Laughlin et al., 2005). Yet, how fire is affecting the carbon storage and vegetation structures of the savanna landscape is poorly understood.

The savanna biome acts as a source or sink of carbon dioxide depending on climatic conditions, land use changes and disturbance regime. Savannas account for approximately 58.7 P g of biomass and 30% of the global terrestrial net primary production (Chen et al., 2003) which is comparable to that of tropical savannas (Grace et al., 2006). Savannas and grasslands are suggested to sequester additional 2.5 Mg CO_2 ha^{-1} annually if allowed to transition into woodlands (McCaw, 2012)

On the global scale, aboveground carbon stocks in savannas are estimated to be one-third of the soil carbon pool and vary widely between 1.8t C/ha at sites where trees are scarce to over 30t C/ha at places with dense tree cover (Grace et al., 2006). Chen et al. (2003) found 61% of the total vegetation biomass to be allocated to aboveground components (trees, shrubs and grasses). Savanna carbon stocks content is highly dependent on the cover of woody vegetation biomass since woody plants can store a substantial amount of carbon (Holdo et al., 2009; Pellegrini et al., 2014) compared to the herbaceous layer. Yet the herbaceous plants make a significant contribution to the soil carbon pool (Knapp et al., 2008). Therefore, changes in the aboveground vegetation structure (herbaceous and woody plants) may influence the belowground carbon, particularly regarding the vertical distribution of soil carbon stocks. The uptake of CO_2 is controlled by the equilibrium of net primary production and the loss of carbon due to heterotrophic decomposition, respiration and fire. Processes such as respiration, decomposition, combustion of fossil fuel and wood, deforestation and biomass burning cause the release of carbon into the atmosphere while photosynthetic activities and diffusion help remove CO_2 from the atmosphere. Therefore, the success of terrestrial uptake as a carbon sink is subject to the allocation of carbon to forms with long residence times (Prentice et al., 2001).

Soil is known to be the largest terrestrial organic carbon pool in the biosphere which stores more than the carbon contained in the atmosphere and vegetation together (Elderfield, 1998). The total below ground carbon pool in the land areas of the world excluding “charcoal and litter layer is estimated to be 2157–2293 Pg C in the upper 100cm (Batjes, 2014). The amount of organic carbon stored in the soil depends on the balance between input from organic compounds and release through decomposition and ecosystem disturbances (Schlesinger, 1977). In addition to this, Chen et al. (2003) recorded soil organic carbon contents in the upper 1m to be (151±33 ton C ha^{-1}), accounting for almost 74% of the total ecosystem carbon content. In a related study conducted in the savanna of northern Australia, total ecosystem carbon stock was 204±53ton C ha^{-1}, with 84% occurring below-ground and 16% above-ground (Chen et al., 2003). Considering the amount of carbon stored in soil, the slightest utterance to the soil carbon pool could cause a drastic change in the current global carbon balance particularly with regards to the vertical distribution of soil carbon stocks.

Fire results from natural factors like lightening, but also humans modify the fire regime through ignition and landscape connectivity (Mistry & Beradi, 2014). Pastoralist, landowners and conservation managers use fire mainly for agricultural and animal grazing purposes (Frost & Robertson, 1985; Hao et al., 1996; Williams et al., 2002). Human-induced fires are recognized as key contributors to biomass burning by accounting for 70% of the yearly fires in the African savanna ecosystem (Van Wilgen et al., 1990). With the increase in human activities in recent decades, biomass burning is predicted to become more frequent and prevalent in savanna ecosystems globally and the majority of human-induced fires are predicted to occur in Africa (Bagamsah, 2005; Reid et al., 2005).

Fire affects the composition, structure, and pattern of vegetation in savannas. Even though burned sites tend to return to the same plant life that existed formerly, post-fire plant community composition and vegetation growth are mainly determined by the fire regimes (Ruthven III et al., 2003; Trabaud, 1994). Low-intensity fires stimulate the growth of herbaceous plants and less damage to woody vegetation whilst high-intensity fires reduce woody plant cover over time (Bowman et al., 2009). There is positive response between fire and savannas with high grass density because grassland with high biomass production allow frequent fire and maintain open canopy (Beckage et al., 2009). The likelihood of natural fires in savannas is controlled by fuel load. This is because, the grass biomass build up more during the wet season and dry up in the dry season creating a lot of dry biomass and increasing the probability of fire occurrences. In contrast, closed savannas where C_4 grasses are excluded creates a moist climate and prevent the build-up of ground level fuel load and hence reducing the rate of vegetation flammability (Bowman, 2000; Ray et al., 2005).

Fire influence the rate of carbon storage in savannas through its effects on growth and post-fire survival of vegetation and litter decomposition (Knicker, 2007). Approximately 20% of the global savanna ecosystem experience high frequency burning on yearly bases (Dwyer et al., 2000) implying that, the majority of plant-derived carbon stored in this ecosystem may be released back into the atmosphere (Chuvieco et al., 2008). As fires continue to consume the aboveground biomass and prevent the establishment of new seedlings, savannas would store less carbon though many woody plants in fire-prone biomes become resilient to fire with time (Clarke et al., 2013). Cook et al. (2015) observed a negative change in aboveground carbon stocks and biomass of savannas that were subjected to moderate and high severity fires. Frequent fires reduced the rate of biomass accumulation of individual trees and hence reduction in above ground carbon stocks. Many studies have documented an increase in carbon stocks due to a reduction in fire frequency and intensity. In an experiment to compare carbon stocks in burnt and unburnt sites, study areas excluded from fire contained 40% -50% more soil carbon stocks in the top 5cm compared to stocks in burnt sites (Bird et al., 2000). Moreover, Rau et al. (2010) realized that prescribed burning resulted in 65% and 85% reduction in aboveground biomass and carbon stocks respectively. Other studies have confirmed the negative response of vegetation and soil carbon stocks to increasing fire frequency and intensity (Fynn et al., 2003; Jones et al., 1990; Mills & Fey, 2004; Peter-rost, 1999). On the other hand, Ansley et al. (2006) observed an increase in soil organic carbon stocks in burned sites compared to unburned control areas due to increased productivity of C_3 grasses in the burnt areas.

A feature of the soil organic carbon storage that is still poorly understood is the depth distribution of stocks in the soil and associated relationships with disturbance regimes and climatic conditions (Jobbágy & Jackson, 2000; Parton et al., 1987). Alongside the release of carbon dioxide through terrestrial respiration, most carbon flux from the ecosystem into the atmosphere is derived from burning of aboveground biomass and the litter layer; components which could have been fused into the soil organic carbon pool (Desjardins et al., 1994).

In the absence of disturbances like fire and herbivory, vegetation type, climate and soil type are the main factors controlling the vertical distribution of soil organic carbon (Jobbágy & Jackson, 2000). The distribution of soil organic carbon with depth is found to correlate with climate, with soil organic carbon distributed deeply as temperature and clay content increases and precipitation decreases (Jobbágy & Jackson, 2000). Butnor et al. (2017) observed soil carbon turnover to be more rapid at shallow depths and slower recycling rate of carbon at deeper depths with climatic factors governing in the surface layers and soil type dominating the deeper layers. In the presence of fire, Jones et al. (1990) documented a reduction in soil organic carbon in the 15cm upper layer. This may be attributed to fire altering the living and nutrient conditions of soil organisms. Whenever there are none or little organisms to decompose soil organic matter or litter layer consumed by fire, soil organic carbon reduces.

There are also instances where soil carbon stocks contained in burnt and unburnt study areas were not different but the reason for these contradictions are still unclear (Richards et al., 2011).

According to Sankaran et al. (2008), fire return interval is one of the most important variables in regulating woody plant cover along an extensive ecological gradient in African savannas. Different fire regimes result in different ecological impacts (Bowman et al., 2009). The frequency, intensity and season of biomass burning are believed to alter the equilibrium between losses and gains of carbon stocks. Inherently, high-intensity fire is suggested to result in greater burning of biomass compared to low-intensity fires (Williams et al., 2012). Fire intensity varies with frequency and season of burning since biomass burning affects fuel load and moisture content of plants (Andersen et al., 2003; Govender et al., 2006) by either promoting or causing a decline in productivity in the savanna ecosystem (Bond et al., 2005).

The rate of releasing carbon to the atmosphere may vary over season since combustion efficiency is lowest during early dry season due to high moisture content of fuel (Hao et al., 1996). In a study conducted by Hoffa et al. (1999), fuel consumed during the late dry season was twice as high as during the early dry season when normally fire spread was at reduced rate and a very low heat released. Moreover, Cook et al. (2015) observed a negative change in carbon stocks of savanna trees that were subjected to moderate and high severity fires. Similarly, increased fire frequency and late dry season fires reduce woody vegetation cover and favour grassy components by suppressing woody plant establishment and subsequent growth in savannas (D'Odorico et al., 2006; Murphy et al., 2010; Sackey & Hale, 2008b) which has impact on the woody vegetation biomass and carbon stocks accumulation.

By shifting the timing of burning to the earlier part of the dry season, fires are less intense since vegetation is not completely dry and fuel load has not peaked to cause damage. Therefore, fire managers who want to increase the recruitment of tree to larger size could set fires during early part of the dry season to decrease fire intensity (Govender et al., 2006). Long term fire return intervals caused build up in vegetation carbon stocks and reduced biomass consumption. Early dry season, low-intensity fires reordered higher carbon stocks and less biomass consumption than late dry season fires (Scheiter et al., 2015). Therefore, active management to reduce the frequency and intensity of fires may lead to increase ecosystem biomass and carbon stocks over time.

Fire regime affects the time it takes plant community to recover after fire disturbance (Gandiwa, 2011). A lot of savanna fires are surface fires which burn almost only the herbaceous layer of the vegetation and the severity of the fire is directly connected to the quantity of fuel load on the ground (Miranda et al., 1993). According to Williams et al. (1998), crown fires are uncommon in properly managed savanna ecosystem due to frequent and moderate intensity fires. However, understory heat from moderate intensity fires can cause significant canopy scorch and successive post-fire leaf fall (Beringer et al., 2004).

Irrespective of reproductive strategies (sprouting or seeding), vegetation recovery is an importance indicator of ecosystem resistance and resilience to fire disturbance (Buhk et al., 2005). Depending on fire regime, ecosystem recovery could be short or long term. Ecosystems that are adapted to fire disturbance usually have a short recovery period. The seeds of most herbaceous plants remain dormant during fire period and germinate during favorable conditions (Heydari et al., 2013) because vegetation recovers faster at areas where fire has little impact and low biomass consumption (Pereira et al., 2016). According to Beringer et al. (2004), canopy resistance to fire doubles with immediate leaf fall during dry season burns and even though canopy recovers rapidly over time, ecosystem carbon stocks do not. Hence the savanna ecosystem changes from sink to source after fire and remains a source despite canopy recovery (Beringer et al., 2004). It is, therefore, crucial to investigate and understand how fire history influence carbon stocks and vegetation structure in fire-prone biomes in and around the globe.

The most dominant vegetation form covering about 61% of Ghana’s land area is the savanna and is mainly found in the northern section of the country (Tom-Dery et al., 2013). Bushfire is known to be the greatest significant disturbance of the savanna ecosystem in Ghana contributing to the loss of vegetation, nutrients and natural resource degradation in this vegetation zone (Bagamsah, 2005; Kusimi & Appati, 2012). Burning is embedded in the cultural values and traditional farming systems of the people in the northern sector of Ghana. Annually, farmers burn with the intention of clearing bushes for cultivation and stimulating the growth of fresh palatable grass for herbivore and livestock. Due to the prolonged dry season in the region (November –April), fuel load tends to be high which makes these fires exceed their intended boundaries and rather burn miles of the landscape.

Mole National Park located in this fire-prone vegetation zone experience bushfire every year but very little is known about the impact of the frequent bushfire on the vegetation’s structure and carbon stocks. The management policy in the park is to burn the vegetation early in the dry season when fuel load is low (Sackey & Hale, 2008b). Nevertheless, late dry season fires with high intensities occur repeatedly over large ranges of the park. Sackey and Hale (2008b) predicted the likelihood that, fire impacts would lead to the decline of woody density in Mole National Park unless the frequency of burning is reduced.

The rise in bushfire frequency in Mole National Park is due to an increase in fires lit by humans utilizing the parks resources, inadequate strategies and lineups to control escaped fires and ineffective fire management policy. Of the little research that has been done about Mole National Park, most of them are on the fauna. Regardless of the potentially significant impact wildfires could have on the structure and carbon stocks of this important vegetation, currently, no research has been done to evaluate the impact of fire management. It is therefore important to understand how fire history affects the carbon stocks and vegetation structure of this fire-prone vegetation.

The most significant contribution of this study is to explore the impacts of bushfire on vegetation structure and carbon storage with regards to the vertical distribution of soil organic carbon. It will provide knowledge on the proper management of the savanna biome and ways of maintaining it as a carbon sink. Understanding the impact of biomass burning on the vertical distribution of soil organic carbon stocks may help improve soil carbon models and consequences of vegetation change and develop a more efficient strategy for managing the coexistence of woody and herbaceous plants in savannas. This paper aims to investigate the research question and hypotheses stated below:

Research Question: How does bushfire affect ecosystem carbon stocks and vegetation structure in Mole National Park in Ghana?

Hypotheses:

1. Unburnt sites in Mole National Park have the highest woody vegetation biomass at the expense of herbaceous vegetation biomass.
2. Ecosystem carbon storage is higher in unburnt sites than in sites that have been burnt
3. Soil organic carbon differs at different depths beneath the surface of the soil and decreases with depth across all treatments.
4. Early dry season bushfires decrease ecosystem carbon stocks less than late dry season bushfires.

METHODOLOGY

Study Area

The study was conducted in the 4,800 km^2 Mole National Park located in the Northern region of Ghana (N 9º12' - 10º06', W 1º25' - 2º17'). The park is the largest protected area in Ghana (Burton et al., 2011). The Mole National Park land was set aside as a game reserve in 1958 and in 1964 the villages in the area were relocated and the land was designated as a National Park. The park is managed by the wildlife division of the Ghana Forestry Commission as a Category II National Park, under the IUCN classification of protected areas. A policy for Collaborative community-based wildlife management was implemented by the forestry division since 2000 (IUCN/PACO, 2010). The park is surrounded by several villages who are largely engaged in subsistence farming of crops and livestock rearing.

The climate of the region is tropical and semi-arid with a single wet season. Mean annual rainfall is between 950 and 1100mm, which occurs mostly from May to October and the mean annual temperature is 29ºC (Burton et al., 2011; Mikkelsen & Langohr, 2004). The park lies between 120-490 m above sea level (Jachmann, 2008). The soils are a mixture of: Ferrosol high in free iron in the B2 horizon and well structured; Nitisol that are well-drained with a blocky structure and about 30% clay content; and, Vertisol with a high content of expansive clay that forms deep cracks during the drier seasons (Bowell & Ansah, 1994). The guinea savanna ecosystem is dominated by open savanna woodland with a grass layer that can be 3m tall during the rainy season (Sackey & Hale, 2008b). Based on the vegetation description of White (1983), Dowsett-Lemaire and Dowsett (2008) classified habitats found within Mole National Park as follows:

(1) **Freshwater swamp**-found on freshwater wetlands; (2) **Bovals**- edaphic grasslands with characteristic species of the Sudanian region; (3) **Wooded grassland and woodland**- open woodland with clear distinction between woodland and wooded grassland where wooded grassland has less than 40% wood cover. *Terminalia avicennioides, Vitellaria paradoxa* are example of species that dominate this habitat; (4) **Semi evergreen forest**- riparian woodland that can grow up to 25 m tall and at least 50 m wide near the Mole river, with an abundance of liane tangles; (5) **Anogeisus groves-** a patchy habitat of tall trees (20-25cm) in dry forest dominated by *Anogeissus leiocarpus*.

Mole National Park is rich in flora and fauna. About 740 different plant species are protected within the Park. Three woody plant species which are endemic to Ghana, namely *Rhinopterys angustifolia*, *Gongronema obscurum*, and *Raphionacme vignei* are all located in the park. There are numerous rivers and streams across the park, which form part of the Volta river catchment. The two major rivers running through the park are the Lovi and the Mole river (Bowell & Ansah, 1994), yet the majority of minor rivers dry out during the dry season. Annually, different parts of the park are burnt before the peak fire season of the region. This typically takes place in the early months of the dry season to reduce the intensity of fire. High intensity late dry season bushfires are also known to occur in the Park because of fires creeping into the park from neighbouring communities and poaching activity.

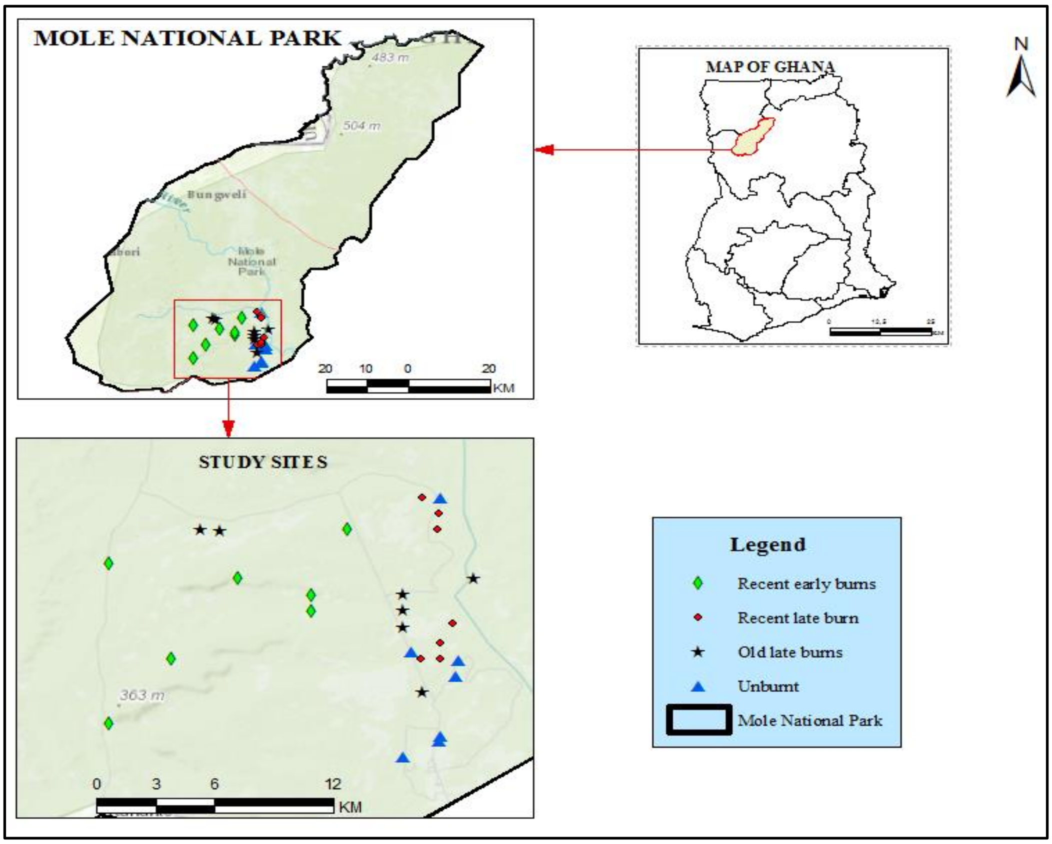

Figure 1: *Map of Mole National Park in Ghana showing study sites. The map on right is the regional map of Ghana showing the location of Mole National Park. The top left map shows sampling location in Mole National Park and the bottom map highlights study sites (n=28) within Mole National Park.*

Site selection and study design

Satellite imagery obtained from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) was used to obtain fire data. Arc GIS version 10.4 from NTNU and Google map were used to detect study sites. (https://earthdata.nasa.gov/earth-observation-data/near-real-time/firms/active-fire-data). The data was sorted and areas with 90-100% confidence level of fire occurrence or not were selected. The shapefile data points were imported into ArcMap and layers created using the *GCS_WGS_1984* coordinate system. The map was projected using Winkel-Triple (NGS-World). The point shapefile with the positioning of sampling areas were uploaded in GPS and latitudes and longitudes of specifically selected sites were located and recorded. Based on the satellite image data and interviews with local people and park official, burnt areas were selected and classified into four categories based on time since last burnt and season of burning:

- Recent early burns: sites burnt early in the dry season from 2012 to 2015
- Recent late burns: sites burnt late in the dry season from 2013 to 2015
- Old late burns: sites burnt late in the dry season from 2003 to 2012.
- Unburnt: areas not known to be burnt for at least between 2000 and 2016

These fire history intervals were used based on the results from (Sackey et al., 2012). They suggested that, a rotational system of three years fire free interval is needed for the survival of most of the woody plant species in Mole National Park. Seven plots were selected from each category of site making 28 plots in total by using stratification method of sampling. A fire map of 375 square meter resolution was used for plot selection. Within each plot, an area of 25m^2 plot was demarcated for sample collection. Within each 25m^2-plot, five subplots of 0.16m^2 each were marked out using a quadrat in the four corners of the plot and the center (Fig.2.)

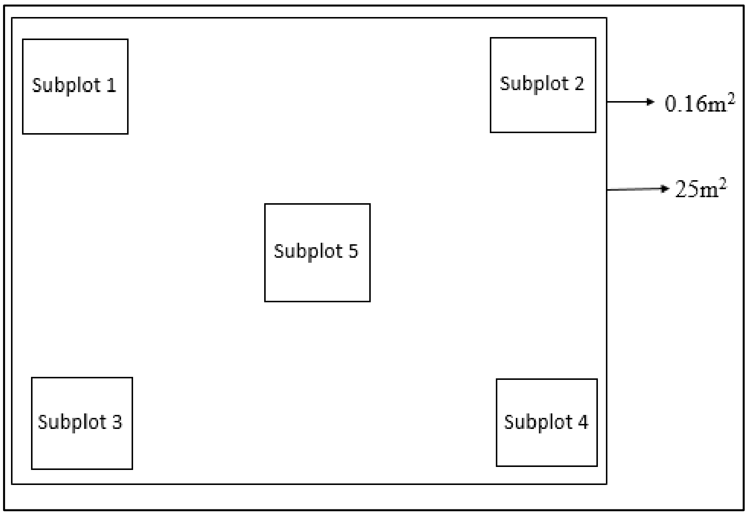

Figure 2*: A diagrammatic figure showing sampling strategy of the study with 5 replicate subplots nested within one study site.*

Data Collection

Fieldwork was carried out between late June and early July 2016, during the middle of the raining season. This time was used for data collection since it is the time of peak growth of vegetation and easy soil sample collection. The data collection took place within the south eastern/samole range of the park because it is the area surrounded by many communities and therefore expected to be exposed to frequent burning.

Woody and Herbaceous vegetation

The woody plants were sampled non-destructively in the 25m^2 plots and classified into shrubs and trees based on height. Shrubs were recorded as the smallest woody plants between 0.5 m and 2m. Shrub height was recorded, as well as diameter at stem base, of all individuals within the plots. For each tree, taller than 2m, diameter at breast height (1.3m) was recorded. All individuals were identified to species and their diameter recorded using a Vernier caliper (± 0.001 cm). The plants were further classified into charred or uncharred and dead or alive based on visual observations. For plants, less than 50cm tall found within each 0.16m^2 subplot, the aboveground parts were harvested with clippers as close as possible to the ground level and stored in paper bags sorted into grass, shrubs and herbs. All sorted plant samples were dried in an oven at 70^{o}C for 72 hours and weighed using analytical laboratory balance (±0.001g).

Deadwood and litter sampling

Litter found in the subplots was collected, cleaned of soil, sorted into leafy and woody litter and stored in paper bags. Additionally, all dead wood debris within the 25m^2 plots were recorded with the diameter at their centers together with their total length. Deadwood debris defined here are fallen dead trees, dead branches and fragments of woods with mid diameter greater than or equals 4cm. Deadwood found across the border of the 25m^2 plot were sampled whenever a maximum portion is found in the demarcated plot.

Soil sampling

Soil samples were taken with a gauge auger with an internal diameter 1.9cm in four subplots to a depth of 12cm and one subplot to a depth of 17cm whenever possible since the soil core could not reach the depth of 17cm in some subplots. The soil from each core was sub-divided into three or four depths: 0-2cm, 2-7cm, 7-12cm 12-17cm. The samples (totaling 448) were kept in separate plastics bags and stored in a refrigerator at 6^{o}C to reduce microbial activity for one and a half month prior to processing.

Aboveground carbon stock estimation

Aboveground carbon was estimated for the tree, shrub, litter, deadwood and herbaceous layers (herbaceous = herbs + grass + shrubs < 50cm). Allometric equations were used to estimate biomass for trees and shrubs greater than 50cm tall found in the plots. The regression equation used for the estimation of tree biomass was selected to match the vegetation type and climatic conditions of the study area as described by Brown (1997)

Tree biomass, $TB = \text{Exp}(-1.996+2.32\times \ln(D)$

Where TB= biomass per tree in kg, and D= diameter at breast height in cm

Shrub biomass was estimated following Guy (1981).

Biomass per shrub= $(\text{diameter}^2 \times \text{height})^{0.7839} \times 0.0890$

The carbon content of herbaceous vegetation was obtained by multiplying the respective biomass by 0.5 and expressed per unit area.

Biomass of each dead wood debris was calculated as the product of volume and decay class specific density. The volume of deadwood was obtained using the formula of a cylinder (Rouvinen et al., 2005). Following the protocol of Harmon et al. (1995), deadwood recorded were found to be under the decay class number (3) of (Pfeifer et al., 2015). The wood density of this decay class with calculated volumes was used to estimate the biomass.

Soil carbon stock estimation

Dry weight was estimated after drying fresh soil samples in an oven at 70°C for 72 hours. Soil samples were sieved to 2mm to remove stones and roots and homogenized using a pestle and mortar. For a sub-sample of on average 2.75±0.03 g, dry weight Loss on Ignition (% LOI) was determined by igniting at 550°C for 5 hours. Soil organic matter was calculated using the weight of the oven dry soil per unit bulk volume, percentage organic matter content and the height of the corer.

Soil organic matter (SOM)= BD × fraction organic matter × depth

Soil organic carbon (SOC) =SOM × 0.58 (Evrendilek et al., 2004).

Data Analysis

Data was analyzed using the R software package version 3.2. All calculated results are recorded as mean ± standard error unless otherwise stated. To obtain a balanced data, all hierarchical data was pooled to site level. Linear regression models were used to assess the impact of fire history on total ecosystem, aboveground and belowground carbon stocks as well as vegetation structure. An exploratory data analysis using Anderson-Darling normality test was carried out to check how normally the data is distributed by using. To meet the assumptions of the model, aboveground carbon stocks and vegetation biomass data were log transformed to base 10 and total ecosystem carbon stock was square root transformed.

To determine differences in carbon stocks between the four fire histories and their sub-samples, one-way ANOVA was used. Multiple comparisons using Tukey’s Honestly Significant Differences test was used to analyze statistically significant differences at an alpha level of 0.05. P-values of Tukey tests are shown in the text inside parentheses.

RESULTS

Effect of fire history on vegetation structure.

Woody vegetation biomass was significantly greater in unburnt sites than other fire histories whilst herbaceous vegetation biomass was highest in recently burnt areas and lowest in unburnt areas (Fig. 3, Table 1). As predicted in hypothesis 1, unburnt study areas have the greatest woody vegetation biomass (5.11±1.9kg/m^2) and the lowest herbaceous vegetation biomass (0.04±0.01 kg/m^2)

Considering the total aboveground carbon stored in the vegetation, unburnt sites had significantly more vegetation biomass [$F_{(19,120)=6.791}$, $P<0.01$,$R^2=0.4418$] than the sites that had been burned within the last 15 years, though there was not significant difference between recent early and old late burnt sites (Table 2). Recent late burnt sites contained less vegetation biomass (2.10±0.39kg/m^2) than recent early burnt (3.42±0.42 kg/m^2) and old late burnt (2.57±0.34kg/m^2) sites in comparison to unburnt sites (7.76±1.80kg/m^2). Biomass of unburnt sites was significantly greater than recent late burnt ($P<0.01$), old late burnt ($P=0.01$) and recent early burnt ($P=0.024$).

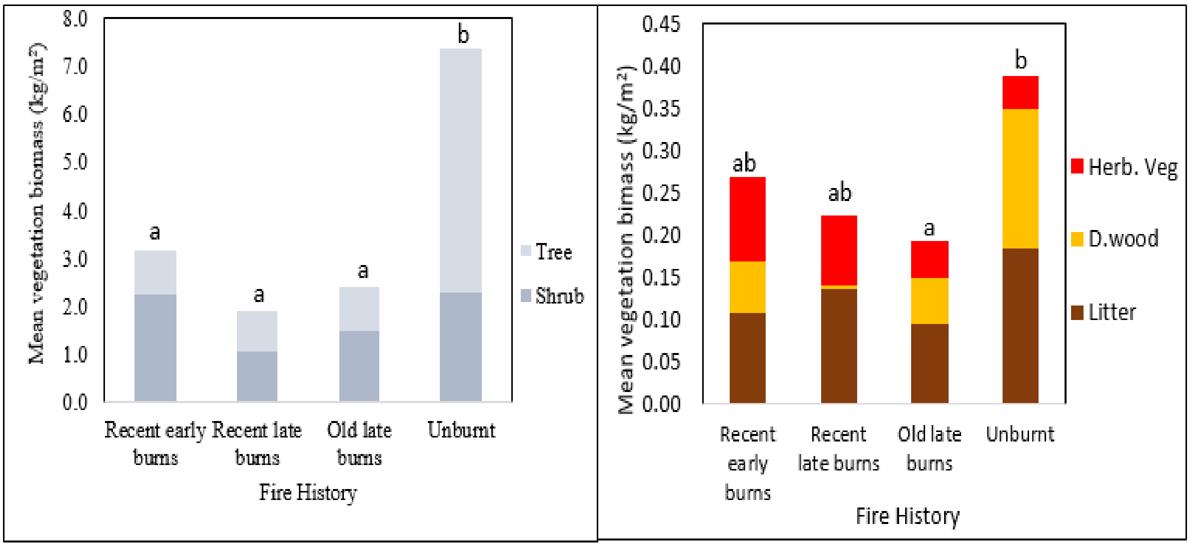

***Figure 3**: Total vegetation biomass (Means in kg/m^2) for the four-studied fire history categories (recent early burns, recent late burns, old late burns and unburned areas) in the savanna within Mole National Park, Ghana. Ecosystem vegetation biomass (Trees, shrubs, herbaceous, dead wood and litter). Bars with different letters are significantly different from each other and bars with "ab" means they are neither significantly different from "a" or "b".*

***Table 1**: Aboveground vegetation structure and carbon stocks presented in kg/m^2 (Means ± SE) for four studied fire history (Recent early burns, recent late burns, old late burns and unburned) in the savanna within Mole National Park, Ghana.*

Fire History	Recent early burns	Recent late burns	Old late burns	Unburnt
Trees (kg/m^2)	0.49±0.17	0.35±0.12	0.72±0.38	2.37±0.96
Shrubs (kg/m^2)	2.52±0.20	1.79±0.46	1.56±0.59	1.43±0.24
Herbaceous veg. (kg/m^2)	0.05±0.01	0.03±0.001	0.03±0.01	0.02±0.01
Litter (kg/m^2)	0.05±0.01	0.03±0.001	0.06±0.02	0.12±0.02
Dead wood (kg/m^2)	0.07±0.04	0.01±0.00	0.05±0.03	0.28±0.11
Soil 0-2cm (kg/m^2)	1.17±0.12	0.85±0.17	1.07±0.13	1.38±0.24
Soil 2-7cm (kg/m^2)	3.34±0.28	1.77±0.47	3.04±0.28	3.32±1.86
Soil 7-12cm (kg/m^2)	3.36±0.26	2.15±0.55	3.23±0.33	3.43±0.32
Soil 12-17cm (kg/m^2)	3.03±0.27	1.34±0.23	2.76±0.55	3.29±0.37

Effect of fire history on total ecosystem carbon stocks.

Total ecosystem carbon storage (above-ground + litter + deadwood + below-ground) was dependent on fire history with unburnt sites having significantly higher carbon stocks (16.85±1.90kg/m^2) than recent late burnt area (7.28±1.03kg/m^2, $P < 0.01$), and old late burnt sites (11.68±1.51 kg/m^2, $P=0.02$) but not recent early burnt sites (13.23±1.07 kg/m^2, $P =0.91$; Fig. 4).

There was no significant difference ($P=0.34$) in total ecosystem carbon stocks contained in recent early and old late burnt sites (Figure 4; Table 1). 85% of the variation found in ecosystem carbon stocks in the study area could be explained by the model [$F_{(35,212)} =41.93$, $P<0.01$, $R^2=0.85$; Figure 4]. Total belowground ecosystem carbon pool was about three times more than carbon stocks contained aboveground.

***Figure 4**: Total ecosystem carbon stocks (Mean ± SE bars) for the four studied fire history categories (recent early burns, recent late burns, old late burns and unburned areas) in the savanna within Mole National Park, Ghana. Total ecosystem stocks are separated into belowground (soil to 17cm depth) and aboveground (Trees, shrubs, herbaceous, live woody and litter).*

Soil organic carbon differs at different depths beneath the surface of the soil and decreases with depth across all treatments.

The total belowground (0-17cm depth soil) carbon stocks contained in unburnt study sites (11.83±1.41 kg/m^2), recent early burns (10.39±0.93kg/m^2), and old late burnt (9.66 ±1.30kg/m^2) were significant ($P<0.01$) greater than the carbon stocks in recent late burnt (5.77± 1.43kg/m^2) areas (Table 1, Figure 5). 46% of the variance found in soil carbon stocks in the study area could be explained by the model (fire history) [$F_{(15,92)}=7.243$, $P<0.01$, $R^2=0.46$]. When zooming in on different depths, we could not demonstrate significant differences ($P>0.05$) between the soil carbon for the top 2cm, 2-7cm and 7-12cm for all studied fire histories. However, at 12-17cm depth, there was a significant difference between carbon stocks contained in the unburnt area (3.29±0.37kg/m^2) and recent late burnt area (1.34±0.23kg/m^2; P=0.01, Figure 5) even though carbon stocks in upper soil layer seem recovered within four years after fire (Table 1, Appendix 2).

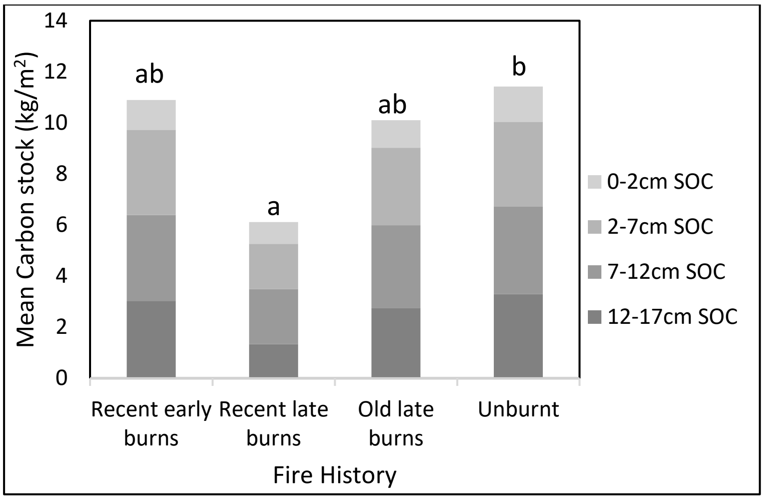

***Figure 5**: Belowground carbon stocks (Means in kg/m^2) for the four studied fire history categories (recent early burns, recent late burns, old late burns and unburned areas) in the savanna within Mole National Park, Ghana. A bar with "a" indicate significant difference and "b" not significantly different from Unburnt site). Bars with different letters are significantly different from each other and bars with "ab" means they are neither significantly different from "a" or "b".*

Effect of Early and Late dry season fires on ecosystem carbon stocks in the study areas.

Analyzing the total carbon stocks contained in sites burnt late in the dry season and sites burnt early in the dry season, early dry season burnt sites had significantly more carbon stocks than late dry season burnt sites [$F_{(19,120)}$=11.19, P<0.01]. Total ecosystem carbon stocks contained in recent early burnt area (13.23±1.07 kg/m^2) was significantly greater than recent late burnt (7.28±1.03kg/m^2; P<0.01) carbon stocks.

Late dry season fires decreased both above and belowground carbon stocks in the study areas (Figure 6; Table 1). Recent late burnt contained less aboveground carbon stocks (1.58±0.35 kg/m^2) compared to recent early season burning (2.84±0.35 kg/m^2) though the difference was only marginally significant (P=0.08). Sites burnt late in the dry season also contained significantly less belowground carbon stocks (5.77±1.43kg/m^2) than sites burnt early in the dry season (10.39±0.93kg/m^2; P<0.01).

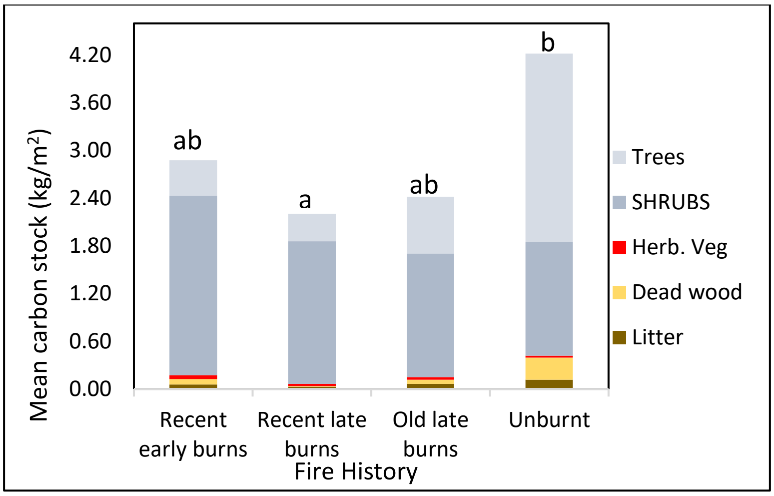

Figure 6: *Aboveground carbon stocks (Means in kg/m^2) for the four studied fire history categories (recent early burns, recent late burns, old late burns and unburned areas) in the savanna within Mole National Park, Ghana. Total aboveground carbon stocks are separated into Trees, shrubs, herbaceous, deadwood and litter). A bar with "a" indicate significant difference and "b" not significantly different from Unburnt site. Bars with different letters are significantly different from each other and bars with "ab" means they are neither significantly different from "a" or "b".*

DISCUSSION

This study shows that aboveground and belowground carbon stocks in Mole National Park are dependent on fire history. After burning, woody vegetation biomass decreases markedly and it takes years for this to rebuild. The carbon pools in herbaceous vegetation layer, however, were higher in plots that have been burned compared to plots with no known burning for the past 16 years. Even though belowground carbon pools were depleted after burning and the depletion is highest at the deeper layers of soils, the top soil layers seem to recover fast after the fire. Late season burns had a much more dramatic effect on carbon pools both above and below ground than early season burns but already around four years after a late dry season burn, much of the carbon pools belowground seems to have recovered.

Woody and Herbaceous vegetation biomass in burnt and unburnt sites.

As stated in hypothesis 1 of this study, unburnt areas in Mole National Park contains the highest woody vegetation biomass compared to burned areas, though the difference was only significant with recent late burnt areas. Unburnt areas had much woody vegetation biomass at the expense of herbaceous vegetation. This finding is expected and consistent with a review of current literature on the effect of fire on vegetation by Bond and Keeley (2005) who also documented a significant dramatic change in woody plants biomass in a long term burning experiment in a savanna ecosystem where fire was excluded for 35 years. Based on the results obtained in this study on the difference between woody vegetation biomass in unburnt and late new burnt sites, it could be predicted that, the guinea savanna ecosystem can turn into forest provided fire can be totally excluded as also suggested by Sankaran et al. (2005).

According to Bond (2008), at the expense of C_4 plants, savannas would accumulate considerable biomass and carbon stocks and closed forest would double if protected from wildfires. Other studies (Bond & Keeley, 2005; Cook et al., 2005; Grace et al., 2006; Higgins et al., 2007; Murphy et al., 2010) also detected a consistently negative relationship between fire frequency and biomass of savanna woody plant biomass due to reduction in plant growth. The observed woody plant biomass reduction with burning may be attributed to the decrease in the woody compartments as the herbaceous vegetation increases. The increase in herbaceous cover after burning makes an important contribution to ecosystem biomass and carbon stocks but does not make up for the biomass reduction in woody plants since they make only 2% of the woody biomass even when at most. The observation is not surprisingly since people normally burn specifically for getting more grassland and less woody cover.

In a frequently burnt vegetation, herbaceous plants are exceptional in their ability to recover after fire since most of the plants mature in only one growing season. It was found that, herbaceous vegetation and multi-stem plant biomass were highest in the recently burnt areas (Recent late and Recent early burnt areas) though the difference was not significant. Grass and herbaceous species increased in biomass at burnt areas compared to unburnt and woody plant biomass reduced in burnt areas. This is because, herbaceous species mostly have their survival buds at or below the surface of the soil and are therefore able to sprout immediately after fire. Also, since woody plants with closed canopy can otherwise prevent the establishment and growth of light depending species, when they are usually damaged by high-intensity fires, there is little competition for nutrient, space and light which help herbaceous plant in these sites to increase in density and biomass (Keeley et al., 2003; Lunt & Morgan, 2002).

Dry season and frequent burning in semiarid savannas stimulate the growth of shorter multi-stemmed plants and herbaceous species which could be due to fires preventing new seedling from growing to their maximum height. (Bond, 2008; Clarke et al., 2013). In summary, unburnt areas have higher woody plant biomass at the expense of herbaceous vegetation biomass while burnt areas have higher herbaceous plant biomass and is consistent with many published results in tropical savannas.

Ecosystem carbon storage in burnt and unburnt sites.

This study shows that total ecosystem carbon stocks were greatest in unburnt areas compared to the areas subjected to the different fire histories though the difference was only significant with recent late burnt areas. Depending on fire regimes, ecosystem recovery could be short or long term. Beringer et al. (2004) found that, canopy resistance to fire doubles with immediate leaf fall during dry season burns and even though canopy recovers rapidly over time, ecosystem carbon stocks do not. Hence many burnt ecosystems change from sink to source after fire despite canopy recovery (Beringer et al., 2004). Yet the results of this study indicate that, carbon stock recovery increases as vegetation covers.

Belowground biomass and carbon stocks are not reduced so much as aboveground carbon stocks. This is caused by the slower recovery of trees after fire disturbance since trees make up the major aboveground vegetation. This could also be due to a more frequent consumption of the aboveground vegetation by fire. The sites that had been recently burned may also have been repeatedly burned than those that had long time since last fire. We did not survey if this was the case due to lack of complete information on fire history in the park. Though most plants can sprout quickly after fire, they are usually burnt by the next seasonal fires causing a delay in recovery. Recorded soil carbon stocks exceeded woody carbon stocks but when the woodland is consistently consumed by fire, there can be a significant fluctuation in the ecosystem carbon stocks. The observation that the soil carbon pool is about two to three times higher than aboveground carbon stocks and division between soil carbon stock and total ecosystem carbon stocks in the study area (75% in soil) is similar to the 70% and 60% reported by Ryan et al. (2011) and Walker and Desanker (2004) respectively. Ecosystem carbon stocks are higher in unburnt study areas and reduce with frequent and late dry season fire.

Soil organic carbon at different depths beneath surface of soil across all fire histories

Total belowground (soil) organic carbon stock was higher in unburnt study sites than in the recent early, old late and recent late burnt sites. Fire showed the same tendency to decrease soil carbon with the severity of the fire but did not show significant differences when compared between the various fire histories at depths 0-2cm, 2-7cm and 7-12cm. However, the at depth 12-17 cm the soil carbon was significantly lower in recent late burnt areas compared to the unburnt. This could be attributed to the post-fire growth rate of the aboveground vegetation. The vegetation biomass data obtained shows that, herbaceous vegetation sprout and grows fast after fire disturbance which implies organic matter in the topsoil builds up fast at the onset of the wet season, therefore carbon content is restored quickly. At depth 12-17cm, unburnt study area had higher carbon stocks than recent early, old late and recent late burnt areas yet the difference was significant for only recent late burnt site. The gradual response of soil to recent late fire suggests that, the 0-12cm soil organic carbon stock depends on how aboveground vegetation recovers after fire disturbance. Since fire seldom burns the soil down to depth 17cm (Jobbágy & Jackson, 2000), the significant reduction in carbon stocks at this depth could be attributed to the reduction in woody vegetation cover. Because woody plants that have long roots that reach deeper depths are reduced in burnt areas, the carbon incorporation by root decomposition at a deeper depth in the burnt areas is minimal, hence the observed significant reduction in carbon stocks at depth 12-17cm in recent late burnt sites. This can also be due to slow recycling rate at deeper depth resulting from insufficient organic matter incorporation, differences in root apportioning and patterns of aboveground litter allocation. Root decomposition is important because root litter is a key source of soil carbon contributing more than aboveground litter. This implies that, the deeper plant roots in the soil, the more they can allocate carbon at deeper depths due to detrital input. Therefore, root detrital input may be an important carbon source for deeper soils (Manzoni et al., 2012; O'Lear et al., 1996; Rasse et al., 2005). Moreover, soil type may also be a factor for the observed reduction in carbon stocks at deeper depths as suggested by Butnor et al. (2017).

The 37% decrease in soil carbon stocks contained in recently late burnt area in relation to unburnt sites in the upper 7cm depth is consistent with a study where soil carbon stocks of fire excluded sites increased from 40%-50% in the top 5cm compared with burnt plots (Bird et al., 2000). Considering the carbon stocks in the top 17cm of soil, recently late dry season fires caused approximately 48% decrease in carbon stocks in relation to unburnt areas. This finding contradicts with the results of Jones et al. (1990) who observed approximately 10% decrease of soil organic carbon in the top 15cm when fire return interval was increased from annual to triannual in Kruger National Park. The observed differences in carbon stock reduction may be because of different fire regimes and climatic conditions in the different studied areas. Late dry season fires are usually high-intensity fires and indeed shows a higher reduction in soil carbon stocks as also seen in the results of this thesis.

In addition to the above, there are many other studies that have reported a decrease in soil carbon stocks under annual burning regimes (Fynn et al., 2003; Jones et al., 1990; Mills & Fey, 2004; Peter-rost, 1999). These findings may be attributed to the fact that late dry season bushfires alter the living and nutrient conditions of soils. Whenever there is little input of organic matter from vegetation (both shoot and root), soil organic carbon is reduced though other factors that are not yet clear may be having an impact.

Nevertheless, Richards et al. (2011) and Coetsee et al. (2010) did not observe a significant difference in soil carbon stocks contained in burnt and unburnt sites. Richards et al. (2011) argued that changes in soil carbon content would be detectable after 100 years of changes in fire management strategies. Also, Ansley et al. (2006) rather reported an increase in soil organic carbon from 2044g/m in unburnt control site to 2393g/m^2-2534g/m^2 in their treatment burnt sites. The results of these studies (Ansley et al., 2006; Coetsee et al., 2010; Richards et al., 2011) contradict with the findings of this study and these are justifiable because the entire fire history of the studied area in this study is not known. It could be that, the recently burnt sites have also been frequently burned in the past years. Also, other savanna determining factors like mean annual precipitation, grazing pressure and soil type in the various studies areas may contribute to the different observations.

The impact of early and late dry season fires on ecosystem carbon stocks.

One important finding of this research is that, early dry season fires had little effect on ecosystem carbon stocks compared to late dry season fires. Late dry season burning damaged aboveground vegetation and caused a reduction in biomass and carbon content and a longer time to build up. This result is comparable with results obtained by Sackey and Hale (2008b) in Mole National Park. They suggested that, unless the frequency of burning in Mole National Park is reduced, relative abundance and density of woody plants would decline. They observed woody plant biomass decline and top-kills of woody plants resulting from regular severe fires and concluded that, three years' fire exclusion is needed to prevent a reduction in woody vegetation density and biomass provided the park management aims to increase woody vegetation cover in the park. The Kruger fire experiment by Higgins et al. (2007) also produced similar results to this study showing that, annual fires caused 1.5% reduction in woody biomass in relation to triannual burns which lead to the build-up of 853 kg/ha. Fire exclusion led to an increase in aboveground woody biomass changes of woody plants. They proposed that, mild fires which usually occurs early in the dry season leads to little change in ecosystem biomass and carbon stocks

Frequent fires have been suggested to reduce the growth rate of trees with the magnitude of the effect increasing with fire severity. Murphy et al. (2010) reported 24%, 40% and 66% reduction in the growth of trees when subjected to Mild, moderate and severe fires respectively. There is world-wide evidence supporting the report of the drastic influence of season of burning (early or late dry season fires) on ecosystem carbon stocks and biomass (Archibald et al., 2010; Scheiter et al., 2015). In support of the finding of this research, other studies have proposed early dry season fires for slower biomass consumption and higher carbon storage than late dry season fires (Kugbe et al., 2015; Russell-Smith et al., 2013; Scheiter et al., 2015). Moreover, the season of burning does not have a significant impact on the vegetation biomass and carbon stocks. Both late and early dry season burnt sites contained approximately equal biomass than unburnt sites Scheiter et al. (2015).

To appreciate the uniqueness of fire in shaping the savanna ecosystem in Mole National Park, it is necessary to consider the impact of herbivory since fire cannot be considered in isolation from grazing effect, particularly in African savannas (Glitzenstein et al., 1995; San José &

Montes, 1997; Sankaran et al., 2008). The distribution of plant biomass is influenced by herbivory to the extent that savanna grasslands that are heavily grazed do not usually burn which could lead to an increase in tree densities. In terms of maintaining aboveground biomass production in grassland ecosystems, Frank et al. (2003) proposed low grazing intensity to be generally advantageous compared with grazing exclusion. Cui et al. (2005) reported that grazing regime did not significantly change soil organic carbon content or stock in grasslands neither did it alter the distribution of soil organic carbon along different soil depths.

On the other hand, large herbivores like elephants are known to open closed woodlands, enhancing grass growth which encourages regular severe fires and affects organic matter content. Considering the combined effect of fire and herbivory on vegetation biomass and carbon storage, it could be assumed that fire causes the decline in woody vegetation whereas grazing inhibits recovery (Belsky, 1995; Scholes & Archer, 1997). In this way, grazing may change carbon allocation pattern affecting the amount of carbon entering the soil (Johnson & Matchett, 2001). As herbivores consume the aboveground vegetation, they equally increase or decrease the soil carbon content by altering the quality and quantity of resource (urine, dung and litter) input into the soil. Nitrogen and other nutrients in urine and dung of herbivores may stimulate decomposition of soil organic matter (Barthelemy et al., 2016; Singer & Schoenecker, 2003). Even though elephants are one of the dominant herbivores in Mole National Park, Sackey and Hale (2008a) found out that, they are not significantly affecting the vegetation cover in the park. It is therefore certain that, elephants have little or no impact on the results presented on vegetation structure and likewise ecosystem biomass in this study. It is therefore suggested that, controlled studies would be needed to separate the impact of fire and herbivory on carbon stocks in Mole National Park.

CONCLUSION AND RECOMMENDATION

In this study, carbon stocks ranged between 1.58 and 5.02 kg/m^2, 5.77 and 11.83 kg/m^2, 7.28 and 16.83kg/m^2 for aboveground, belowground and total ecosystem carbon stocks respectively. Sites that were burnt had lower ecosystem carbon stocks and biomass and this was observed in both aboveground and belowground components. The reduction in soil organic carbon stocks was observed all the way down to 17cm and was greatest the first years after intense fires but within four years, soil carbon stocks were restored. Yet aboveground carbon stocks were not completely recovered since tree biomass and carbon stocks were still showing a reduction after the four years. On the other hand, the results of this study indicate that, early dry season fire has little or no impact on vegetation structure and carbon stocks. Further study is needed to describe the mechanisms of the belowground carbon pool and its interactions with herbivory for the carbon stocks. Also, it would be vital to assess the effect of fire frequency and intensity on belowground carbon stocks in Mole National Park by assessing plant roots since part of the carbon stocks are incorporated in plant roots.

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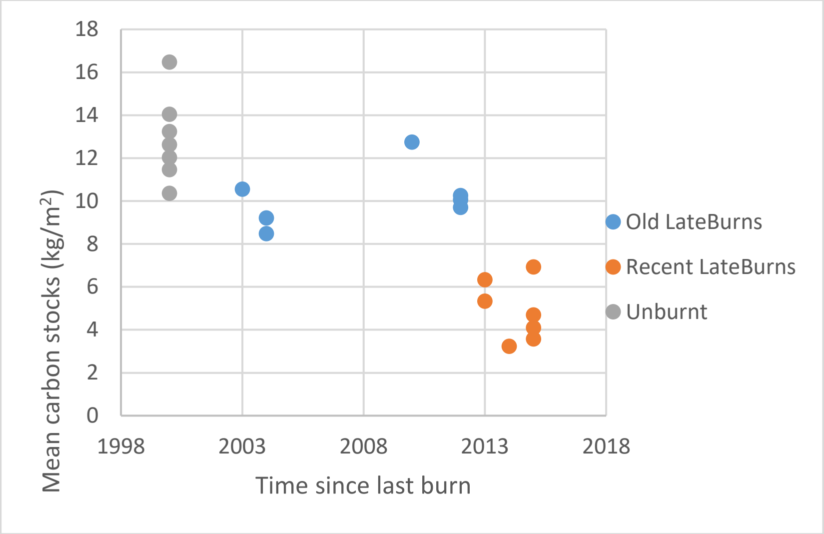
APPENDIX



Appendix 1: *Belowground carbon stocks for time since last burnt in three studied fire history (old late burns, recent late burns and unburnt) sites within Mole National Park, Ghana.*

Appendix 2. *Table showing statistical values for Vegetation biomass, aboveground, belowground and total ecosystem carbon stocks at α =0.5*

Samples	Degree of freedom (DF)	F-statistic	Adjusted R-squared	P-value
Vegetation biomass	120	13.13	0.62	2.2e-16
Aboveground carbon stocks	132	28.2	0.578	<2.2e-16
Belowground carbon stocks	92	7.243	0.46	3.149e-10
Total ecosystem carbon stocks	212	41.93	0.85	2.2e-16