Above-ground carbon stocks, species diversity and fire dynamics in the Bateke Plateau

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Thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy
School of GeoSciences
The University of Edinburgh, 2019

Declaration

I declare that this thesis has been composed solely by myself and that it has not been submitted, either in whole or in part, in any previous application for a degree. Except where otherwise acknowledged, the work presented is entirely my own.

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December 2018

Abstract

Savannas are heterogeneous systems characterised by a high spatial and temporal variation in ecosystem structure. Savannas dominate the tropics, with important ecological functions, and play a prominent role in the global carbon cycle, in particular responsible for much of its inter-annual variability. They are shaped by resource availability, soil characteristics and disturbance events, particularly fire. Understanding and predicting the demographic structure and woody cover of savannas remains a challenge, as it is currently poorly understood due to the complex interactions and processes that determine them. A predictive understanding of savanna ecosystems is critical in the context of land use management and global change.

Fire is an essential ecological disturbance in savannas, and forest-savanna mosaics are maintained by fire-mediated positive feedbacks. Over half of the world's savannas are found in Africa, and over a quarter Africa's surface burns every year, with fires occurring principally in the savanna biome. These have strong environmental and social impacts. Most fires in Africa are anthropogenic and occur during the late dry season, but their dynamics and effects remain understudied.

The main objective of this research is to understand the floristic composition, carbon storage, woody cover and fire regime of the mesic savannas of the Bateke Plateau. The Bateke Plateau is savanna-forest mosaic ecosystem, situated mainly in the Republic of Congo, with sandy Kalahari soils and enough precipitation for potential forest establishment (1600 mm/yr). Despite occupying 89,800 km^2, its ecology and ecosystem functions are poorly understood. This study combines two approaches: firstly experimental, setting up long term field experiments where the fire regime is manipulated, and then observational, using remote sensing to estimate the carbon storage and study the past history of the fire regime in the region. I established four large (25 ha) plots at two savanna sites, measured their carbon stocks, spatial structure and floristic composition, and applied different annual fire treatments (early and late dry season burns). These treatments were applied annually during 3 years (2015, 2016 and 2017), and the plots were re-measured every year to estimate tree demographic rates and the identification of the key processes that impact them, including fire and competition. Field data were combined with satellite radar data from ALOS PALSAR, and the fire products of the MODIS satellites, to estimate carbon stocks and fire regimes for the entire Bateke Plateau. I also analyse the underlying biophysical and anthropogenic processes that influence the patterns in Above-Ground Woody Biomass (AGWB) and their spatial variability in the Bateke landscape.

The total plant carbon stocks (above-ground and below-ground) were low, averaging only 6.5 ± 0.3 MgC/ha, with grass representing over half the biomass. Soil organic matter dominate the ecosystem carbon stocks, with 16.7 ± 0.9 Mg/ha found in the top 20 cm alone. We identified 49 plant species (4 trees, 13 shrubs, 4 sedges, 17 forbs and 11 grass species), with a tree hyperdominance of *Hymenocardia acida*, and a richer herbaceous species composition. These savannas showed evidence of tree clustering, and also indications of tree-tree competition. Trees had low growth rates (averaging 1.21 mm/yr), and mortality was relatively low (3.24 %/yr) across all plots. The experiment showed that late dry season fires significantly reduced tree growth compared to early dry season fires, but also reduced stem mortality rates. Results show that these mesic savannas had very low tree biomass, with tree cover held far below its climate potential closed-canopy maximum, likely due to nutrient poor sandy soils and frequent fires.

Results from the remote sensing analysis indicated that multiple explanatory variables had a significant effect on AGWB in the Bateke Plateau. Overall, the frequency of fire had the largest impact on AGWB (with higher fire frequency resulting in lower AGWB), with sand content the next most important explanatory variable (with more sand reducing AGWB). Fires in the Bateke are very frequent, and show high seasonality. The proportion of fires that occurred in the late dry season, though smaller predictor, was also more important than other factors (including soil carbon proportion, whether or not the savanna area was in a protected area, annual rainfall, or distance to the nearest town, river or road), with a larger proportion of late dry season fires associated with a small increase in AGWB. The results give pointers for management of the savannas of the Bateke Plateau, as well as improving our understanding of vegetation dynamics in this understudied ecosystem and help orient policy and conservation.

Lay Summary

Savannas cover the majority of the land surface of the tropics, and about 20 % of the land area of the world. They are characterised by the co-existence of tree and grasses. The proportion of tree cover in savannas is very variable, and we do not fully understand what causes tree cover to vary across the landscape. An area with the same soil type and rainfall could have no trees, or almost total tree cover. We do know that climate (rainfall, and the time of the year when that rainfall happens), soil characteristics and nutrient content, the density of herbivores, and fire, all play a role regulating the coexistence of tree and grasses. However, we do not know their relative strength, nor how they interact with each other. In fact, one of the main challenges in savanna ecology is to explain the effects of these complex environmental mechanisms functioning at many temporal and spatial scales to understand the distribution of tree cover.

Mesic savannas, defined as those with a mean annual precipitation of 1000–2000 mm, are highly dynamic and unstable systems, where both forest and open savannas are possible states. It is likely that fires are fundamental in determining the tree cover in these savannas. Fires are a frequent and natural phenomenon in savannas, normally occurring in the dry season and triggered by either human burning or lightning strikes. In savannas, normally only the grasses burn, with large trees potentially damaged but normally surviving. Research has shown that early dry season fires tend to have lower intensities, and are less likely to kill trees, than fires late in the dry season, when they have greater dry grass fuel loads and are thus more intense and potentially deadly for trees. Low intensity fires further tend not to burn whole areas, and therefore create patchiness in the landscape, and as such are beneficial for biodiversity.

The subject of this thesis is a large savanna covering the Bateke Plateau. This is one of the least studied areas of tropical Africa – few scientists have studied its plant diversity or how the trees, grasses and animals in it coexist. It is dominated by sparse wooded savanna on sandy soils originating in the Kalahari Desert to the south, with a relatively high annual precipitation (about twice that of Edinburgh in the UK). Located mainly in the Republic of Congo, but extending into Gabon and Democratic Republic of Congo, it is surrounded on three sides by the second largest tropical rainforest in the world. Its importance comes as a

result of its extent, biological diversity, and providing ecosystem services, but it is threatened through human pressure and climate change. The aim of the research was to improve our understanding of how fire influences the carbon stocks and tree dynamics of these savannas, in order to help governmental, NGOs and national park agencies manage them in the future.

The research was performed in field plots I set up in two protected sites, dominated by sparse wooded savanna. In these, I identify the floristic diversity, carbon stocks and spatial structure. These plots were subject to different fire treatments, altering the fire seasonality by doing early and late dry season burns. By re-measuring these plots, I estimated rates of tree growth, tree death, and regeneration, and identify the effect of fire seasonality and tree-tree competition on growth and survival rates. Reliable estimates of tree growth and death rates are important for developing effective models of savanna ecosystem dynamics. I combine the field plot data with data from a radar satellite to map the woody biomass stocks in the Bateke Plateau, and used a different satellite that can map the area that burns each year to investigate how the fire regime influences woody biomass at a large scale. These data were combined with biophysical and anthropogenic variables (fires, soil properties, precipitation, topography, protected status and distance to towns and roads), to improve our understanding of what principally determines patterns in woody biomass across the Bateke landscape.

Overall, my study shows that these savannas have low tree carbon stocks and that tree growth and mortality rates are low. These savannas are dominated by one fire tolerant tree species, *Hymenocardia acida*. Fires in the Bateke are very frequent, mostly occurring during the dry season. I demonstrated the importance of the sandy soils and frequent fires in causing this low tree biomass. Results also show multiple explanatory variables had a significant effect on tree biomass; and both the experiment and the satellite imaging analysis show that higher fire frequency reduce the woody biomass of an area, if everything else is equal.

Over the past years, many studies have used the existing field plot data sets, together with the data from Earth observation satellites, and combined with models, to generate estimates of the carbon stocks in tropical savannas and how they are changing over time. However, the Bateke Plateau remains a highly unpredicted landscape. Therefore, this thesis

will help increase the poor existing knowledge of this understudied ecosystem, for a better understanding of the dynamics that regulate them. It will also be useful for future studies and for management, conservation and decision-making, and contribute to savanna science.

Acknowledgements

There are many of people who have provided encouragement, advice and support over the past 4 years. I would like to thank my supervisor Ed Mitchard for guiding me through the PhD, and for always providing invaluable advice, many ideas and encouraging words when most needed. I would also like to thank Casey Ryan, my second supervisor, for providing helpful advice and ideas. They have introduce me to African savannas, and I have learnt a lot from both their experiences. Thank you both for all your inputs, for providing many important insights and developing my scientific skills. I have also received academic assistance from a number of other sources throughout my PhD; my thanks are due in particular to Kyle Dexter, Mat Williams, Sarah Sawyer.

This PhD would not have been possible without the financial and logistical support of the USFS and WCS Congo. Additionally, I would like to acknowledge the financial support to the project provided by The United States Agency for International Development (USAID) and the Central Africa Regional Program for the Environment (CARPE). The fieldwork for the research chapters in this thesis was performed with the help from many people in Republic of Congo. Particular thanks go to Tim Rayden, for all the help, inspiring talks about Congo and conservation, logistic arrangements, and support during fieldwork. I’m very grateful to the people of WCS Congo and the field staff in Lefini and Lesio Louna reserves, who were indispensable during the field campaigns. I was lucky enough to be supported by some fantastic field assistants, including Roland Odende, Marcelle Armande Batsa Mouwembe, Ledia Bidounga, Onesi Samba, Fiacre Mouaba, Fred Edimma, Marlene Gotene and Smith Diafouka; all providing assistance and friendship during field work. Mireille Breuer, for managing the fieldwork when I couldn’t be there, and John Godlee (from University of Edinburh) for his great work assisting in one of the field missions in 2017. Sarah from USFS provided advice and inspiring conversations. The eco-guards Prime Mobie and Denis Ngatse provided help and shared many stories the Bateke Plateau. Mr. Gilbert Nsongola for helping with the species identification. Lastly, to all the people who made my stay at Congo fun and who shared their time with me, I thank you. The work would not have been possible without your hard work and great company.

In Edinburgh, friends from Crew have always been there for support, inspiring talks and for laughs. Too many to name them all, but I have learn a lot from them. Thanks to Sara, Pedro, Jamie, Rosa and Hemant for the great times, dinners, yoga, meditations. Hemant and Sam, thanks for all the help, support with R and proofreading some chapters.

Special thanks to Sam, for your invaluable help and support, for being there during the toughest times, for making the PhD that little bit easier, for putting up with my ups, and more often downs, for the trips, adventures, and many more to come. No words are enough to describe how grateful I am to have you in my life.

Finally, I would like to thank my family for their continuous support and encouragement, without which I would never have made it through. I dedicate this thesis to my parents, Amparo and Pablo, and to Kuku. Their love for nature, other cultures, and travels have been the source of my curiosity and attraction to the natural world. And their ethics and support have made it possible for me to leave my comfort zone and try new experiences. Os quiero.

Paula Nieto

December 2018

"Look deep into nature, then you will understand everything better"

Albert Einstein

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List of Abbreviations

AGB – Above-ground biomass

AGWB – Above-ground woody biomass

AIC - Akaike information criterion

ALOS - Advanced Land Observation Satellite

BGB – Below-ground biomass

C - Carbon

D_{10} - Diameter 10 cm above the surface

DBH - Diameter at breast height

DPM - Disc Pasture Meter

DRC- Democratic Republic of Congo

FBD – Fine Beam Dual

GLS - Generalised linear model

IRSEN - Institut de Recherche en Sciences Exactes et Naturelles

LLR - Lesio Louna Reserve

LWR - Lefini Wildlife Reserve

MODIS - Moderate-resolution imaging spectroradiometer

NMDS - Non-metric multidimensional scaling

PALSAR - Phased Array type L-band Synthetic Aperture Radar

PNPB - Parc National Plateaux Bateke

REDD+ - Reducing emissions from deforestation and forest degradation

RoC - Republic of Congo

SAC - Spatial autocorrelation

TAMSAT - Tropical Applications of Meteorology using SATellite data

TM - Landsat Thematic Mapper

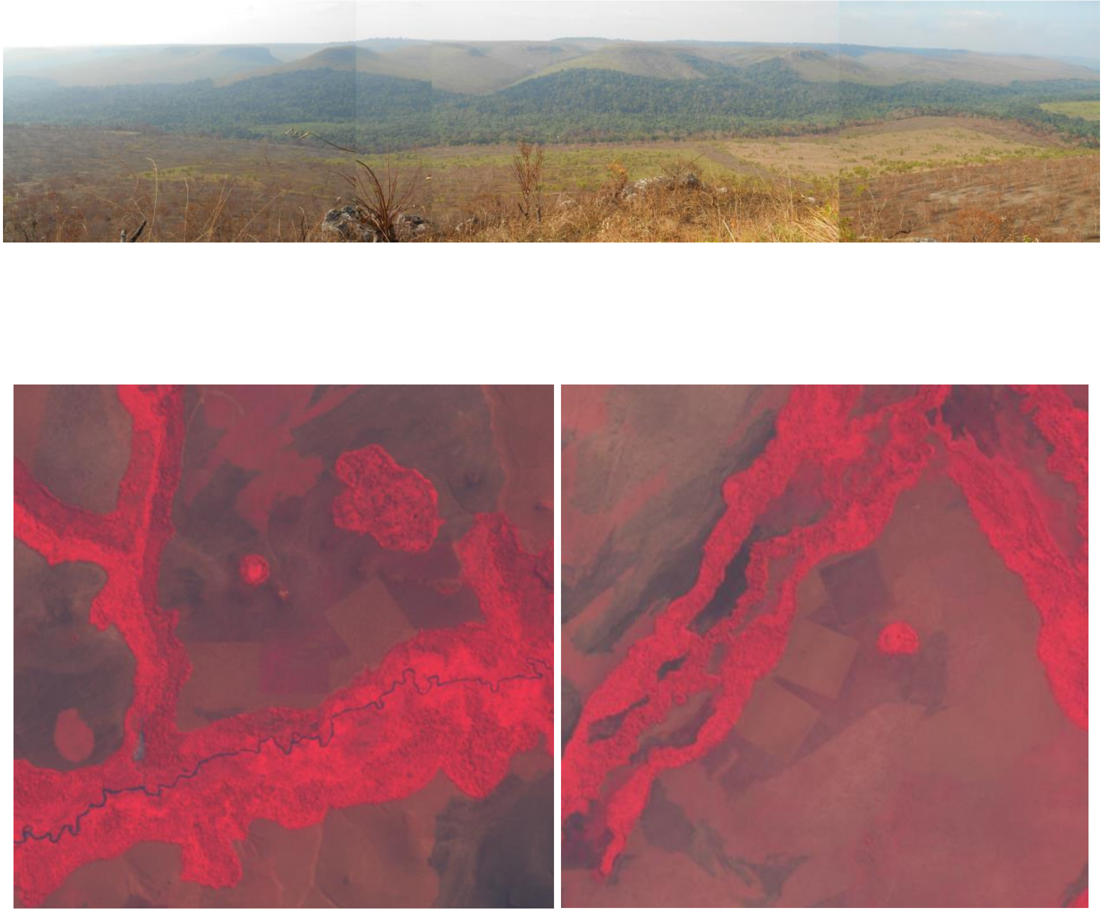
TPI – Topographic Position Index

TRMM - Tropical Rainfall Monitoring Mission

USFS - United States Forest Service

WCS – Wildlife Conservation Society

Chapter 1 Introduction



Top: The experimental plots in Lefini Wildlife Reserve.
Bottom: Sentinel 2 false color composite (R = near infrared, G = visible red, B = visible green), for the plots in Lefini Wildlife Reserves and Lesio Louna Reserve (30/7/2016). The six large (25 hectare) plots are visible a three squares in the centre of each image where experimental fires have been ignited or excluded.

1.1 - General Introduction

1.1.1 The ecology of tropical savanna ecosystems and woodlands

Tropical savannas are characterised by a co-dominance of a continuous herbaceous layer, composed mostly of C4 grass species, and a discontinuous overstorey of disturbance tolerant trees (Frost et al., 1986). Savannas are highly heterogeneous and complex systems, with a large variability of plant spatial structures at local to continental scales (Scholes & Archer, 1997; Sankaran et al., 2005; Bucini & Hanan, 2007). This heterogeneity is both a driver and an effect of complex environmental mechanisms functioning at many temporal and spatial scales. The main ecological factors that determine savanna structure and function are climate, water availability, nutrient supply, soil characteristics, herbivore type/density, and fire. There are numerous studies on the effects of these on savanna structure, but their relative importance remains uncertain, and their effects and interactions clearly varies between sites and on the temporal and spatial scale of its influence (Sankaran et al., 2005; Bond, 2008; Furley et al., 2008; Woollen et al., 2012).

One of the key questions in savanna science is about the mechanisms driving tree-grass coexistence and savanna distribution (Walter, 1971; Scholes & Archer, 1997; Higgins et al., 2000; Sankaran et al., 2005; Hanan & Lehmann, 2010). Trees and grasses respond differently to environmental influences, and these interact by many negative and positive feedback mechanisms, whose strength and sign varies in space and time (Scholes & Archer, 1997; Bond, 2008). Historically, ecologist’s opinions were divided into supporters of bottom-up (water, soil nutrients) or top-down (fire, herbivory) control (Scholes & Archer, 1997; Bond, 2008). In the bottom-up framework, competition for water and resources allows tree-grass coexistence through root niche partitioning, as they source soil and water resources from different soil layers (Walter, 1971). Generally, trees root deeper than grasses, but this is not always the case, and there is still some competition in the top soil layer (Walter, 1971; Holdo & Brocato, 2015). Temporal niche differentiation might also be a factor determining tree-grass coexistence, with trees and grasses responding differently to seasonal precipitation (Scanlon et al., 2005; Archibald & Scholes, 2007), and soil texture affecting the availability of water throughout the year (Fensham et al., 2015). Under the top-down framework, in contrast, the coexistence of trees with grasses results from disturbances like fire and herbivory limiting woody vegetation (Higgins et al., 2000; Bond & Keeley, 2005). Alone these frameworks don't appear to be able to explain all variation in savanna woody cover, and it is now recognised that they should be integrated, as woody cover in savannas is determined by resource-based dynamics and disturbances, together with interactions between them (Staver et al., 2017).

Savannas occur in locations with strong seasonal rainfall climate patterns, and this rainfall and its seasonality are assumed to be the primary determinants of tree cover and woody biomass distribution (Sankaran et al., 2005; Bucini & Hanan, 2007; Lehmann et al., 2011; Staver et al., 2011a). At an African continental scale, it has been documented that tree cover increases with rainfall (Sankaran et al., 2005; Bucini & Hanan, 2007; Lehmann et al., 2014). Sankaran et al. (2005) in his systematic review of African savannas concluded that in semi-arid savannas within a range of Mean Annual Precipitation (MAP) from around 100 to 650 mm, maximum realized woody cover increases with MAP until an upper bound, with soil moisture and seasonality being the main limitations to tree cover. These savannas are defined as stable or climatically determined. For areas above a MAP of 650 mm, mesic savannas, savannas are unstable systems in which MAP is sufficient for woody canopy closure, and disturbances (fire, herbivory) maintain the savanna structure (Fig. 2a) (Lehmann et al., 2011). In these mesic areas, savannas persist even though climate can support forest, and the edaphic conditions and perturbations like fire inhibit tree establishment (Lehmann et al., 2011; Staver et al., 2011a; Veenendaal et al., 2015). Mesic savannas with strong seasonality generally present higher fire frequencies and intensities than arid savannas (Higgins et al., 2000; Van Wilgen et al., 2000; Balfour & Howinson, 2009; Oliveras & Malhi, 2016), as grass production (and fuel availability) tends to increase with increasing rainfall in savannas (Rosenzweig 1962).

Actual vegetation cover distributions in savannas may differ from those predicted by climate in large scale studies (Bond, 2008; Staver et al., 2011a), especially in tropical areas of intermediate rainfall (1000-2000 mm) and moderate seasonality (Lehmann et al., 2011). This observation led to the emerging ecological paradigm of Alternative Stable States, which states that under a wide range of environmental conditions, fire maintains savannas and forests as alternative biome states, by means of a positive feedback mechanism between fire, tree cover and grass fuel (Staver et al., 2011b; Hoffmann et al., 2012; Dantas et al., 2015;

Staal & Flores, 2015). Fire maintains a low tree cover, which facilitates the growth of grass, and these serve as fuel for fires in a positive feedback maintaining savannas in open-canopy savannas (Staver et al., 2011b). Alternately, high tree cover shades out understory grasses, which excludes fire and promotes canopy closure to maintain forest areas. In many tropical areas, forest soils are more fertile than savanna soils, and when forests expand into savannas, trees increase the nutrient availability in savanna soils, creating a positive feedback favouring forests (Murphy & Bowman, 2012).

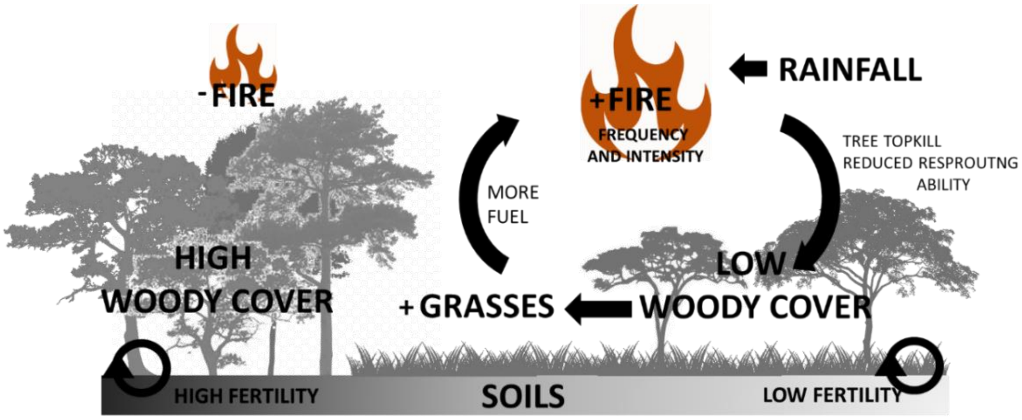


Figure 1.1. Representation of the main controls of savanna structure and their feedbacks. Tree cover is reduced by frequent fires, promoting more grass growth which serves as fuel for more intense fires, which further reduce tree cover. Low fire frequency leads to higher tree cover, which supresses grasses, leading to low intensity fires and a dominant forest tree layer and an increase in soil fertility.

There is ongoing debate about the alternative stable states paradigm in savannas, and while the idea is accepted by some authors (Staal & Flores, 2015), with evidence from the analysis of remote sensing data showing a bimodal tree-cover frequency distribution across the tropics (Staver et al., 2011b), other authors have posed some criticisms. They suggest that, although fire is an important modulator, soil physical and chemical properties better explain the vegetation structure in forest-savanna transitions, and that fire has a reinforcing effect (Lloyd et al., 2008; Veenendaal et al., 2015).

All these views on the savanna biome are not exclusive, and this debate highlights the complexity of this dynamic ecosystem, and the need to understand the multiple complex vegetation-environment interactions at a range of scales. Such understanding is important for quantifying carbon stocks of African savannas and their role in the global carbon budget, to inform effective management of savanna landscapes, and to predict the future savannas under climate change. A representation of the main controls in savanna structure and their feedbacks is included in Fig. 1.1. Figure 1.2. shows the distribution of savannas and other vegetation types in Africa, the distribution of stable and unstable savannas from Sankaran (2005), the annual precipitation and the fire frequency in Africa.

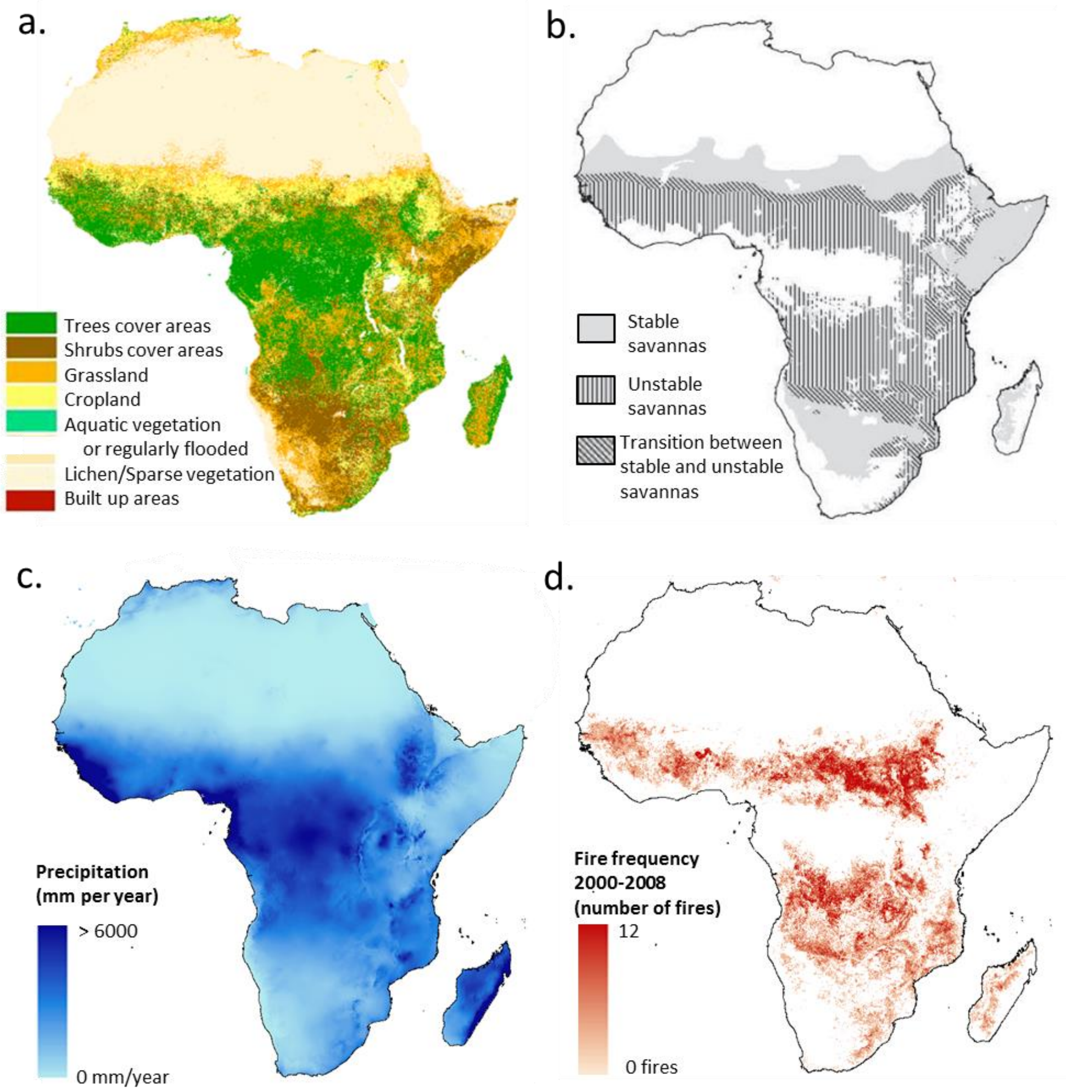


Figure 1.2. a) Land Cover map of Africa 2016 (ESA S2 prototype based on Sentinel-2A at 20 m) b) Distributions of savannas in Africa (grey areas), differentiating disturbance determined 'unstable' savannas (vertically shaded), and MAP-determined 'stable' (grey areas not shaded) and transition between them (cross-shaded areas (Sankaran et al., 2005); c) Total precipitation for Africa, obtained from average monthly precipitation for 1970-2000, Bioclim (WorldClim); d) Fire frequency (number of fires) from 2000-2008 from MODIS (Mitchard 2012). The majority of fires occur in savannas.

1.1.2 Disturbances in the African savannas, fires and herbivores

Fire and herbivores are natural perturbations defining the vegetation structure and composition of savanna ecosystems. While both appear to most dramatically influence grass, the herbaceous layer has evolved to tolerate grazing, and to die off in the dry season before burning and then resprout the following year. Trees, by contrast, are more likely to receive permanent damage or be killed by herbivores or fire, especially when young. However, their relative impacts on vegetation structure are poorly quantified. Knowing the role that these disturbances have on savanna vegetation dynamics is important to better understand and predict the dynamics of the savanna biome under different climate, herbivore and fire regimes.

1.1.2.1. Herbivores

Herbivores have a strong impact on woody canopy cover (Sankaran et al., 2005), driving tree mortality of all size classes of trees, particularly impacting nutrient rich areas, and affecting the landscape in patches (Asner et al., 2009; Staver et al., 2011a). The impact of herbivory depends on whether grazing or browsing predominates, but both limit woody plant regeneration, reducing grass biomass and fuel loads, thus decreasing fire frequencies and intensities (Skarpe, 1991; Scholes & Archer, 1997). Grazing can, in some cases, favour tree cover as it decreases competition from grasses and helps tree seed dispersal (Staver et al., 2011a).

In the following sections, I will focus on the impact of fire, given it is the main disturbance in the study area of this thesis, as herbivore densities are low.

1.1.2.2. Fires

Africa is often referred to as the “fire continent” due to frequent and widespread vegetation fires (Komarek, 1972). Most fires in Africa’s savannas are started by humans for a variety of agricultural, pastoral, and management activities (Archibald et al., 2010), but their intensity and rate of spread is also influenced by traits of the vegetation, the climate, and recent rainfall and temperatures.

Fires have important impacts on African savannas, affecting vegetation composition and structure and altering soil characteristics (Bond, 2008; Beckage et al., 2009; Santín & Doerr, 2016). Woody vegetation is mainly resistant and adapted to fire, with numerous annual plants, and geophyte and suffrutescent species (those with large underground structures, protecting most of the plant's resources and allowing resprouting after fire) (White, 1977). However, the flammable fast growing grasses cure rapidly in the dry season, supporting high fire frequencies (Bond, 2008; Lehmann et al., 2011).

The impact of an individual fire on vegetation is related to the fire intensity, which is closely associated to season and fuel conditions (Bond, 2008). Due to the high fire frequency in savannas, juveniles of woody plants can be topkilled (leaves and branches), but thanks to their ability to resprout repeatedly they can sometimes persist in a suppressed state for years (Higgins et al., 2007; Hoffmann et al., 2012). If there is a fire-free interval of sufficient duration to allow a sapling to reach a critical size at which it is less susceptible to top kill, it can then grow into an adult size and persist given frequent fires (Hoffmann et al., 2012). Thus, fire limits the rate of saplings' transition to adults, when they are mostly resistant to the common mild fires (Hanan et al., 2008; Hoffmann et al., 2009). The influence of fire on savanna vegetation is uncertain, with particular uncertainty about the degree to which existing fire regimes in savannas are sustainable, and with difficulty in identifying the optimal management strategy, and little knowledge of how location-specific the effects of fires are.

The influence of fire regimes on vegetation structure and species composition has been shown to be complexly linked and to be site specific (Furley et al., 2008). The obvious way to understand the role of fire in shaping vegetation is to perform long-term fire experiments (Furley et al., 2008). Controlled fire experiments in African savannas are however quite uncommon, especially long term experiments, and they normally focus on different fire frequency rates, and rarely focus on different fire seasonality treatments. They, have, however, been performed in Africa for decades and provide valuable information about the effects of fire on savanna composition and structure (summaries of the observations in fire experiments in Appendix 1.1, also in (Furley et al., 2008; Veenendaal et al., 2018). These experiments have shown that fires can modify vegetation structure and result in a strong reduction to above-ground biomass (Higgins et al., 2007; Bond, 2008; Smit et al., 2010; Ryan et al., 2011).

In general, there is evidence that species composition, tree cover and plant biomass in most savannas are dependent on the fire regime (Bond, 2008), but the exact effects remain uncertain and vary depending on the location. Additionally, fire is an ancient phenomenon in savannas, and sensitive to small climatic variations, which requires long time series to fully understand its effects, hence the importance of long term fire experiments.

1.1.2.3. Fire regimes

Fire and vegetation affect each other in a series of positive and negative feedbacks that depend on the frequency, seasonality and intensity of the fires (Beckage et al., 2009). The characteristics of fires at a given site is termed the fire regime, defined mainly by frequency, intensity, size, seasonality, type, and severity (Bond & Keeley, 2005). Fire frequency is the occurrence of fire for an area over a time period; intensity refers to the energy released; severity is a measure of ecosystem or vegetation impact; and seasonality is the variation of the timing of fire within the year (Bond & Keeley, 2005).

Frequent fires generally promote less woody cover (Sankaran et al., 2005), as it prevents recruitment of juveniles into adult size classes (Higgins et al., 2000). Areas with very sandy soils, however, are likely to have higher woody cover (Sankaran et al., 2005). Sandy soils, like the ones of the Kalahari sands, normally have lower nutrient availability, but they can stimulate a higher tree cover in cases where its greater water percolation to soil layers below grass roots can overcome the mentioned negative effects of lower fertility (Sankaran et al., 2005), and tilt the competitive balance against short-rooted grasses towards deep-rooted trees. The mean fire return interval across all Africa’s savannas is estimated to be around 4 years (Laris & Wardell, 2006; Furley et al., 2008), but fire frequency in savanna woodlands in Africa varies widely, being sometimes annual or even semi-annual (Archibald et al., 2010). A sufficient fire return interval of 3 years or more allows trees to reach a sufficient dimensions to escape the fire trap (Bond & Keeley, 2005). Variations in fire intensity or frequency might create patchiness in the landscape supporting different vegetation states and increasing biodiversity (Parr & Andersen, 2006).

In addition to fire frequency, the seasonality of a fire regime impacts vegetation dynamics. At the start of the dry season grassy fuels are only partially cured and still retain humidity, and thus fires burn at low intensity and tend to cause less damage to the vegetation. These fires generally only result in the mortality of young shrubs and saplings, but rarely impact larger stems, and allow roots to survive and plants to resprout during the following rainy season (Menault et al., 1995, Ryan & Williams, 2011). Fires in the early dry season also tend to fragment the landscape, creating a patchwork of burned and unburned areas, impeding the spatial diffusion of high intensity fires than can occur later in the season (Bucini & Lambin, 2002). However, early dry season fires can be disadvantageous to grass meristems, and can promote the establishment of woody species which may be undesirable (Roques et al., 2001; Pricope et al., 2012). Fires that occur in the late dry season burn on fully-cured and dry fuels, resulting in intense fires that have greater impacts on woody vegetation (Govender et al., 2006; Laris et al., 2016). High intensity fires can burn tree branches, destroy tree bark, and can result in the top-kill or mortality of large tree stems (Ryan & Williams, 2011). Such fires occasionally pass into adjacent closed canopy forests where vegetation is not physiologically adapted to fire, resulting in widespread tree mortality.

The most common type of fire in savanna areas are surface or ground fires, fires that burn through the grass layer with low flame height. Ground fires burn dry grasses, surface litter, shrubs, and occasionally small trees (Laris & Wardell, 2006). These fires do much less damage to established trees than crownfires, fires that pass through the crowns of trees of shrubs (Bond, 2008). Crownfires are rare, occurring under extreme weather conditions.

1.1.2.4. Fire management

Given the above, it is clear that changes to a fire regime have the potential to have dramatic effects on tree cover (Louppe et al., 1995; Hoffmann & Solbrig, 2003; Furley et al., 2008). In the absence of frequent fires, savannas can be encroached by forest fire sensitive trees (Hoffmann et al., 2012), provoking a loss in habitat for open area associated species. As most savannas in Africa are inhabited by people, or else directly managed, the fire regime of the vast majority of Africa’s savannas is subject to management decisions.

Since hominids evolved in African savannas and gained the ability to manipulate fire, they have impacted the fire regime (Archibald et al., 2012). Active fire management in African savannas has been practiced for long time (van Wilgen, 2009). Traditionally, local authorities controlled the use of fire in many parts of sub-Saharan Africa by restricting its use to certain planned occasions like hunting (Walters, 2010a). In West Africa, these traditional burning practices normally used varying fire regimes across the landscape, at different times of the year causing patchiness (Laris & Wardell, 2006). However, new fire legislation introduced during colonial times, in Western and Southern Africa, revoke local practices and control mechanisms, restricting or supressing fire, causing environmental impacts (Bond & Archibald, 2003; Laris & Wardell, 2006; van Wilgen, 2009).

Management of savannas in Africa has evolved over the recent decades, due mainly to a better understanding of this ecosystem thanks to new research and experiments, and to changes in ecological mentality (Bond & Archibald, 2003; Parr & Andersen, 2006). Recent studies have presented fire as an inevitable and necessary natural process to maintain savannas (van Wilgen, 2009). Early burning management techniques are now used in some parts of Africa (Laris & Wardell, 2006; Diouf et al., 2012). Although few protected areas are under controlled burning regimes, fire management of protected areas aims to promote landscape heterogeneity, trying to imitate natural conditions (van Wilgen, 2009). Understanding the impact of fire management remains a challenge due to the limited understanding and future uncertainties. In order to effectively manage fire in an area, there should be an assessment and understanding of its fire regime, its dynamics and their response to change.

1.1.3 African savannas in the global carbon cycle, and their future with climate change

Anthropogenic emissions of carbon dioxide (CO_2) into the atmosphere has increased over the past few centuries, mainly from fossil fuel emissions and land use change activities, resulting in an increase of atmospheric CO_2 (Le Quere et al., 2018). This unprecedented change to the global carbon (C) balance has changed the climate of the Anthropocene (Steffen et al., 2007; Lewis & Maslin, 2015), and has resulted in global warming and rapid climate change (IPCC, 2014). In this context, there is a crucial need to better understand and further research the global carbon cycle in order to make more reliable predictions of future climate at both local and global scales, and to mitigate and adapt to environmental changes. In the savannas of Africa these challenges include rapid increase in Africa's population (UN, 2017), and high rates of deforestation and land use change.

Savannas and woodlands account for about 27.5 PgC (or 45.9%) of the total above-ground carbon stocks in tropical Africa (Baccini et al., 2012), and due to their large extent, frequent fires, and strong interannual variability, African savannas play a prominent role in the global carbon cycle (Grace et al., 2006; Williams et al., 2007; Ciais et al., 2011). However, the knowledge of the C stock estimates and annual fluxes remains limited (Williams et al., 2007; Ciais et al., 2011). Uncertainty in the C cycle of African savannas results from a limited existing observational network and lack of long-term measurements (Williams et al., 2007; Ciais et al., 2011), and is related to the spatial heterogeneity in vegetation structure of savannas.

Estimates of the annual carbon budget of savannas range from a small source, to a small sink, with substantial interannual variability (Williams et al., 2007; Bombelli et al., 2009; Ciais et al., 2011; Valentini et al., 2014), with the majority of estimates suggesting that savannas worldwide are a small net sink of carbon. In Africa, where savannas are the dominant land cover, a lack of in situ measurements result in particularly large uncertainties to the carbon cycle. The annual African carbon balance averages −0.61 ± 0.58 PgC/yr (Valentini et al., 2014), but with substantial spatial variability relating biome distribution and anthropogenic impacts. Focusing on African savannas, Ciais et al., 2011 estimated savannas and woodlands to be a sink of 0.8 ± 1.6 tC/ha/yr. This C sink is partly offset by losses from land use change (Valentini et al., 2014), with deforestation rates estimated to be higher in African savanna woodlands than in tropical rain forests (Brink & Eva, 2009; Ciais et al., 2011; Bouvet et al., 2018; McNicol et al., 2018). Fire also plays an important role in the African C cycle, with emissions from vegetation fires the largest source of atmospheric carbon in Africa (Williams et al., 2007). The vast majority of fire emissions originate in savannas and woodlands (Valentini et al., 2014).

African ecosystems are expected to undergo major changes in the future due to climate change, and are predicted to be one of the parts of the world most vulnerable to the impacts of climate change (IPCC, 2014; Niang & Lennard, 2014; Baudena et al., 2015).

Projections of the future of African ecosystems are widely divergent and highly uncertain, mainly because these projections need to incorporate the complex and interacting effects of atmospheric CO_2, precipitation, together with the disturbances from fire and herbivores (Niang & Lennard, 2014; Midgley & Bond, 2015). Predictions for African climate by the end of this century indicate a general warming, frequent occurrence of extreme heat events, and high regional rainfall variability, as some regions will get drier (Serdeczny et al., 2017).

With climate change, an increase in temperatures, and in rainfall variation (Jolly et al., 2015; Serdeczny et al., 2017) will likely result in fires that are more intense and extensive (Bowman et al., 2009), resulting in ecosystem changes such as alterations to species composition and vegetation structure. It is predicted that increased atmospheric CO_2 concentrations may affect the balance between grasses and trees (van Wilgen, 2009). Recent studies indicate that many savannas are experiencing a CO_2 fertilization effect, whereby increasing atmospheric CO_2 concentrations are stimulating plant growth (Buitenwerf et al., 2011). By growing faster, trees increase their chances of reaching a sufficient height to escape the fire trap (Bond & Midgley, 2000). This effect might result in rapid structural change over extensive areas of grasslands and savannas in Africa, with a potential loss of bistable savanna and forest states across wide areas (Higgins & Scheiter, 2012). Woody encroachment into previously savanna areas has been observed in many African ecosystems, and the effect will likely accelerate as atmospheric CO_2 concentrations continue to increase (Mitchard et al., 2009; Mitchard & Flintrop, 2013; Stevens et al., 2016).

1.2 - The Bateke Plateau

This section includes a description of the Bateke Plateau landscape, with its historic and present ecological background, and the environmental and the human factors that shape this landscape.

The Bateke Plateau extends from the east of Gabon to the southwest of Democratic Republic of Congo (DRC), with most situated in Republic of Congo. With an area of approximately 89,800 km^2 (Fig. 1). It extends between the parallels of the Equator and 5° S, and the meridians of 14 and 17° E. The Bateke intrudes into the Congo basin, the second largest block of continuous tropical forest after the Amazonian basin, and an important biodiversity hotspot. It is part of the Guineo-Congolian regional centre of endemism (White, 1983), with most of the Bateke included in the Western Congolian forest-savanna mosaic ecoregion (Olson et al., 2001). The landscape comprises 5 different savanna plateaus (Koukouya, Djambala, Nsa, Ngo and Mbé/Batéké) with most of them draining into the Congo river (Descoigns, 1960; CBFP, 2006). It consists mainly of rounded hills punctuated by erosion cirques, with an elevation that ranges from 259 to 872 m above sea level (mean of 545 m), each separated by deep valleys mainly associated with rivers (Descoigns, 1960; CBFP, 2006).

1.2.1 Precipitation

This area has a tropical transitional climate, characterized by an average annual precipitation of 1627 to 1966 mm and a mean annual temperature of approximately 25°C (all calculated in Chapter 3). There is a main dry season from June to September, and a short dry season in January and February (Vande Weghe et al., 2009, and Fig. 1.3.). The average annual precipitation for the years 2015-2017 derived from TAMSAT (Tropical Application of Meteorology Using Satellite Data and Ground-Based Observations) is shown in table 1.1. The presence of savannas here might seem unexpected due to their very high rainfall which potentially could support closed canopy forest, but it is thought to be a result of edaphic and anthropogenic factors (Sankaran et al., 2005).

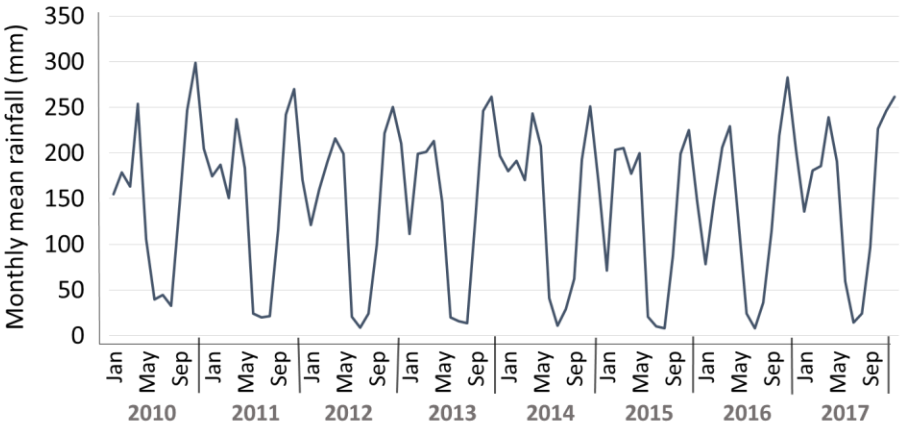


Figure 1.3. Mean monthly rainfall (derived from TAMSAT for the Bateke Plateau for years 2010-2017).

Table 1.1. Mean annual rainfall and standard deviation (derived from TAMSAT for the Bateke Plateau for years 2015-2017).

	Mean rainfall (mm)	S.D.
2015	1553.37	80.91
2016	1678.34	86.29
2017	1860.11	83.99

1.2.2 Soils

The Bateke landscape is located on the most northern part of the Kalahari Sand, an ancient sand dune system (Haddon, 2000), with the deepest sand deposits on Earth (Fig. 1.4). Soils are mainly sandy in texture and ferralitic (Schwartz & Namri, 2002), identified as Ferralic Arenosols (FAO-UNESCO), and typically have very little organic matter. These sands have high percolation rates, resulting in potentially less water available for plants despite the high rainfall. Part of the soils, however, are podzols located in the lower areas, in small closed depressions or in valley bottoms and terraces (Schwartz, 1988).

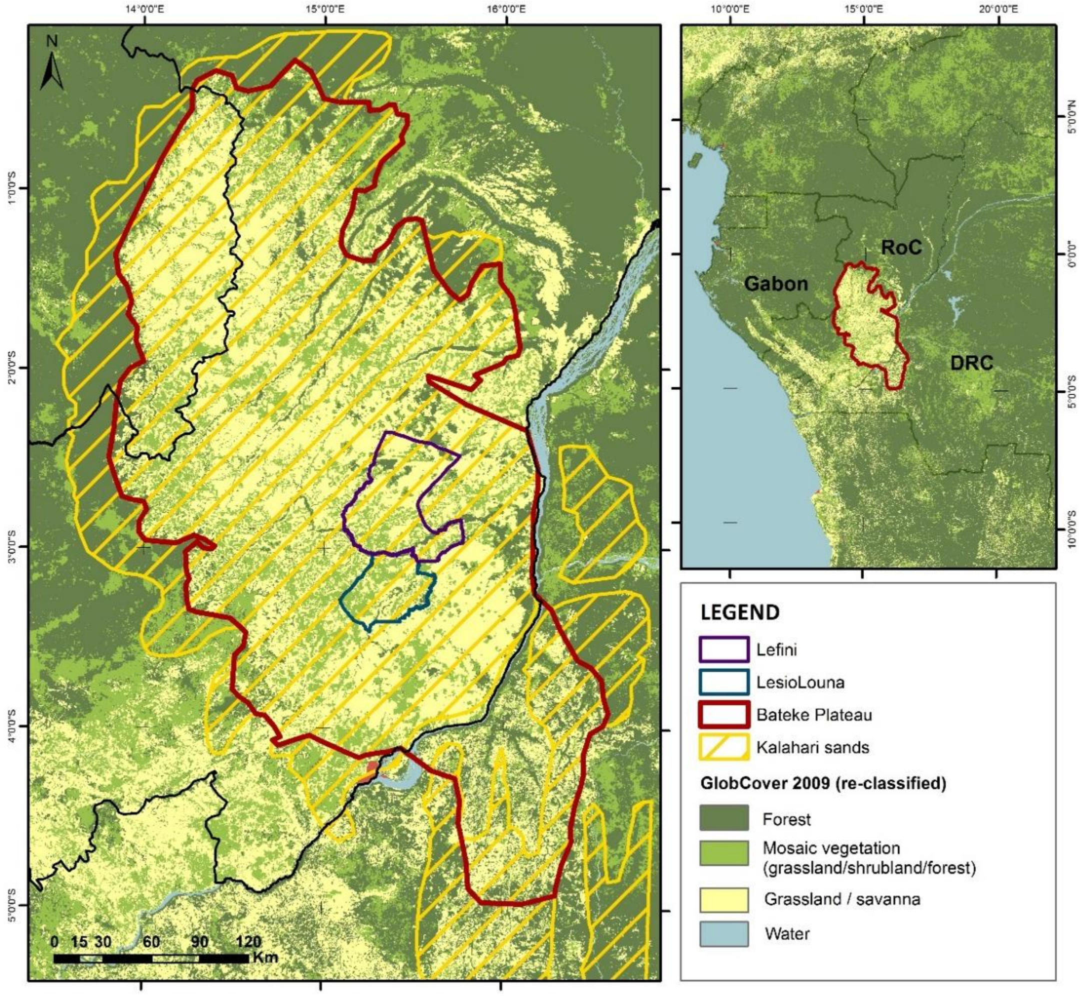


Figure 1.4. Distribution of the Kalahari sands over a land classification map (Globcover 2009 reclassified). Lefini and Lesio Louna are the two protected areas where the field sites in this thesis are located (more information in Chapter 3).

Note: In this thesis, "Bateke Plateau" is used to refer to the geographic entity of the Batéké Plateaux area. The Bateke Plateau landscape doesn't have official delimitations, so for this thesis I have opted to create an extent of the geographical area of the Bateke Plateau by taking into account the delimitation of the savanna-forest mosaic bordered by the rainforest, the extensions of the Kalahari sands, and including the 5 plateaus that correspond to this landscape (Fig. 2).

1.2.3 Vegetation

The vegetation of the Bateke Plateau is predominantly a mosaic of savanna with patches of closed-canopy forest. Savannas cover the majority of the Bateke Plateau, whereas forests occur normally surrounding rivers. The savanna woody vegetation is composed of trees and perennial bushes, most of them fire resistant (Makany, 1973), with an understory of grasses and forbs. The herbaceous vegetation consists of annual plants and perennials, some of which only survive the dry season underground (geophytes).

The several different habitat types have been identified by researchers in the Bateke Plateau are included next in more detail (information from: (Duvigneaud, 1949, 1953a, 1953b; Koechlin, 1960; Aubréville, 1961; Makany, 1973; Vande Weghe et al., 2009; Walters, 2010a) (Photos 1-12):

- Herbaceous savanna (or steppes): Open grasslands with or without limited woody cover, often occupying the higher part of hills, in the poorest and more arid soils. Grasses vary in height and in dominance, with Poacea being the main family. The most abundant grass species are *Loudetia simplex* and *Hyparrhenia diplandra*. Other species belong to the genres *Hyparrhenia, Andropogon, Beckeropsis, Cterium* and *Panicum.* Herbaceous savannas can be further divided in:
    - Island savannas: relatively small and surrounded by forests;
    - La Grande Savanna: large continuous savannas divided by forests, roads, and rivers. They cover most of the Bateke landscape.
- Wooded savanna: Savannas with woody vegetation that ranges from more open to dense. It is found normally at valley bottoms or bordering riverine forests. Trees are normally small or shrubs. Tree species diversity is low, with around a dozen species, dominated by *Hymenocardia acida Tul. (Europhorbiceae)*. *H. acida* can grow up to six meters tall, and is particularly resistant to fire. It normally forms clumps that sprouts after the passage of fire, with the survivors reproducing vegetatively. In the past, its wood was used for charcoal and its bark as a dye. Nowadays, it is sometimes used for medicinal purposes, and Teke woman occasionally collect their fruits.

  The second most abundant species is *Annona senegalensis*, which also resists fire well. Less frequent tree species are: *Maprounea africana*, *Ochna afzelii*, *Bridelia ferruginea*, *Syzygium guineense*, and *Vitex madiensis*. There are also some small shrubs like *Painari capensis* and *Anisophyllea quagensis*. Leguminosiae are not very abundant (*Albizia adianthifolia* and *Dialium englerianum*). After the passage of fires, the aerial parts of these plants can be completely destroyed but their roots can rapidly resprout and produce shoots with fruits shortly after the fire.

- Forest: The transition between forest and savanna is normally very abrupt. There are three types of forests, with the main species being *Millettia laurentii*, *Pentaclethra eetveldeana*, *Hymenocardia ulmoides*, *Chaetocarpus africanus*, *Greenwayodendron suaveolens* and *Dacryodes yangambiensis*:
    - Forest fingers and Riparian forest: they exist mainly along rivers and some lakes, where soils are less sandy and have a deeper organic layer. They form an extensive forest edge (photos 1, 3 and 6);
    - Recent forest: occur at the forest-savanna edge where forest is encroaching. Includes isolated *Hymenocardia acida* trees;
    - Small forests patches often around former village sites: they are frequently located on hill tops. The vegetation of these is mainly secondary species including fruit trees like avocado and sapho (*Dacryodes edulis*).
- Humid grassland: there are some wet grasslands or peat bogs in the catchments of hills, dominated by grasses of the genera *Xyris*, *Utricularia*, and *Mesanthemum*.
- There are also some marshes around a few small lakes, but these are not extensive.

1.2.4 Fauna

Herbivore densities in the Bateke Plateau are low and do not cause much disturbance due to historic and current hunting, though there probably were once high herbivore densities that could have had a role in shaping the landscape we now see (Vande Weghe et al., 2009; Walters, 2010b). Poaching for bushmeat, trade and ivory has severely depleted many species. Herbivores probably had an impact on the vegetation, although these savannas possibly never maintained a fauna as diverse as those of eastern and southern Africa, as the rain forest to the north and the Congo River to the south form impassable barriers for most species from the Sudano-Zambezian savannas (Vande Weghe et al., 2009).

Mammals in the Bateke Plateau savannas are represented by widely distributed species in Africa, but rare in the Congo Basin. Ungulates typical of these savannas are the bush duiker (*Sylvicapra grimmia*) and the bushbuck (*Tragelaphus scriptus*). Other mammal species are the hippopotamus (*Hippopotamus amphibious*), buffalos (*Syncerus caffer*), elephants (*Laxodonta sfricana*) living mainly in gallery forests but that can venture into savannas, and small populations of spotted hyena (*Crocuta crocuta*) and jackal (*Canis adustus*) (Vande Weghe et al., 2009). There are also some populations of leopard (*Panthera pardus*) and golden cat (*Felis aurata*) associated with the gallery forests. Lions (*Panthera leo*) were thought to have disappeared from the area since 1996, but in 2015 there was camera footage of a single male lion from the Plateaux Batéké National Park (PBNP) (Hedwig et al., 2018). The Bateke host a big population of birds, with 267 species recorded (Christy, 2001; King, 2011). There are other species associated with forested areas, including the chimpanzee and the western gorilla (CBFP, 2006). Termites don't generally like sandy soils and are not abundant in the Bateke Plateau (Vande Weghe et al., 2009).

In recent years, conservation programs are aiming to improve the state of the wildlife in this landscape. Some projects are the megafauna restoration project in the Batéké Plateau of Gabon and Congo (Aspinal Foundation), the reintroduction programme of Western lowland gorillas both Gabon and RoC (The Aspinall Foundation) and multiple wildlife surveys by Wildlife Conservation Society (WCS) and the Congolese Ministry of Forestry Economy and Sustainable Development (MEFDD).

1.2.5 Past history

The origin and dynamics of savannas are not well understood, although savannas have existed in Africa for millions of years (Bond, 2008). Some research using paleosols in Africa suggest that there is strong evidence for relatively sparse woody cover habitats in the Late Miocene to early Pliocene (around 6 to 4 M years ago) (Cerling et al., 2011). A global expansion of savannas occurred during the late Miocene (Staver et al., 2011a). Various studies (e.g. Keeley and Rundel (2005)) have theorised that late Miocene climate changes (increased rainfall seasonality followed by a dry season and a monsoon climate) created a fire climate capable of replacing woodlands with C4 grasslands. This hypothesis is supported by paleosol data and by charcoal sediment profiles (Keeley & Rundel, 2005). Other studies, however, suggest that fire was responsible for driving the late Miocene expansion of C4 grasslands in the context of low CO_2 levels which could have slowed the rate of tree recovery after fire, relative to C4 grasses (Bond & Midgley, 2000; Keeley & Rundel, 2005).

Until about half a century ago, the dominant theory about the origin of the Bateke landscape stated that it was created by people burning the forests (Aubreville, 1949), a theory that still has some support. This theory might be the reason why this area is very poorly known ecologically and biologically, as it was considered secondary and therefore less interesting. However, since then, more recent studies are suggesting that these savannas are not new, but this forest savanna mosaic constitutes an ancient landscape (Koechlin, 1960). These savannas existed even during the wettest periods of the at least last tens of thousands of years (Koechlin, 1960). They have periodically expanded or contracted, but the savanna never disappeared (Schwartz, 1992; Maley & Willis, 2010; Maley et al., 2018).

The past biogeography of the Bateke landscape is discussed more in detail in Chapter 3. In summary, several studies suggest that the Bateke Plateau savannas are at least 20,000 years old, with a last great expansion around 3200 years ago, following a dry climatic event (Maley, 2001). This climatic event was accentuated in the sandy areas with high percolation rates that significantly amplified the effect. Elenga et al. (1994) summarises the main conclusions of the major climatic and vegetation changes of the recent past based on geomorphological, pedological and archaeological studies and on remains of macroflora In Republic of Congo (Table 1.2). Human influence probably started later, with regular anthropogenic fires maintaining savannas.

Table 1.2. Major climatic and vegetation changes of the recent past in Congo (Elenga et al., 1994)

YEAR B.P	MAJOR CHANGES
40,000-30,000	humid period - forest expansion
30,000-12,000	arid period - extension of wooded savanna
12,000-3000	humid period - new forest expansion
CA. 3000	climate and vegetation reach present state

Wetter conditions, and less seasonality, have promoted the encroachment of forest into the savannas across much of Central and West Africa in the last millennium (Stevens et al., 2017). In recent decades, anthropogenic impacts (e.g. agriculture, fire, land clearing) have reduced the forested area in some areas of the Plateau (Vande Weghe et al., 2009).

1.2.6 Protected areas

The Bateke landscape contains 5 protected areas:

- Lefini Wildlife Reserve: One of the oldest parks in Africa. Described in more detailed in Chapter 3;
- Lesio-Louna Reserve: Also described in more detail in Chapter 3. This reserve has some areas where fire has been excluded for about 20 years, around the main camp;
- Parc National Plateaux Bateke (PNPB). Located in Gabon, on the border with RoC. Proposed for conservation due to its exceptional landscape, its potential for tourism and the presence of unique animals (Vande Weghe et al., 2009). Officially designated in 2002, includes collaboration management activities with the Projet de Protection des Gorilles (run by the John Aspinall Foundation).
- Ogooué Leketi National Park: This park, located in RoC, is a cross-border park contiguous with the PNPB. It was established in November 2018, being delayed for several years due to conflict with forestry concessions located in the park. It's expected to reduce the problematic of border conflicts with Congolese hunters (WCS Congo Program, 2018);
- Bombo-Lumene Game Reserve: situated in the south of the Bateke, in the Democratic Republic of Congo, this protected area is located 130 km from Kinshasa.

WCS-Congo, together with Ministry of Forestry Economy and Sustainable Development (MEFDD), manages the Lefini, Lesio Louna reserves and the Ogooué Leketi National Park. Additionally, the CARPE program, within the framework of the Congo Basin Forest Partnership (CBFP), identified in the year 2000 12 priority landscapes for conservation in forested Central Africa. The PNPB and the Lefini Wildlife Reserve were linked in the so called "Léconi-Batéké-Lefini Landscape", covering a total area of 3.5 million hectares, and a large part of the Bateke Plateau. Within the Bateke Plateau area the Leketi-Mbama Ramsar site (wetland of international importance) is found, located in the North of the Bateke, and the Ibi-Batéké Carbon Sink project (I-BCS) in the Ibi Village (in DRC). The I-BCS project is an integrated rural development programme to promote sustainable development.

1.2.7 People

The Bateke Plateaus are occupied by the Teke people, the oldest of the Bantu tribes in the Republic of Congo. The Bantus appeared in the area about 3000 BP, with large-scale Bantu migrations into the Bateke Plateaux ending around 1000 AD (Schwartz, 1992). The increase of commerce on the Congo River during the 1500s, the colonisation by France and Belgium, and the large concessions to exploit timber, minerals, or rubber, changed the structure of this landscape (Vande Weghe et al., 2009). More recently, there was a rural exodus to the cities and a ‘reagroupment’ of villages by the state in the 1930-1970´s, moving larger settlements near roads to ensure better access to health and education (Vande Weghe et al., 2009). Although the forest areas have high social and cultural values (with historical sacred and cultural sites), populations living in the savanna (i.e. the Teke people) didn’t like the forests, and consequently they usually abandon and change village location as soon as they feel too enclosed by vegetation (Walters, 2010a). These abandoned villages became normally invaded by vegetation, forming forest patches of species including mango trees and oil palms, and shaping the landscape (Vande Weghe et al., 2009).

The present-day Bateke Plateau is influenced by people living throughout the area, although the population density has historically always been low (Vande Weghe et al., 2009). The average density of the human populations is around 0.2 inhabitants/km^2, but their distribution is uneven (CBFP, 2006), and more people live in the savannas than in the forests (Sautter, 1966). This low population density could be related to low animal density, low water availability, migration, catastrophic disease events, the slave trade, or poor soil quality (Sautter, 1966; Walters, 2010a). Human influence likely decreases with increasing distance from roads and villages, which provides access to transportation, sending and receiving products to larger populated areas, but nearly every part of the landscape is currently influenced by people to some extent (Sawyer & Menakis, 2014).

Today, the value of the savanna for the local people is high, since it is a source of sustenance and part of their culture (Walters, 2010a). Batéké populations mainly practice subsistence agriculture, gathering, fishing and hunting, with natural resources playing a significant role in the economy (Walters, 2010a; Rayden et al., 2014). These activities have however changed in nature, a transformation associated with access to new technologies, like hunting with guns (Vande Weghe et al., 2009).

1.2.8 Role of fire in the Bateke Landscape

Fire has long been part of the Bateke Plateau ecosystems. Palynological studies show the appearance of vegetation fires in Africa around the end of the Cretaceous period, 65 million years ago (Beerling & Osborne, 2006). Fires were normally ignited by thunderstorms, mostly at the end of the dry season, burning huge areas.

Humans started modifying the fire regimes in Africa since they began occupying these areas. In African savannas, the use of fire by hominids probably increased the fire frequency starting around 2.5 million years (Scholes & Archer, 1997). However, humans are thought to have started to have substantial influence on burning regimes around 4000 BP (Archibald et al., 2012). There is limited information about the fire regimes in the Bateke until the first Western explorers arrived in the 1880s. Since then, several ethnographic and explorer accounts discuss the ways in which fire was controlled in the Bateke, and Walters (2010a) provides a summary of them and the social side of fires in the Bateke in Gabon. According to these, the land chief had strict control over the timing and location of fires, customary fire laws were respected, many villages participated in an annual fire drive that resulted in a mosaic of burned and unburned areas bounded by domains, and the largest fires were set during the dry season for communal hunts (Walters, 2010a). Burning without authorisation was heavily punished. More recently, human fire intensity has intensified (Vande Weghe et al., 2009). The communal fire hunts disappeared in the 1960´s, following the collapse of the traditional land use, the removal of lands from the local communities, the introduction of guns and the limitation of the power of the chief (Walters, 2010a). Today, land chiefs of the Bateke Plateau don’t have the power to control people and, consequently, fires have become less seasonal and unregulated, although hunting fires typically peak at the end of the dry season as they did in the past (Walters, 2010a).

In the present day almost all of the fires in the plateau are caused by humans, with most of the savanna normally burning at least annually, mainly in the long dry season (June to September), although there is a very small secondary peak in the short-dry season (January to February), as shown in Chapter 5 and in (Vande Weghe et al., 2009; Walters, 2012; Sawyer & Menakis, 2014). Some fires in the rainy season are possible due to the highly permeable soils (Vande Weghe et al., 2009). Savanna areas are regularly burned by local populations and managers for a range of purposes, including for subsistence (hunting, gathering, agriculture), safety (visibility, habitat removal, path clearing, ease of travelling), and for pleasure. Lightning fires can occur, but are mainly during the rainy season and therefore probably not extensive (Walters, 2012).

Most of the fires are probably extinguished by weather, through changes in wind direction, relative humidity, and/or precipitation (Sawyer & Menakis, 2014). Barriers to fire spread on the Bateke include forests, roads, rivers, and areas that have recently burned, but under certain weather conditions, even these barriers might not be able to stop fire spread (Sawyer & Menakis, 2014). Sometimes, very intense fires burn also the forests, with the rivers acting as the only barrier. In this landscape, early dry season fires tend to burn patchily, and burn incompletely either due to immature fuel (grasses) or to weather. Early season fires are normally short lived, whereas dry season fires can burn for days, covering large areas. Semi-annual fires normally burn incompletely, creating zones of unburned land and a patchy landscape (Walters, 2010b).

Currently, most of the management of fuels on the protected areas in the plateau employs fire, and this is either direct (burning on or near the area being managed) or indirect (fire entering the managed area from elsewhere) (Posner et al., 2009). Given the culture, ecology and fire dynamics of this landscape, trying to remove fire from it would be impossible and possibly undesirable, as fire is essential to maintain the forest-savanna biome (Posner et al., 2009). Fires are imperative for some savanna vegetation and some animals in the Plateau. Thus, it was suggested that the most appropriate tool to manage fire in this system could be the use of fire under controlled and monitored conditions (Posner et al., 2009).

WCS and USFS are working for an improved understanding of fire dynamics in the Bateke Plateau, with the goal of using fire to maintain and conserve savannas in some areas and allow forest regeneration in others. This will potentially have important consequences for the role of the Bateke Plateau in the national carbon emissions reduction strategy. This PhD project was funded with this objective in mind. Now, the USFS and WCS's Batéké Project have initiated a planning process, together with the government and local communities, to better coordinate the use of fire in this landscape. In 2018 they hosted a validation workshop for a simple fire management plan for the Lefini Reserve and organised a technical fire commission made up of local communities, government agencies and civil society organizations to discuss the development of a fire management plan for communities living in and around the Lefini Reserve. The goal is for this plan to be used as an example for other areas across the country (the work is funded by the U.S. Agency for International Development's Central Africa Regional Program for the Environment USAID/CARPE). In Lesio Louna Reserve, staff apply regular preventive prescribed burns, sometimes twice or three times per year in some areas. They do these burns to protect forest fragments from escaped or intentional fires, but with little scientific basis for their burning programme.

1.2.9 Threats to the Bateke Plateau

The Bateke Plateau, even with a low population density, is threatened due to its proximity to two large capital cities, Brazzaville and Kinshasa, with populations estimated at 1.8 and 9.5 million respectively, and a subsequent high demand for charcoal and bush meat (Hoare 2007). The improvement of road transport to Brazzaville in 1996 has increased the pressure in this landscape, making possible the transport of wood and products to Brazzaville or Kinshasa (WCS, 2015). Agro-economic activities such as manioc, peanut, pineapple, yam and wood charcoal production, logging, hunting, slash and burn agriculture and bush fires have widely impacted this landscape, being important drivers of forest degradation and deforestation (Rayden et al. 2014). In the protected areas there is an increased threat by mechanized agriculture, harvesting for firewood and artisanal logging (WCS, 2015). The fauna is highly endangered by local and commercial hunting to supply urban markets in RoC, DRC and Gabon (WCS, 2015). The alterations of the fire regimes pose another source of threats to this area. Additionally, logging concessions have increased the threats to this landscape. In RoC, three logging concessions have been established in the Bambama and Zanaga forest, which overlap with the new national park. In DRC there is an abuse of illegal artisanal logging permits (CBFP, 2006).

Remote sensing data (MODIS and Landsat) indicate that the Congo Basin does not suffer from the large-scale clearing found in other humid tropical forest zones (Hansen et al., 2013). However, extensive and fragmented forest clearing is still occurring, with significant implications for the region's biodiversity (Posner et al., 2009). There is evidence of some areas the south of the Congo Basin suffering woody cover reductions (Mitchard et al., 2009; Mitchard & Flintrop, 2013). In the Lefini Wildlife Reserve, for example, the surface area of forest at the east and north has diminished (WCS, 2015). There is also some evidence of forest encroaching into the savanna in tropical savanna mosaics in Africa (de Foresta 1990; Delègue et al. 2001; Favier et al. 2004; Maley 1990; Mitchard et al. 2009). Favier et al. (2004) observed encroachment in the littoral region of RoC, and Schwartz et al. (1996) found evidence of forest advancing into the savanna in the Congolese Mayombe at a rate of 20-50 m per century.

Photo 1. The Lefini river, an example of riverine forest.

Photo 2. A Bai in the Lefini reserve, used by forest elephants.

Photo 3. Lac Bleu, In Lesio Louna, with its surrounding forest.

Photo 4. An orphan Gorilla in Lesio Louna, in the orphan gorilla Aspinall Camp.

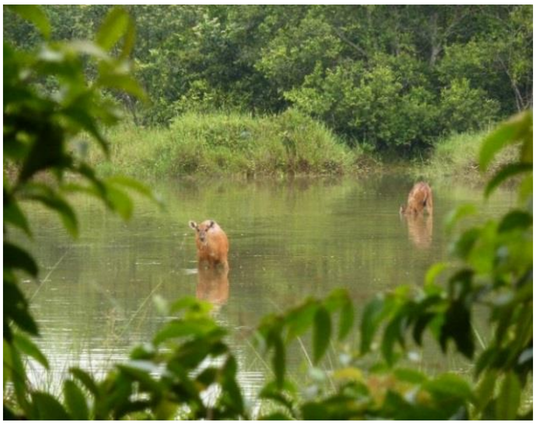


Photo 5. A lake close to the Ibou Briko camp, in Lesio Louna.

Photo 6. River in the Lesio Louna Reserve.

Photo 7. View over plot LWR1 in Lefini Wildlife Reserve.

Photo 8. Lefini Wildlife Reserve.

Photo 9. Lefini Wildlife Reserve.

Photo 10. A fire in an island savanna, Lesio Louna Reserve.

Photo 11. Lesio Louna, plot LLR1.

Photo 12. Lefini Wildlife Reserve.

1.3 - Thesis outline and key questions

The aims of this thesis are to improve our understanding of the Bateke Plateau savannas focussing on the mechanisms that control tree cover, and the effects of fire seasonality and frequency on savanna vegetation and carbon stocks. There are two main methods used to investigate these: field experiments and observations through remote sensing. This thesis mostly presents results through field experiments, where fire frequency and seasonality can be controlled and replicated. This is the approach followed in Chapter 3 and 4 of this thesis. Field plots provide the most reliable estimates of AGWB (Above-Ground Woody Biomass) carbon stocks, but due to limitations on time and resources they don't often capture the full landscape variability, particularly in remote areas. The second approach is observational, and remote sensing offers a tool to investigate this across wide areas and in different parts of the landscape with different environmental characteristics. In Chapter 5 I combine the field plots with satellite data (optical and radar) and environmental data to conduct basic research on the characteristics of the whole Bateke Plateau, and use the variation in these factors in space to attempt to elucidate their influence on AGWB.

More specifically the main objectives of this thesis are:

I. Determine the carbon stocks and floristic composition of a mesic savanna in the Bateke Plateau (chapter 3);
II. Estimate the rates of tree growth and mortality under different fire seasonality, the tree spatial structure, and determine the importance of tree-tree competition (chapter 4);
III. Analyse the above-ground woody carbon stocks and fire regime of the Bateke lansdcape, and identify the main determinants that regulate tree cover (chapter 5).

I expected to observe a significant effect of fire dynamics and soils on species composition and carbon stocks at plot and landscape scales. I hypothesed that late dry season fires would be more intense, resulting in reduced growth and increase mortality rates of trees, and be associated with lower carbon stocks, relative to early dry season fires.

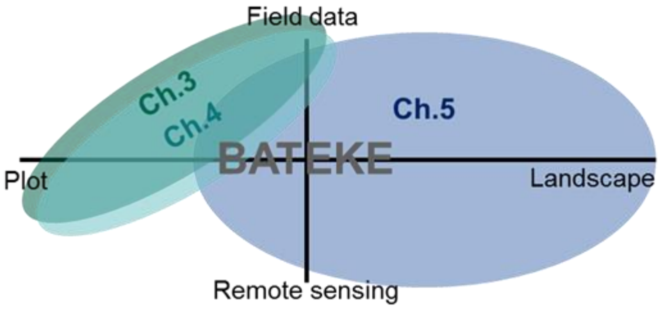


Figure 1.5. Diagram illustrating the different chapters in this thesis, using field data and remote sensing data to attain the objectives at plot and landscape scales.

This thesis is structured as a series of three core chapters presented in the style of scientific journal articles as they are either published or intended for publication. Each paper stands alone as an independent research article, and therefore there is some overlap between introductory and methodological sections. Chapter 1 is an introduction to savanna science, focusing on the effect of fire. It also introduces the unique landscape of the Bateke Plateau, to help us understand better this system before going in deep into the three research chapters. Chapter 2 describes the fire experiment and the protocol followed, enabling the future continuation of the experiment. Chapters 3 through 5 are research articles that address the key aims and objective of the thesis, and Chapter 6 provides a summary of the results, discusses their wider implications, and identifies potential areas for future research.

1.4 - Thesis motivation and approach

This PhD thesis was originally developed and funded by the University of Edinburgh, the United States Forest Service, and the Wildlife Conservation Society, coming out of a request for information and research from the Wildlife Conservation Society to the University of Edinburgh about how to manage fire within some new Reserves in the Bateke Plateau that they had just begun managing. It was created with the main objective of improving the understanding of fire dynamics in the Bateke Plateau, with the future goal of potentially using this understanding in order to manage fire in the Bateke Plateau to assist Congo’s national carbon emissions reduction strategy, and potentially even to generate carbon credit sales that could be used for conservation. It was expected that the results could be immediately used by the WCS to promote better management of this area to enhance biodiversity and carbon storage, as well as driving forward basic scientific research in this understudied ecosystem.

On an early examination of the literature it was found that there had been no fire exclusion/management experiments carried out previously in this region, and little baseline data on carbon stocks or biodiversity. The main approach of this thesis was therefore first to set up field fire experiments in the Bateke Plateau, involving large vegetation plots with different treatments, and later use modelling and satellite image analysis combined with the field data to quantify the relationships between fire intensity/frequency, woody cover and above-ground biomass. The thesis chapters and objectives were designed knowing that only 3 years of data would be available from this experiment by the end of the PhD. I designed the experiment and ran the first field missions. The goal was to train staff from WCS in the field protocols to continue the experiment every year. The initial campaigns passed successfully, and the fire treatments were implemented. However, as time went on a few problems were encountered (explained in detail in Chapter 2), that slightly modified some of the analyses that could be performed. However the overall aims of the thesis remained consistent throughout, and the results presented do greatly enhance our knowledge of the influence of fire on the carbon storage of the Bateke Plateau.

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1.6 - Appendix 1.1

This appendix includes a table with a literature review of the fire experiments in savannas around the world reported in literature.

Area		Years	Scale	Characteristics	Reference	Main results
AFRICA	**Ndola, Zambia**	1933 for 9-12 yrs		4 woodland plots and 8 coppice plots. Under fire protection, annual early or late dry season burning.	Chidumayo, 1988	No significant differences in stem mean girth at breast height of canopy species under fire protection and early burning. Decrease in dbh and basal area increment with increasing age of miombo coppice.
	Marondera Zimbabwe	1953-1991	36x60 m	10 subdivided plots plus control plots, with replicates. Grazing was excluded. Treatments of four fire return intervals (1, 2, 3, 4 years, and no burn). Burns at the end of the dry season.	Barnes, 1965; Furley et al., 2008.	Plots burned at 3 and 4-year intervals recovered to greater mean heights than unburned plots. No significant variation between treatments. Frequent fires (especially annual and biennial) had a marked impact on vegetation structure and tree density, Fire affected composition of herbaceous plants, but not the number of species. All in miombo.
	Mozambique, Nhambita	2007	1.4 ha	8 adjacent plots in a 4 X 2 grid Nested triangular measurement scheme.	Ryan & Williams, 2011	Miombo woody biomass may be preserved or enhanced by burning in low-intensity conditions. Tree populations and biomass are very sensitive to fire intensity. Large (>5 cm dbh) stems are vulnerable to fire. Resprouting was very common and not obviously linked to fire intensity.
	Matopos, Zimbabwe	From 1947	30x27 m and 27x23 m	2 plots in 2 areas (thornveld and sandveld). Burning/mowing at different times of the year and at different frequencies. Replicated 3 times.	Kennan, 1972	Basal cover was affected by fire frequency. Sandveld vegetation was more resistant to burning than the thornveld.
	Bateke Plateau Gabon	2007-2008	1 m^2	3 study areas, plus one not burned. In each, 15 plots with 5 treatments (EDS and LDS, EDS, LDS and no burn).	Walters, 2012	Annual fires were intense and burn completely, semiannual fires were cooler and patchy, favoring re-sprout survival.
	Kruger National Park	1954-	7 Ha	High replication, long-term studies and extensive associated botanical and wildlife studies. Burns at varying return intervals (12 types) and seasons in 4 types of savanna vegetation. No fire, annual, biannual, triennial.	Over 70 papers. Higgins et al., 2007; Van Wilgen et al., 2007.	Fire return period was critical to maintaining savanna structure. Fire frequency, fire season and complete exclusion did not affect the size of trees and there was no decrease in tree density with increasing fire frequency. Resprouting increased with fire intensity. Constant fires lowered the size of individual species, but rarely killed them. Increased fire occurrence promoted landscape heterogeneity.

Area		Years	Scale	Characteristics	Reference	Main results
AFRICA	**Bulawayo, Zimbabwe**	1994-2003	20 × 20 m	Randomised block design of 10 plots in two study sites. Burnt (dry season annual hot fires) vs unburnt.	Gandiwa, 2011	Repeated dry season annual fires lead to thinner and short-plants. Repeated burning increased the proportion of multi stemmed plants and of dead stems. There were no significant differences in density, number of species between the burnt and unburnt sites.
	Kokonde-kro, Ivory	1937	100 x 200 m	3 plots (1 protected from fire, 1 burned EDS, 1 LDS. Repeated over 40 years	Louppe et al., 1995; Aubreville 1947,1949, 1953	Fire was decisive in the regression of topical dry forest to grass-dominated savanna. Grasses dominated the vegetation on LDS burns. EDS burns were similar to the protected site but with fewer trees and more grass.
	Mali	2002-2003		Landsat ETM to map fire regime	Laris & Wardell, 2006	Early fires produced highly fragmented burn patches.
	Tanzania	1979-1984	2 m^2	Deep/shallow disturbances, early dry-season burning, and removal of grass species, in and out mammal exclosures.	Belsky, 1992	Protection from grazing and physical disturbance had greater impacts on species cover and diversity than removal of dominant species or fire.
	Windhoek, Nami	2005-2006		Burnt and unburnt, species richness in one year.	Nepolo & Mapaure, 2012	Short term fire had a significant impact on grass cover and insignificant impact on grass biomass production, forb densities, species richness and diversity in short term.
	Namibia		$1m^2$-$25m^2$-625 m^2	Plots: grass (1 m^2), shrub (25 m^2) and tree (625 m^2) cover. Fire return interval 0-5 years, 5-10 and >10 years.	Sheuyange et al., 2005	Frequent fires reduced shrub cover temporarily and promoted herbaceous cover. The effects on tree cover were less dramatic.
	Witfonte in farm, SA	1995-2001	9 plots 3×10 m	Back fire, head fire and no burning.	Snyman, 2004	Fire caused a decrease in basal cover. Seasonal above-ground phytomass production and litter were significantly decreased by fire over all growing seasons.
	Ukulinga, SA	48 yrs.	1 and 100 m^2	Plots in mesic, montane and semi-arid grasslands. Range of treatments and no burn.	Uys et al., 2004	Forbs in all three grasslands were resilient to fire.
	Others:					Nyamandhlova station and Tuli Kennan, 1972.

Area		Years	Scale	Characteristics	Reference	Main results
AUSTRALIA	**Kakadu National Park**	1973-1996	1-ha	4 plots across 2 savanna types (woodland and open forest). Treatments: annual EDS, LDS, biennial EDS, and exclusion.	Many references, including: Russell-Smith et al., 2003; Andersen et al., 2005.	A range of responses to differences in fire regime is possible, no single fire regime can optimise all biodiversity.
	Kidman Springs	1993 - 2013	160m x 160m	2 sites with different fire intervals (every 2, 4 and 6 years) and season of fire (EDS and LDS), and no fire. 16 plots arranged in a 4 x4 grid	Many references, including: Cowley et al., 2014.	Once woody plants get taller than two meters they become very resistant to fire. Late burns every 4 years was the most effective. Burning more often, or too early in the dry season, damages pastures. Early fire promoted biodiversity but can cause pasture decline.
	Kapalga	1989-1995	10-20 km^2	Range of fire treatments, with annual (EDS, LDS and no fire) with replicates.	Numerous studies, results summarised in Andersen et al., 2003; 2005.	Annual late fires reduced tree basal area. Both timing and intensity were key determinants of species survival, with both early and late fires reducing the number of seeds produced.
	Bowling Green	1997-2001	10ha	3 fire regimes	(Williams et al., 2003)	The abundance of most species was stable irrespective of the fire regime. The density of trees increased in the absence of fire.
	Others					There are several other smaller-scale experiments (less than 1Ha.). These included: relative efficacy of wet season burning and fuel reduction (Williams and Lane 1999); role of soil as a determinant of savanna-to-rainforest succession (Bowman and Paton 1993); fire intensity and sapling survival in a common rainforest tree (Fordyce et al. 1997) and fire intensity and mortality of invasive woody species (Grice 1997).

Area		Years	Scale	Characteristics	Reference	Main results
SOUTH AMERICA	**Bahia Reserve, Brazil**	1991-2004	20 x 50 m	13 plots. Structural and floristic changes of fire-protected cerrado.	Roitman et al., 2008	Floristic changes were significant. Species number rose. New species migrated to the area, and there was an expansion of many fire-sensitive species. Woody layer expanded.
	Llanos Venezuela	1961-1977	3 Ha.	Plot, protected against fire and cattle grazing for 16 years.	San Jose & Farinas, 1983	Increase in tree species population and change in floristic composition with fire protection. Gradually changing into a denser arboreal community.
	Mato Grosso, Brazil	2009 – 2011	50 Ha.	Annually burn plot with a control plot	Balch et al. 2008, Brando et al. 2012 and other studies	Total net primary productivity was lower on the burnt plot than on the control. Importance of fuel input rate and timing relative to fire frequency.
	IBGE, Brazil	1992-2008	200 × 200 m	Unburned (control), fire once every 4 years (quadrennial fires) during the middle of the dry season, and fire once every 2 years (biennial fires) in early, middle or late dry season.	Gonzales et al. 1997, Pivello, 2010	Evidence of long-term fire effects in soil pH.
	Other					Ramos-Neto & Pivello, 2000; Santos et al., 2003; Barradas 2017; Fidellis et al. 2018.

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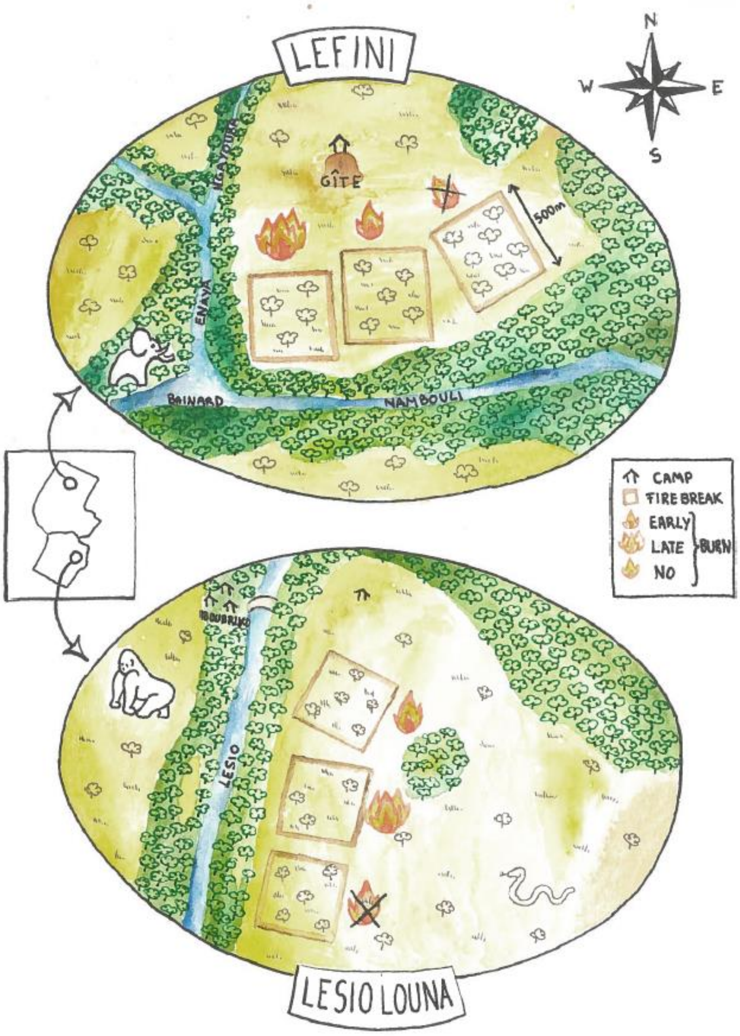
Chapter 2

Designing a long-term fire experiment on the Bateke Plateau



Painting of the fire experiments in the Bateke Plateau (Paula Nieto)

2.1 - Thesis Experimental approach

The main experimental approach of this thesis was to design and implement a fire experiment and establish vegetation plots. The fire experiment was designed with the main aim to quantify the effect of fire seasonality on carbon stocks, with additional aims of measuring demographic rates and calibrating remote sensing data to upscale estimates to the Bateke Plateau. The plots were also used to quantify species composition, soil characteristics and grass biomass. For this, first the USFS performed a scoping study of potential locations, before final sites in Lesio Louna and Lefini were selected. During the design phase of the field experiment, it was a priority to ensure appropriate replication while balancing costs for maintenance and monitoring of the plots, as the goal was to establish a long term experiment that would continue beyond this PhD.

Fire experiments are difficult to implement, and even more difficult to maintain for long periods. During this present research there were a number of issues that have influenced the operation of the fire experiment and the design of the research chapters. These are detailed in section 2.7.

2.2 - Introduction to the fire experiment

This Chapter includes a detailed description of the methodology I designed in order to set up a fire experiment in two protected areas of the Bateke Plateau. This information can be used to continue the experiment. The fire experiment was originally designed as a long term experiment, so I include at the end of this chapter recommendations for its successful continuation. The information obtained in this experiment was used in all research chapters, and helps provide valuable information for fire management activities in the Bateke, which I include in Chapter 6 Discussion and conclusions.

As far as we know, there has never been a fire experiment in the Bateke Plateau, except for the fire manipulation study in PNPB in Gabon, conducted in 2007-2008 (consisting of small plots of 1 m^2, with burning in the wet season, early dry season, late dry season and a no-burned plot (Walters, 2010)). This represents a significant knowledge gap, as the Bateke is an unusual savanna system typified by very sandy soils but relatively high rainfall (>1500 mm/year), well above the minimum required for canopy closure in the absence of fire (Sankaran et al. 2005). The Bateke savannas are typified by low above-ground woody biomass and tree diversity, and it is unclear if this is caused predominantly by the fire regime, the soils, some combination of the two, or other factors. We therefore decided to set up a fire experiment in this ecosystem, as one critical method for helping to understand the current savanna dynamics and make predictions for future changes for the Bateke Plateau. The experiment was designed to provide unique information about the functioning of this ecosystem. We learned from the methods and results of other fire experiments in designing ours, in particular focussing on the use of very large plots (25 ha) to capture the small scale heterogeneity in woody cover, demographic changes and replicating the plots and experimental treatments across two separate sites.

2.3 - Methods

Six large scale (25 ha) field plots were established in two sites in the Bateke Plateau, Republic of Congo, in the year 2015. This was a replicated fire experiment, with 3 fire treatments implemented across two sites. Field plots were established in May 2015, and six field missions have been completed since (two in 2015, two in 2016 and two in 2017). In order to allow the experiments to continue in the future, a Wildlife Conservation Society (WCS, the organisation that manages the national parks) team in Congo was trained on the experimental methodology, including fire control and woody plant/grass mensuration, and assisted in all the field campaigns. The size of this plots was selected to be sufficient for a remote sensing analysis of the biomass data.

The field plots were located in two protected reserves in the Bateke Plateau, the Lefini and the Lesio Louna Reserves (Fig. 2.1). At each site, 3 experimental plots were set up and different annual burn regimes were applied: one plot burned in the early dry season, one in the late dry season, and one was protected from burning. As discussed in section 3.8, the inventories of the unburned plots (LWR3 and LLR3) were not completed, and have not been used for this research, although the plots have been demarcated, most trees inventoried, and fires controlled to some degree, so we hope these plots may be used in future.

A summary of all the plots, their location, treatment, date inventoried and the date the fire treatment was applied is included in Table 2.1.

Table 2.1. Summary of the experimental plots and their treatments

Plot	Location	Treatment	Dates Inventoried	Dates burned
LWR 1	Lefini Wildlife Reserve	Late Dry Season Burn	May 2015/Sept 2016/Sept 2017	24/09/2015; 19/09/2016; Sept 2017
LWR 2	Lefini Wildlife Reserve	Early Dry Season Burn	May 2015/June 2016/June 2017	24/05/2015; 10/06/2016; 13/06/2017
LWR 3	Lefini Wildlife Reserve	No Burn	Sept 2016 (incomplete)	Accidental Fire 12/09/2015
LLR 1	Lesio Louna Reserve	Early Dry Season Burn	June 2015/June 2016/June 2017	15/06/2015; 8/06/2016; 06/06/2017
LLR 2	Lesio Louna Reserve	Late Dry Season Burn	Sept 2015/Sept 2016/Sept 2017	19/09/2015; 28/09/2016; Sept 2017
LLR 3	Lesio Louna Reserve	No Burn	May 2016	Accidental Fire August 2016

2.3.1 Location

The Lefini (CO: 2°30’13.4”S, 15°28’55.2”E) and the Lesio Louna (CO: 3°16’51.3”S, 15°28’04.9”E) reserves are both located within the Bateke Plateau (Fig. 2.1), and are situated about 160 and 110 km north of Brazzaville respectively. The reserves range from 300 m to 740 m in altitude, with a topography consisting mainly of large plateaus, with small hills, two large rivers and some valleys. The main habitats are open Loudetia or Hyparrhenia grassland, with the dominant tree *Hymenocardia acida* (King, 2011, King et al. 2004), and forests mainly associated with rivers and uphill areas. Both reserves are listed as IUCN Category IV (IUCN & UNEP, 2015).

The location of the plots was chosen in areas close to the field stations, with comparable and sufficient density of big trees, and with a minimum distance to the forest of 30 m. The plots at each site were placed close to each other, but with at least 20 m between them, in order to have space to make the fire breaks. The treatment assigned to each of the plots was chosen randomly.

All the plots were signed and marked in the following way:

- The corners of each plot were marked with a 1.5 m iron bar (rebar), itself labelled with flagging tape (photo 1);
- A pole and a small rebar were placed on every 100 m, and labelled with fluorescent tape to be more easily seen during the field campaign. The small rebar was hammered below the ground, so it could be located and revisited by using a metal detector in future years;
- Subplots were marked with a bamboo of around 2 m high cut in half (photo 2).

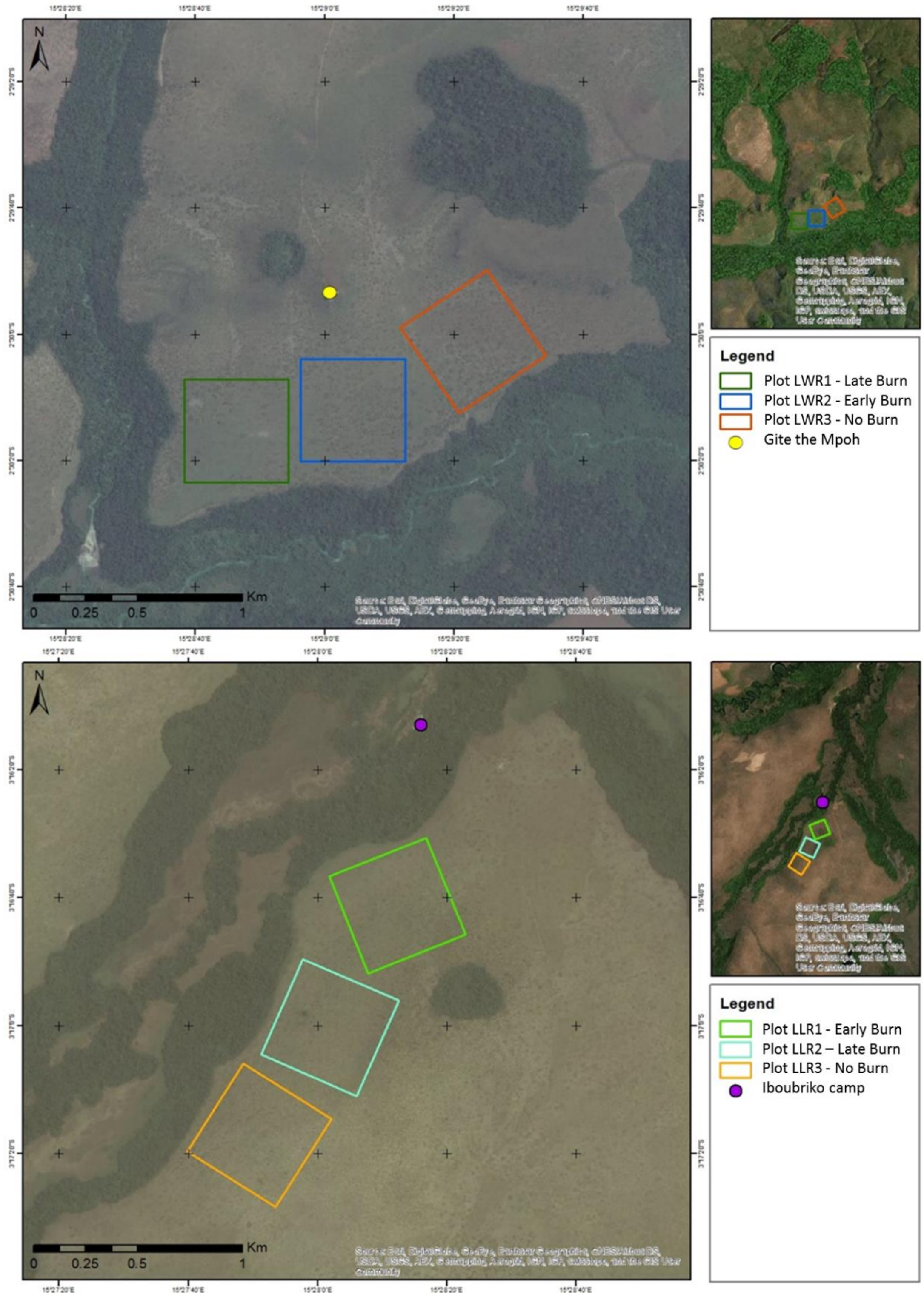


Figure 2.1. Location of the experimental plots in Lefini (top) and Lesio Louna (bottom) reserves, over a Digital Globe image.

2.3.2 Sampling method

The size of each plot was 500 x 500 m. Within each plot, 16 permanent circular subplots with a radius of 4 m (50.3 m^2) were established every 100 m (Fig. 2.2). This size was considered sufficient for the analysis of grass, saplings and soils, taken into account time limitations.

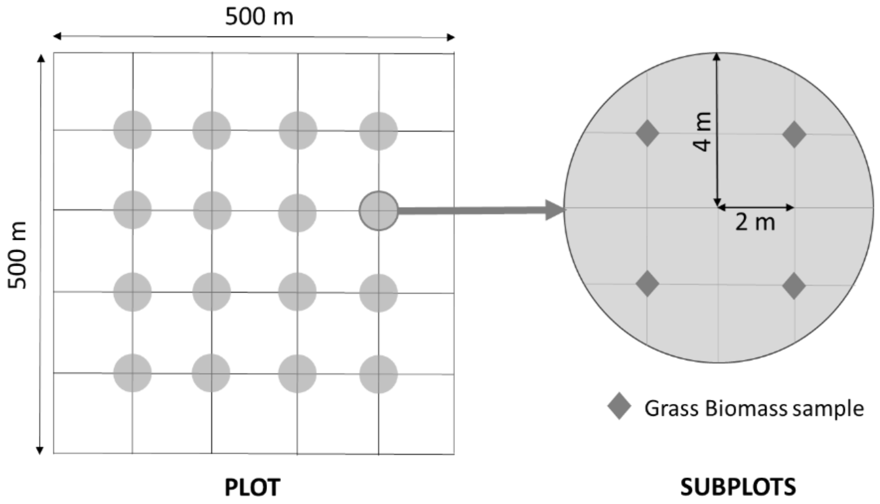


Figure 2.2. Plot layout and Sampling protocol for subplots

The following data were collected at each plot (Table 2.2), following the sampling method detailed in section 2.2.3 and 2.2.4:

In the plots:

- Inventory of all tree stems with a Diameter at Breast Height (DBH) ≥ 9 cm (11 cm in the No Burn plots LWR3 and LLR3). 9 cm was chosen, even though 10 cm was used for all analysis, to increase the probability of identifying new recruits (trees that grow from below to above the 10 cm threshold for analysis) between censuses.

In the subplots:

- Inventory of saplings/shrubs;
- Species presence/absence data for grasses and plants;
- Grass biomass;

- Soil data (organic carbon and nitrogen content).

Table 2.2. Data inventoried in all plots and subplots. *DBH > 11 cm. [1] Inventory not finished.

	LWR1	LWR2	LWR3	LLR1	LLR2	LLR3
Plots						
Trees (DBH > 9 cm)	✓	✓	✓*[1]	✓	✓	✓*
Subplots						
Woody plants (D_{10} < 2 cm)	✓	✓		✓	✓	
Grass biomass	✓	✓		✓	✓	
Species composition	✓	✓		✓	✓	
Soils	✓	✓		✓	✓	

2.3.3 Vegetation measurements in the plots: Big Trees

All trees greater or equal than 9 cm DBH were tagged and measured (DBH ≥ 11 cm for the no burn plots) in 2015 (photo 5). This threshold was derived from the field observation to capture most of the trees observed, and in order to measure a sufficient density of trees for statistical analysis and remote sensing purposes. For all the tagged trees, the tag number, GPS location, DBH, species, status (standing/fallen, whole/broken, dead/alive) and height was recorded. DBH was measured at 1.3 m, and if the tree forked below this, each stem was measured independently and treated as different trees in further analyses. Tree height was estimated using a Nikon Forestry Pro laser.

2.3.4 Vegetation measurements in the subplots: Saplings and Grasses

Saplings:

In the circular subplots of 4 m radius all the woody species (saplings/shrubs) with a DBH < 10 cm, and with a diameter at 10 cm above ground (D_{10}) greater than 1 cm, were inventoried. Measurements of height, location with GPS, species and status, and DBH where applicable, was recorded. Trees were identified to species level by Roland Odende, with the help of a botanist (Gilbert Nsongola), and where identification was nor possible on site, samples were taken to the National Herbarium of the Institut de Recherche en Sciences Exactes et Naturelles (IRSEN) for identification, as described in Odende (2016).

Grasses:

All the grasses in subplot were identified to species level with the help of Mr. Gilbert Nsongola (Herbier National du Congo). When specimens could not be identified on site, samples were taken to the National Herbarium of IRSEN for identification. The percentage of the most abundant species was also recorded.

Grass biomass was estimated by taking measurements with a Disc Pasture Meter (DPM) (Bransby & Tainton 1977, Dörgeloh 2002) (Photo 3). The DPM was constructed locally and first calibrated by taking 35-40 grass samples at each plot. For each sample, all the grass under the DPM was cut, and weighed (wet weight). A subsample of these was weighted, dried in a paper bag, re-weighed in order to determine dry mass based on percent moisture loss from the samples. This data was used to calibrate the DPM, by calculating the relationship between mean disc settling heights (mm) and grass biomass per quadrat using simple linear regressions. Four measurements were taken at each subplot immediately before burning, at NW, NE, SE and SW cardinal directions. More details about the calibration and construction of the DPM are included in Appendix 2.1.

2.3.5 Soils

Analysis of soil properties was conducted in Plot LWR2 (Lefini) and LLR1 (Lesio Louna). Sample collection was performed in the transects numbered 2 and 4, in a total of 8 subplots (Fig. 2.3). Using a soil auger (Photo 4), two soil cores samples were taken in each subplot, at two horizons (0-5 cm) and (5-20 cm). These were taken 2 meters east and west from the center of the subplots. A total of 32 samples per plot were collected. Analysis were performed by Marcelle Batsa from the University of Marien Ngouabi (Batsa et al. (2017). Samples were dried, sieved and analysed in IRSEN, at Pointe-Noire, in order to determine total organic carbon and nitrogen content and bulk density (measured with a cylinder core to assess the volume of the soil and determine the weight after drying (Blake & Hartge 1986)).

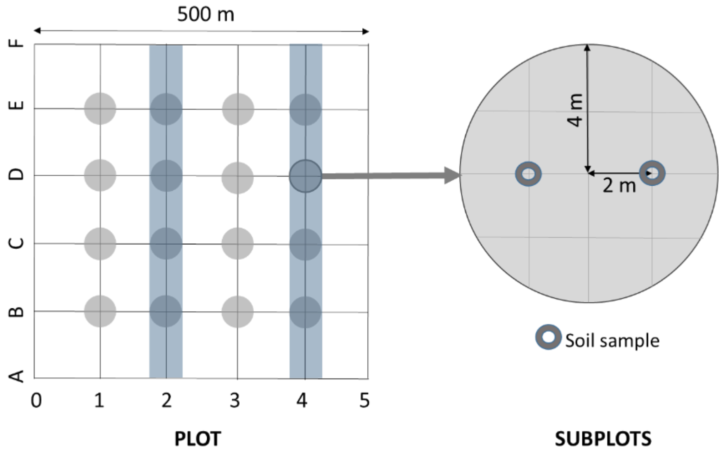


Figure 2.3. Soils samples were taken from subplots along transects 2 and 4 (marked in blue).

2.4 - Fire breaks

Fire breaks were constructed around all plots, to prevent fire burning outside the boundaries of the plot and to protect the plots from external fires. The fire breaks were periodically maintained in 2015, 2016 and 2017, by repeating the procedure at the beginning of the dry season, and also before the short dry season in January/February.

A team of approximately 10 people from the nearby villages was employed in each site to clear the fire breaks. The fire breaks were constructed in the following way (photo 6):

- Grasses were cut with a strimmer to a width of around 2 m surrounding the plot. All the cut grasses were removed. These method was later substituted for digging a ditch as this was estimated to be more efficient;
- At a distance of 10 m from the line cut with the strimmer, a small ditch was dug;
- The area between both lines was burned.

2.5 - Fire treatment and fire measurements

Fires were started in a traditional way by the team from the village, by collecting some tall dry grasses, tying them together and igniting with matches (photos 7-12). Then, multiple people lit small fires in a straight line along the sides of the plot, starting in the upwind side. Fires were always started at roughly 11 am.

Data recorded from each fire was: date and time of the burn, meteorological conditions (temperature, wind and rainfall) before and during the fire, the time the fire was started and when it was finished.

2.5.1 Measurements after the fire

Following the fire, all of the subplots were revisited. Subplots were recorded along 4 transects across each plot, being therefore also able to estimate the percentage of the plot burned.

At each subplot the following was recorded (Table 2.3):

- Estimation of the percentage of area burned;
- The height of the burn scar in the bamboo, in order to estimate the flame height (photo 15).

Table 2.3. Fire measurements: percentage burned, duration of the fire and height of the flames based on the bamboo. All values are averages for all years.

	% Burned (mean)	**Duration of fire (minutes)**	**Flame height (mean in m)**
LWR 1 (LDS)	100	42.00	1.80
LWR 2 (EDS)	75	70.10	0.40
LLR 1 (EDS)	50	45.00	0.95
LLR 2 (LDS)	100	24.30	1.40

2.6 - Re-measurements

Each year (2016 and 2017) the plots were revisited to measure growth, mortality and resprouting rates, before the fire treatment was applied. The following protocol was followed:

In the plots:

- Tree re-inventory: recording species, DBH, Status (standing/fallen, whole/broken, dead/alive, or tag lost). If the tag was log, it was replaced. New recruits (trees that have grown beyond the DBH threshold since the last inventory) were tagged, measured and GPS point was recorded.
- Mortality: A tree was considered dead when there were no signs of life above 1.3 m (top killed). A dead tree may therefore be able to resprout in subsequent years. For dead trees the type of death was recorded following this methodology:
    - Type of death:
        - R - Topkilled, resprouting
        - T - Topkilled, no sign of resprouting
        - D - Totally killed
    - Mode of death:
        - U - Up-rooted
        - P - Snapped (break)
        - S - Standing
        - V - Vanished
        - Q - Can’t tell
    - Cause of death:
        - F - Fire
        - O - Others: Human (cut), termites, wind, etc.
- If a tree is dead the degree of wood decay was recorded based on the RAINFOR codes, and modifications for fire, as shown in Table 2.4. This, however, was not done in 2017.

Table 2.4. Wood decay score (from RAINFOR)

Score	Name	Condition if burned	Condition if rotting
1	Intact.	No sign of fire damage	There is more than 75 % of the wood intact and/or hard.
1.5	Slightly damaged	Bark burned but wood mostly intact	The surface of the bark has some damage, but the heartwood is still hard.
2	Damaged and in bad condition	Only heartwood remains	The log has experienced some decay.
2.5	Somewhat rotten	Hartwood badly charred	Part of the wood is easily crumbed.
3	Rotten	Turned to ash. Ghost tree	There is more than 75 % of the wood soft and rotten, wood collapses when stepped on.

In the subplots:

- Sapling/shrub re-inventory: recording species, D_{10}/DBH, Status (alive, dead, or tag lost). The tag was replaced if needed. New recruits (trees that have grown beyond the D_{10}/DBH threshold since the last inventory) were tagged and measured.
- Grass biomass: Estimated using the Disc Pasture Meter. This was calibrated during each field season.

Photo 1. Rebar with flagging tape marking the corner of Plot LWR1 in Lefini.

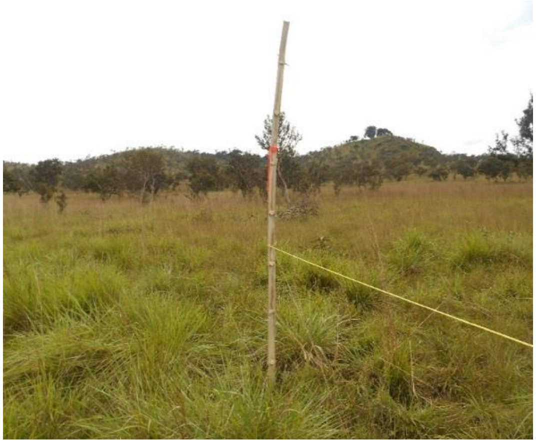


Photo 2. Bamboo stick in a subplot of Plot LWR2.

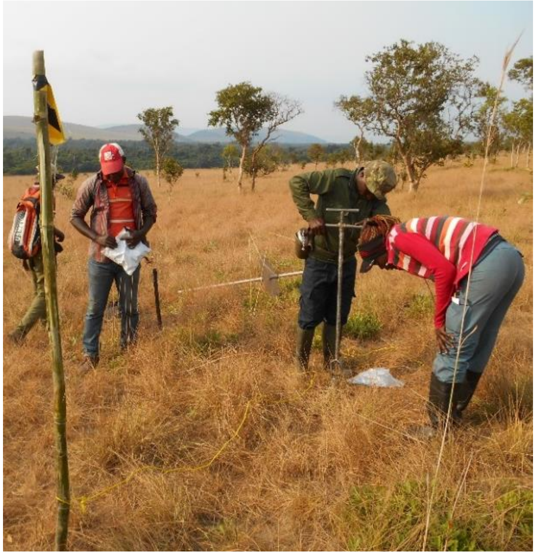


Photo 3. Taking soil samples in one subplot (Lesio Louna).

Photo 4. Using the Disc Pasture Meter for calibration.

Photo 5. Measuring and tagging the trees in Plot LWR2.

Photo 6. Making the fire breaks.

Photo 7. Starting the fire at Lesio Louna.

Photo 8. Starting the fire at Lefini.

Photo 9. Fires were started the traditional way.

Photo 10. Images of Lefini fire in Plot LWR2, early dry season fire.

Photo 11. Images of the fire at Lesio Louna.

Photo 12. Images of the fire during June 2015 at Lesio Louna.

Photo 13. Image of the fire in Lesio Louna.

Photo 14. Images of the fire at Lesio Louna.

Photo 15. Images of the fire at a subplot in Lefini and the bamboo stick showing the burn scar to give an estimation of the flame height.

Photo 16. Plot LWR1 after the fire in Lefini.

Photo 17. After the fire in plot LLR2.

Photo 18. Photo taken in Lefini after the 2015 accidental fire. Soon after the fire (couple of weeks), vegetation starts resprouting.

2.7 - Difficulties and constraints during the fire experiment

Operating a successful fire experiment in the Bateke Plateau is difficult. Field operations are remote, availability and continuity of funding is limited, and maintaining a well-trained team requires dedicated in-country support. Whilst the primary goals of the experiment were achieved, the scope has to be limited in a number of areas. Here I detail the main challenges and constraints encountered during the implementation of the fire experiment that influenced this thesis:

- No burn plots: Due to management difficulties, both unburned plots LWR3 and LLR3 were only inventoried the first year 2015. Additionally, plot LWR3 was not fully inventoried (with about 1 hectare missing). Although these two plots were not used in the research chapters, they remain very important for long-term monitoring and to examining the consequences of fire in this systems over time.
- Accidental fires: During the dry season in 2015 in Lefini and 2016 in Lesio Louna, there were external fires affecting both sites, that started outside the study area and burned the No Burn plots (not yet measured at that point). The Lefini fire, in particular, was very intense, and even burned some of the forest adjacent to the plots (Fig. 2.4). These fires, which were probably anthropogenic, emphasize the importance of effective maintenance of fire breaks for the achievement of long-term results.
- Grass Biomass was measured every year for the early and late dry season burn plots at both sites. Unfortunately, this data was not complete, and the grass biomass measurements for one site in 2016 and another in 2017 are missing. For this reason, grass biomass measurements were not further used in this thesis to calculate productivity or grass biomass change.
- Meteorological data were originally planned to be collected at each site. A temporary meteorological station working with batteries was placed in each site at the beginning of the experiment, with the plan to be changed to permanent solar powered stations. The temporary meteorological stations collected precipitation and temperature data, but can only store around 20 days of data, and batteries required frequent replacement. I collected meteorological data in 2015 for a period of around

20 days before the fires, but in 2016 and 2017 this data was not completely collected due to logistical challenges.

Figure 2.4. Some images of the gallery forests close to the plots in Lefini that accidentally burned in 2015. The fire was only stopped by the river.

2.8 - Participants

This fire experiment was designed by me, with support from my primary supervisor Dr. Edward Mitchard (UoE), Dr. Casey Ryan (UoE, secondary supervisor) and Tim Ryan (Wildlife Conservation Society - Congo). Additional support was provided by the US forest Service

(USFS) and Wildlife Conservation Society (WCS), providing feedback and logistical support during the field experiments. Participants in the fire experiments were:

From WCS-Congo:

- Tim Rayden: WCS representative responsible for the Bateke Plateau (later substituted by Patrick Boundja). Supervised the project and assisted with the logistics of the fire experiments.
- Mireille Breuer: Managed the team during part of the 2016 and 2017 mission. Other participants of this mission were Fiacre Mouaba, Fred Edimma, Marlene Gotene and Smith Diafouka.
- Marcelle Armande Batsa Mouwembe: Master's student from the University of Marien Ngouabi, focussed on the study of soils.
- Roland Odende: Master's student from the University of Marien Ngouabi, performed a comparative study of the floristic composition of Lefini and Lesio Louna. He also managed the team during part of the third field mission.
- Ledia Bidounga: The GIS expert from WCS and World Resources Institute (WRI), assisted during the 2015 field seasons.
- Onesi Jared: Local WCS staff, assisted during the 2015 field seasons.
- Mr. Gilbert Nsongola: From the Herbier National du Congo, Institut National de Recherche en Sciences Exactes and Naturelles (IRSEN). He helped with the species identification during the first field campaign.
- We also had the help of the reserve's Eco-guards: Denis Ngatse (Lefini) and Prime Mobien (Lesio Louna).
- For the creation and maintenance of the fire breaks, people from Mpoh and Mâh villages were employed.

From USFS:

- Dr. Sarah Sawyer: participated in the second field providing support and feedback throughout the experiment.

From University of Edinburgh:

- John Godlee: Participated in the fire experiment mission in June 2017.

2.9 - Data accessibility

Data obtained from this experiment is archived via the SEOSAW project (Socio-Ecological Observatory for Southern African Woodlands), and are available for use in line with the SEOSAW Code of Conduct (https://seosaw.github.io). The data used in Chapter 3 is also archived at the Dryad Digital Repository: doi.org/10.5061/dryad.2122768 (Nieto-Quintano et al. 2018). Information on using the vegetation data prior to the end of the embargo can be found at seosaw.github.io.

For other data, please email me (paula.nieto@ed.ac.uk) or Edward Mitchard (edward.mitchard@ed.ac.uk).

2.10 - References

Batsa, M. A., Ifo, S. A. Binsangou, and Koubouana, F. (2017). Variabilité spatiale des stocks de carbone organique du sol des savanes dans les réserves de Lésio-Louna et de Léfini, plateaux Tékés, République du Congo. Afrique SCIENCE 13: 297-307.

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Walters, G. (2010). The Land Chief’s embers: ethnobotany of Batéké fire regimes, savanna vegetation and resource use in Gabon. Doctoral thesis. University College London.

2.11 - Appendix 2.1. Calibration and construction of the Disc Pasture Meter

Grass biomass was measured using a disc pasture meter (DPM), a common technique widely used to make rapid measurements of phytomass (Bransby & Tainton 1977, Dörgeloh 2002). Four measurements were taken at each subplot (totalling 64 measurements per 25-ha plot). All measurements were performed when the grasses were dry, avoiding the first hours of the morning where there is a lot of moisture. Although measurements were originally taken every year, 2015 was the only year with complete data, and therefore only the 2015 grass measurements were used throughout this thesis.

Calibration

The DPM was calibrated in each plot before its use. For this calibration, all the grass under the disc was cut and weighed. A subsample of grass was weighed, then dried to the point of no further weight loss, and re-weighed in order to determine dry mass based on percentage moisture loss from the samples. For each plot, the relationship between DPM height (cm) and dry grass biomass was determined using linear regression (Fig. 1.A1 linear calibration curve, n = 35–40 for each plot, r^2 = 0.35–0.75). This model was then used to establish the grass biomass in each subplot by only measuring the height and using the appropriate plot calibration equation.

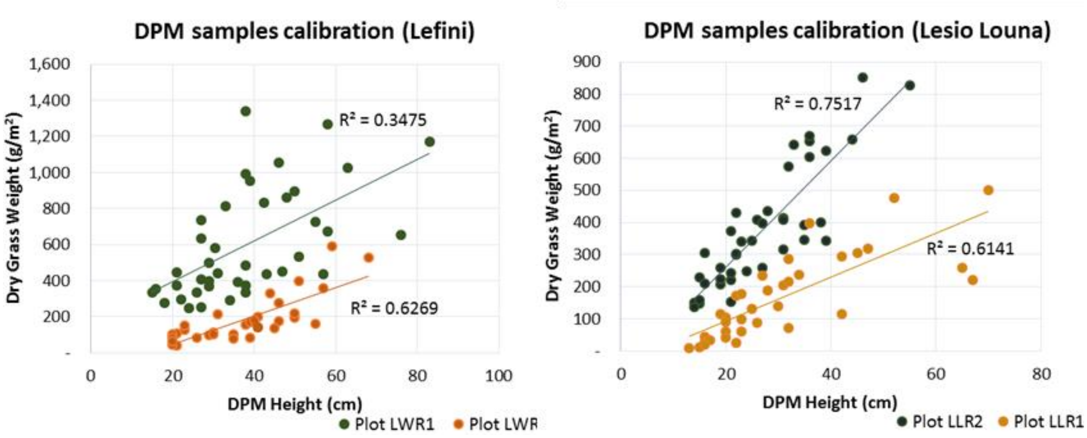

Figure 1.A1. Linear calibration curves for the Disc Pasture Meter for data collected in 2015. N = 35–40 for each plot, r2 = 0.35–0.75.

Disc Construction

I chose to construct a simple, inexpensive DPM using material available in Brazzaville. This was a robust and easy-to-use rising plate pasture meter (Fig. 1.A2 and Photo 1.2.1). The DPM was constructed by buying and cutting two plastic tubes, one with a slightly larger diameter than the other. Height marks were drawn on the inner tube to record the settling height of the disc in the field. In between the two tubes, bubble wrap was placed and adjusted so that the tube with the disc attached could slide down slowly, without falling fast and crashing into the grass layer. A light wood was chosen for the disc, and cut to the appropriate dimensions (two types of wood were chosen initially with different weights and tried on site to see which one was more appropriate for the grass measurements). The disc was cut to a diameter of 50 cm, making the total area of the disc 1963.5 cm^2. A hole was drilled in the center of a disc the same size as larger tube. The disc was attached to the tube with tape. It is important to make sure the disc doesn't get wet during the field measurements, so that its weight doesn't change.

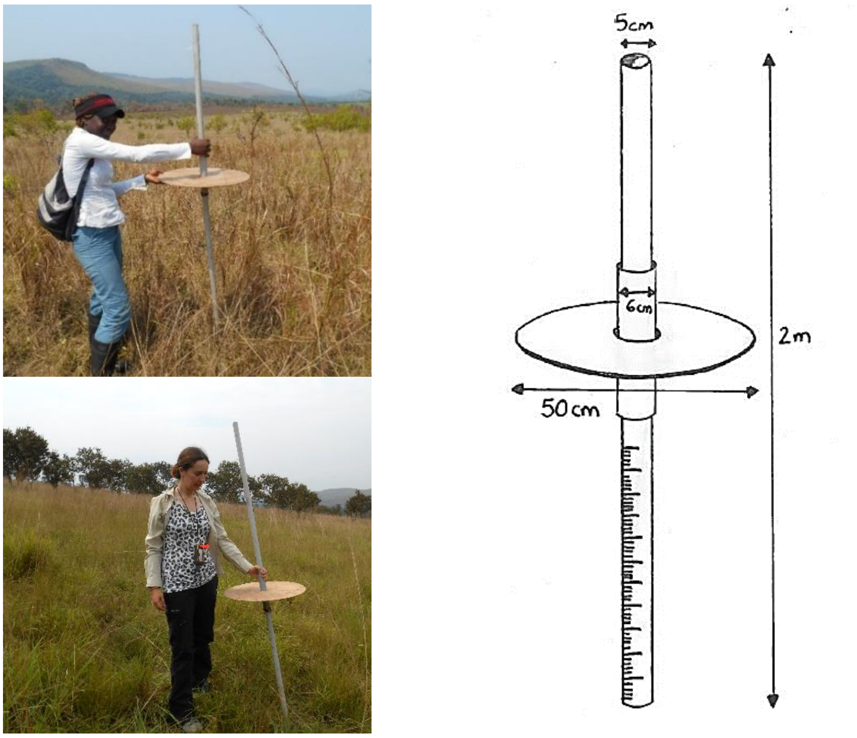

Figure 1.A2. Photos and sketch of the Disc Pasture Meter.

Chapter 3 Biomass stocks and floristic composition of mesic savannas in the Bateke Plateau

Nieto-Quintano, P. , Mitchard, E. T., Odende, R. , Batsa Mouwembe, M. A., Rayden, T. and Ryan, C. M. (2018), The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition. Biotropica, 50: 868-880. doi:10.1111/btp.12606

This chapter is as published in the journal Biotropica and the co-authors are listed above. I conducted all analyses and led the writing of the manuscript, with advice and feedback from co-authors. I led the design of the experiment, with the collaboration of other co-authors. Marcelle Batsa Mouwembe led the soil sampling and analysis, and Roland Odende the species identification study.

Data used in this study are archived at the Dryad Digital Repository: doi.org/10.5061/dryad.2122768 (Nieto-Quintano et al. 2018). Information on using the vegetation data prior to the end of the embargo can be found at seosaw.github.io

3.1 - Abstract

The Bateke Plateau in the Republic of Congo is one of the last frontiers for ecology, being among the botanically and structurally least known areas in Africa. Despite occupying 89,800 km^2 and its importance for local livelihoods, its ecology and ecosystem functions are poorly understood. The Beteke belongs to the Kalahari sands, and has a complex evolutionary history, being mainly isolated from other savannas for much of its past, with currently unresolved ecological implications. Here we assess the biomass and floristic diversity of this savanna. We established four large (25 ha) permanent sample plots at two savanna sites, inventoried all trees, and assessed shrub, forb and grass species and biomass, and characterised the soils. The total plant carbon stocks (above-ground and below-ground) was only 7.4 ± 0.3 MgC/ha, despite precipitation of 1600 mm/yr. Over half the biomass is grass, with the remainder divided between trees and shrubs. The carbon stock of the system is mostly contained in the top layer of the soil (16.7 ± 0.9 MgC/ha in 0-20 cm depth). We identified 49 plant species (4 tree species, 13 shrubs, 4 sedges, 17 forbs and 11 grass species), with an average species richness of 23 per plot. There is tree hyperdominance of *Hymenocardia acida* (Phyllanthaceae), and a richer herbaceous species composition dominated by *Loudetia simplex* and *Hyparrhenia diplandra*. The low carbon stocks are likely maintained by the sandy soils and frequent fires. The species composition of the Bateke could relate to its historical spatial geography and paleoclimatic origin.

3.2 - Introduction

The Bateke Plateau is a savanna-covered plateau located mainly in the southern republic of Congo, but also extending into the east of Gabon and the southwest of Democratic Republic of Congo (DRC), and with an area of approximately 89,800 km^2 (Fig. 3.1). It comprises five different savanna plateaus (Koukouya, Djambala, Nsa, Ngo, and Mbé/Batéké), with an elevation that ranges from 259 to 872 m (mean of 545 m), each separated by deep valleys (Descoigns 1960, Congo Basin Forest Partnership, 2006). The landscape is located on the northern part of the Kalahari sands, an ancient sand dune system (Haddon 2000), with soils that are mainly deep, sandy in texture and ferralitic (Schwartz & Namri 2002), providing rapid drainage. There are also some podzols in lower areas (Schwartz 1988). This area has a tropical transitional climate, characterized by an average annual rainfall of 1500–1800 mm (obtained from Harris et al. 2014). There is a main dry season from June to September and a short dry season in January and February (Walters 2010b). The Bateke Plateau has historically low human population densities, around 0.2 inhabitants/km² (Congo basin forest partnership 2006). Batéké populations mainly practice subsistence agriculture, gathering, fishing, and hunting (Walters 2010a, Rayden et al. 2014). Agro-economic activities, charcoal production, logging, hunting, and bushfires have widely impacted this landscape, driven by the demand from the large capital cities of Brazzaville and Kinshasa (populations of 1.8 and 9.5 million, respectively) (Hoare 2007).

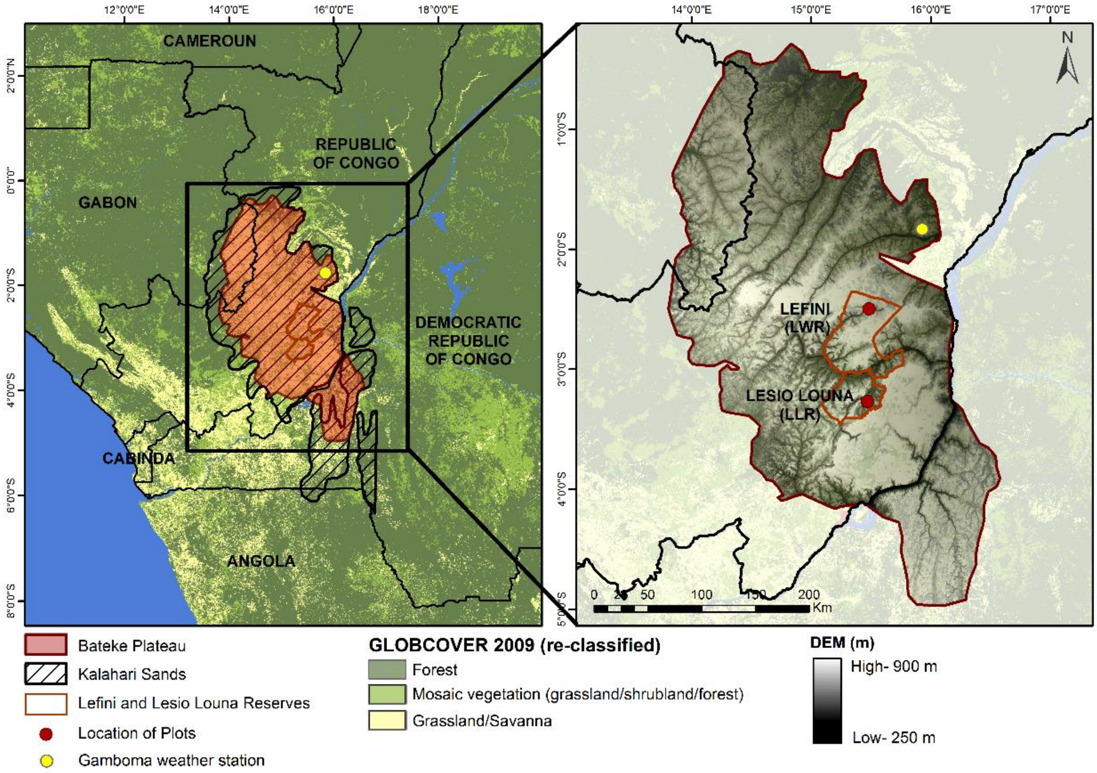

Figure 3.1 Map of the study area, the Bateke Plateau, located mainly in the Republic of Congo. The left hand map shows the extent of the Bateke Plateau (red), the Kalahari sands (dashed), and the weather station of Gambona used for the analysis of the temperature and precipitation data (yellow dot). The right hand panel shows the location of the Lefini and Lesio Louna reserves, where the sampling plots were placed (red dots), over a Digital Elevation Model (DEM) and the land use cover (GlobCover 2009, reclassified).

The vegetation of the Bateke Plateau is predominantly a mosaic of woody savanna and grasslands, with patches of closed canopy forest, the latter confined to rivers and valley floors, pockets at the top of hills, and surrounding settlements, where there is greater water availability and protection from fire (Duvigneaud 1953b). The wooded savanna is dominated by an open canopy of *Hymenocardia acida Tul.* (Phyllanthaceae) and *Annona senegalensis Pers.* (Annonaceae) trees, with an understory of grasses and locally endemic forbs (Walters 2012). The grasslands are typically dominated by *Loudetia simplex* and *Hyparrhenia diplandra* (Duvigneaud 1953b).

The Bateke Plateau intrudes into the Congo Basin rainforest and has a precipitation clearly suitable for closed canopy forest establishment. Here, savanna and forest coexist under the same climatic and edaphic conditions with sharp transitions (Schwartz et al. 1995). This has made it problematic to define the origin of this savanna, with conflicting hypotheses as to the lack of tree cover, which have important consequences for its conservation (Veldman et al. 2014, 2015, Bond & Zaloumis 2016). Some authors (Aubreville 1949, Duvigneaud 1953b, Elenga et al. 1994) have suggested an anthropogenic origin, caused by the arrival of human populations. Conversely, the weight of recent evidence supports an origin caused by arid events in the past, though humans could have played a role (Koechlin 1960, Aubreville 1962, Foresta 1990, Elenga et al. 1994, Schwartz et al. 1995, Vincens et al. 1999, Oslisly et al. 2013). The recent climatic history of the region is complex. There is evidence of a humid period with mainly forests covering the region from 40,000 to 24,000 years BP, followed by a drier period from 24,000 to 12,000 years BP when herbaceous communities expanded (Dechamps et al. 1988, Schwartz 1988, Elenga et al. 1994, Schwartz et al. 1995). From 12,000 years BP onwards, humid conditions encouraged new forest development (Dechamps et al. 1988, Elenga et al. 1994), supported by studies suggesting that, as recently as 4000-3500 years BP, the Bateke Plateau was forested (Dechamps et al. 1988, Schwartz et al. 1995, Vincens et al. 1999). These forests were likely replaced by open grasslands around 3000 years BP, when a major arid event occurred with greater seasonality, causing extension of grasses (Elenga et al. 1994, Schwartz et al. 1995, Vincens et al. 1999, Maley 2001), and coincident with the arrival of increased human populations (Schwartz 1992). However, even during the most humid episodes of the past 40,000 years, there is evidence that some savanna still existed in the area (Dechamps et al. 1988, Vincens et al. 1999).

The Bateke belongs to the Guineo-Congolian center of endemism (White 1983), with most of the Bateke being in the Western Congolian forest–savanna mosaic ecoregion (Olson et al. 2001). These savannas have been fairly isolated from other savanna formations, especially from West Africa by the Congo Basin rainforest. In the Guineo-Congolian region (White 1979) and in southern Kalahari areas, endemism is high (Walters et al. 2006), with many sand-adapted and pyrophytic species. This suggests potential for endemism in the Bateke, and indeed this is supported by recent findings (Bamps 2013). In Gabon, there have been recent reports of more than 30 new plant records from savannas, and six globally rare species restricted to Kalahari sands or moist savannas (Walters et al. 2006, van der Maesen & Walters 2011), and in South Congo, Koechlin (1960) found 12 % endemic species. However, Bateke savannas were considered by White (1983) as secondary with some being edaphic and by Schwartz et al. (1995) as inclusive or edaphic, and original, without equivalent in the past. The theory of Bateke savannas being secondary would contradict potential endemism, as secondary savannas tend to have lower plant species richness and absence of geoxylic suffrutices (Zaloumis & Bond 2016). Plant species with a geoxylic suffrutex growth form are plants with large woody underground structures and short-lived aerial shoots, with a high capacity to resprout stimulated by fire, thus providing an alternative escape from fire (White 1977). They are mainly endemic to the Kalahari sands of the Zambezian region and occur almost exclusively in higher rainfall savannas with frequent fires (White 1977, 1979, Revermann et al. 2017).

There is evidence from charcoal that fires have occurred in the Bateke since 2100 BP, and almost certainly they occurred frequently far further back in time (Schwartz 1988, Walters 2012). Nowadays, fires are mostly anthropogenic, occurring mainly in the dry season for hunting and gathering (Walters 2010a, 2012). Frequent fires, fuelled by the continuous layer of grasses, have unclear effects on species richness (Higgins et al. 2000, Smith et al. 2013) and probably encourage specialization (Walters et al. 2006). Herbivore densities are low and do not cause much disturbance due to historic and current hunting, though there probably were once high herbivore densities that could have shaped the landscape (Walters 2010b).

3.2.1 Biomass stocks and botanical studies in the Bateke Plateau

Savannas cover around half of the African continent (Menaut 1983), but despite their importance to the global carbon cycle, current knowledge of African savanna biomass stocks and floristic diversity is limited (Hall & Scurlock 1991), especially in the understudied ecosystems of the Bateke Plateau.

We searched and collated the published and gray literature of the Bateke to provide a first comprehensive review of the biomass stocks in the Plateau and found eight studies that have previously quantified some aspects of biomass stocks of these savannas (Makany 1973, Apani 1990, Schwartz & Namri 2002, Yoka et al. 2010, 2013, Gigaud 2012, Lokegna 2015, Ifo 2017). These values are in general low for African savannas. There have been still fewer estimates of soil carbon stocks in the Bateke Plateau (Namri 1996, Schwartz & Namri 2002, Ifo 2017). The spatial scale of all these studies is restricted, and none have assessed all ecosystem carbon storage elements together, limiting their ability to provide understanding of the system.

We have better knowledge of the plant species of the region, with floristic inventories of Gabon (Aubréville 1961) and DRC (Robyns 1949), and a Checklist for Gabon (Sosef 2006). In RoC, there is a published inventory for the vascular flora of the Republic of Congo (Sita and Moutsambote (1988)), which provides a list of 4397 species (198 families and 1338 genera), but with the vast majority being forest species and no indication of their distribution. This inventory has been slightly updated since then, with 84 species added by Champluvier and Dowsett-Lemaire (1999), and 64 by Lachenaud (2009). More usefully, there is an illustrated list of plants of the Lesio Louna and Lefini reserves, which are major reserves covering 6% of the Bateke Plateau, that list 457 species belonging to 119 families (Nsongola et al. 2006). Some old botanical studies in French of this landscape also exist, but they are limited to the South of the Bateke (Koechlin 1960, Descoigns 1972), the Cuvette region (Descoigns 1960, Yoka et al. 2013), and the Teke Plateau (Makany 1973, Apani 1990), and in more recent some masters' theses (Lokegna 2015, Mampouya 2015). However, all these studies are limited in scope, contributing to the Republic of Congo being one of the botanically least known and inventoried countries in tropical Africa (Lachenaud 2009, Sosef et al. 2017).

Due to the lack of basic data on this ecosystem, it is difficult to understand its function, conservation value, and the transformations it could undergo with climate change and management changes. Our main objective was to characterize the structure of the vegetation and floristic diversity of the Bateke Plateau using data collected from four very large (25-ha) inventory plots, located within two protected areas and designed as a long-term fire experiment. Our research questions were as follows: (1) What is the carbon storage of our two woody savanna study sites, and how is it distributed between vegetation and the soil? (2) What is the species diversity of the study sites, and how does diversity vary by plant life form type? (3) Can we explain the structure of these savannas in the context its biogeographical history and human influence?

Due to frequent fires and intermediate rainfall, we expected these savannas to have a low tree biomass but higher grass biomass and understory diversity, with the presence of pyrophytes and geoxylic suffrutex species. Moreover, if these savannas are ancient as recent evidence suggest, with a fluctuating savanna/forest cover for at least past 40,000 years, and because of its geographical position, we would anticipate high plant and forb diversity, presence of geoxylic suffrutex, and some endemism. We would expect floristic similarities with the southern savannas due to the Kalahari sands acting as a corridor.

Overall, we provide a baseline biomass and diversity inventory for these savannas that we hope will be useful to other scientists interested in their structure and function, and assist with their management and conservation.

3.3 - Methods

3.3.1 Site description

We conducted the study in two protected areas in the Bateke Plateau, the Lefini and the Lesio Louna reserves (Fig. 3.1), situated about 160 and 110 km north of Brazzaville, respectively. These sites have a precipitation of 1627 to 1966 mm/yr and a mean annual temperature of approximately 25°C (all calculated for the period 1996–2016 from data of Climate Research Unit (CRU) for the station of Gamboma (Harris et al. 2014), see Fig. 3.1 for location). The Lefini Wildlife Reserve (LWR) has a total area of 5010 km^2 (IUCN & UNEP 2015) and was established in 1951 as a hunting reserve. The Lesio Louna Reserve (LLR) has a total area of 1730 km^2 and was established in 1993 as a sanctuary for the reintroduction of orphan gorillas by the Aspinall Foundation and later as a Natural Reserve in 1999. Both reserves are listed as IUCN Category IV and aim to maintain, conserve, and restore species and habitat (IUCN & UNEP 2015). They feature typical Bateke habitats: rolling hills studding a plateau dissected by river valleys, with open savanna dominating, and with forest patches around rivers and on the top of hills.

CARBON STOCK ASSESSMENT

We established four 25-ha permanent sample plots (500 m x 500 m) in the savanna, two in each protected area, in the year 2015 as part of a long-term fire experiment (plots LWR1 and LWR2 in Lefini and plots LLR1 and LLR2 in Lesio Louna). The plots were not randomly located, selected to be in wooded savanna, easily reachable by foot from research camps, and sufficiently large to encompass much of the natural variability of the savannas. All four plots were located with one edge running about 30 m away from the edge of closed canopy forest, associated with nearby rivers. Data collection took place in 2015 in the beginning of the dry season (May/June) for plots LWR2 and LLR1 and in the end of the dry season (September/October) for plots LWR1 and LLR2.

In these plots, we inventoried all living trees with a diameter at breast height (DBH) greater than 10 cm, recording: species, DBH, height, status (alive/dead, standing/fallen, and broken), and spatial location (by GPS). DBH was measured at 1.3 m height above-ground, and if the tree forked below this, each stem was measured independently and treated as different trees. Trees were identified to species level by Roland Odende, and their height was estimated using a Nikon Forestry Pro Laser. For the estimation of the above-ground biomass (AGB) from these measurements, we used the generic pan-tropical allometric equation from Chave et al., (2014) with wood density obtained from the Wood Density Database (Chave et al. 2009, Zanne et al. 2009) based on the species determination. This was considered the most appropriate for the study site as there are no locally defined allometric equations for this location. As height was estimated individually on the ground for every tree, there was no need to use diameter measurements to estimate tree height through a locally derived or regional relationship. However, we did compare DBH and height values in order to test the strength of this relationship in this ecosystem and to develop a model for use by others. Below-ground tree biomass (BGB) was not measured in the field, but estimated using a root-to-shoot ratio (R:S = 0.42) described by Ryan et al. (2011) for miombo woodlands. We consider this equation was appropriate as the trees are subject to similar ecological pressure and constraints, and due to the absence of a local equation or one for Central African savannas. To survey grasses and saplings/shrubs, the latter defined as woody plants with a DBH < 10 cm and with a diameter at 10 cm above-ground (D10) greater than 1 cm, 16 permanent circular subplots with a radius of 4 m (50.3 m^2) were established within each plot, on every 100 m vertex (Fig. 3.2). In these subplots, saplings were tagged; measured (D10) using a calliper, height, and DBH where applicable; and identified to species level. To estimate the biomass of the saplings (stems and roots), the allometric equations from Ryan et al. (2011) were applied for saplings with DBH < 5 cm.

$$SBs = 0.0007645 * D_{10}^2 + 0.004645 * D_{10} + 0.03876 \qquad \text{Equation 1}$$

$$SBr = 0.001784 * D_{10}^2 + 0.0001413 * D_{10} + 0.15839 \qquad \text{Equation 2}$$

where, SBs and SBr is the stem and root wet sapling biomass in kg, respectively. This was converted to biomass Mg/ha using the dry mass fraction (DMF) of 0.61 determined in the same study. For saplings with D10 ≥ 5 cm and DBH < 10 cm, the Chave et al. (2014) Equation 1 was used for the AGB, and the ratio R: S = 0.42 for roots. Grass biomass was measured using a disc pasture meter (DPM) (Bransby & Tainton 1977, Dörgeloh 2002), by taking four measurements at each subplot (therefore 64 measurements per 25-ha plot). The DPM was calibrated in each plot before its use. In order to perform this calibration, all the grass under the DPM was cut and weighed (wet weight). A subsample of grass was weighed, then dried to the point of no further weight loss, and re-weighed in order to determine dry mass based on percentage moisture loss from the samples. The relationship between mean disc settling heights (cm) and grass biomass per quadrat was determined separately for each plot using linear regression (linear calibration curve, N = 35–40 for each plot, $r^2 = 0.35–0.75$). BGB was not measured in the field, but it was estimated using the ratio calculated by Apani (1990) for grasses in the Teke Plateau (R:S = 2.5).

Biomass was converted into carbon stocks using a conversion factor of 0.47 (Ryan et al. 2011) for woody plants and 0.42 for grasses (Ryan 2009). All biomass values are given in metric tonnes of carbon per ha (MgC/ha).

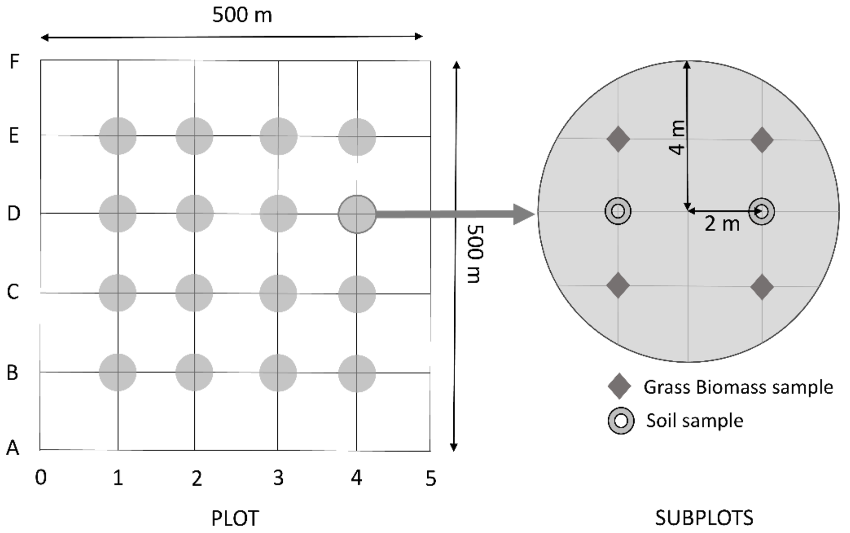

Figure 3.2. Sampling method. Plots were 500x500 m (25 ha), with subplots placed every 100 m. Each subplot had a radius of 4 m in which grass and soil (transects 2 and 4 only) measurements were taken.

SOIL ANALYSIS

Soil analysis was performed in Plot LWR2 (Lefini) and LLR1 (Lesio Louna), by taking two soil samples (4 m apart) in each subplot located in the transects numbered 2 and 4 (Fig. 3.2), at two different horizons, h0 (0–5 cm) and h1 (5–20 cm), giving 32 soils samples per plot. Samples were dried, sieved, and analysed in the physiochemical laboratory of the Institut de Recherche en Sciences Exactes et Naturelles (IRSEN) at Pointe-Noire, in order to determine total organic carbon, nitrogen content, and bulk density (measured with a cylinder core to assess the volume of the soil and determine the weight after drying, (Blake & Hartge 1986) (Batsa et al. (2017).

SPECIES COMPOSITION.

We performed a survey of the floristic composition by identifying all plant species within the subplots (presence/absence), first in situ, and where not possible samples were taken to the National Herbarium of IRSEN for identification, as described in Odende (2016). For six species, the identification was only possible to genus level. For the species nomenclature, the Sita and Moutsambote (1988) flora inventory and the Plant list data base (The Plant List, 2013) were used. Species were further categorized into the different life forms (trees, shrubs, sedges, forbs, and grasses). To further categorize shrubs and trees as geoxylic suffrutex, we used the definition of White (1977) as plants with a 'massive, woody, underground axes but only annual or short-lived shoots aboveground', and use the list provided in (Maurin et al. 2014). Species diversity was calculated using species richness for all presence/absence data, as the total number of unique species observed in each subplot.

DATA ANALYSIS

We investigated the within-plot variances using linear models and one-way analysis of variance (ANOVA). To evaluate to what extent species were well sampled, we constructed rarefied species accumulation curves. Dissimilarity in species composition between sites (beta diversity) was calculated using Sørensen dissimilarity index. Compositional patterns were visualized using a non-metric multidimensional scaling (NMDS), and correlations between the floristic composition and environmental characteristics were assessed with multiple regression, by fitting the ecological variables to ordination scores using the 'envfit' function of the vegan package (Oksanen et al. 2013). All data analyses were performed using the R statistical software v. 3.1.3 (R Core Team, 2015, http://cran.r-project.org), using the vegan (Oksanen et al. 2013), spatstat (Baddeley & Turner 2005), pgirmess (Giraudoux 2017), and iNEXT (Hsieh et al. 2016) packages.

3.4 - Results

3.4.1 Biomass Stocks

In total, we inventoried 4120 live tree stems with a DBH ≥ 10 cm in our 100 hectares field plots (LWR1 = 726, LWR2 = 1480, LLR1 = 1022, and LLR2 = 892), with a maximum DBH of 39.3 cm. The tree, grass, and saplings/shrubs carbon stocks on a plot basis are summarized in Table 3.1, with a mean total of 6.47 ± 0.33 MgC/ha. Grass carbon stocks were in general about equal to that of tree, shrub, and sapling biomass combined, though there was considerable variation both within and between plots. Plots had significantly different above-ground biomass for trees (ANOVA single factor, $P < 0.05$) and grasses ($P < 0.01$).

Approximately 90% of the tree AGB was stored in trees with a DBH between 10 and 22 cm, with large stems rare (Supplementary Information Fig. S3.1). The stem density of the plots varied from 29.0 (plot LWR1) to 59.2 tree stems per hectare (plot LWR2) (Fig. S3.2).

Table 3.1. Summary of the average biomass stocks per hectare. For grasses and saplings/shrubs, ± indicates the standard error per plot of 16 x 50.3 m^2 subplots; and for tree stems it is the standard error of 25 x 1 ha subplots.

	Biomass stock (Mg/ha)				
	LWR1	**LWR2**	**LLR1**	**LLR2**	**MEAN**
Grasses					
Stems	1.58 ± 0.25	5.35 ± 0.22	3.28 ± 0.16	1.37 ± 0.09	2.89 ± 0.22
Roots	3.96 ± 0.63	13.36 ± 0.55	8.20 ± 0.39	3.42 ± 0.21	7.24 ± 0.55
Total	**5.54 ± 0.68**	**18.71 ± 0.59**	**11.48 ± 0.42**	**4.79 ± 0.23**	**10.13 ± 0.59**
Saplings/Shrubs					
Stems	1.10 ± 0.27	1.40 ± 0.72	1.36 ± 0.60	0.55 ± 0.21	1.11 ± 0.25
Roots	1.84 ± 0.44	1.22 ± 0.52	1.52 ± 0.70	1.13 ± 0.59	1.34 ± 0.28
Total	**2.94 ± 0.52**	**2.61 ± 0.89**	**2.89 ± 0.92**	**1.68 ± 0.63**	**2.45 ± 0.38**
Trees					
Stems	0.90 ± 0.20	2.14 ± 0.23	1.64 ± 0.33	1.44 ± 0.14	1.57 ± 0.13
Roots	0.38 ± 0.08	0.89 ± 0.10	0.69 ± 0.14	0.52 ± 0.06	0.62 ± 0.05
Total	**1.28 ± 0.22**	**3.03 ± 0.25**	**2.33 ± 0.36**	**1.96 ± 0.15**	**2.19 ± 0.14**
TOTAL	**9.76 ± 0.88**	**24.35 ± 1.10**	**16.70 ± 1.08**	**8.43 ± 0.68**	**14.77 ± 0.71**

3.4.2 Soil Carbon and Nitrogen

The mean bulk density of the 0–20 cm horizon was 1.48 ± 0.01 Mg/m^3 (LWR2) and 1.44 ± 0.01 Mg/m^3 (LLR1) (soil analysis results summarized in Table S3.1). Carbon stocks and the C:N ratio were very low in both sites. Soil carbon content estimations were very similar in both profiles, being slightly higher in the h0 profile than in the h1, with an average of 16.74 MgC/ha. Carbon stocks and C:N ratios were not significantly different between sites (ANOVA single factor, $P > 0.05$).

We also found that DBH was a predictor of tree height, although with a weak positive relation (R2 = 0.14, $P < 0.001$) in all plots (see Fig. S3.3 for graph and equation). Ninety percent of the inventoried trees with a DBH ≥ 10 cm were taller than 3.1 m.

3.4.3 Species Characterization

We identified 49 species in total (4 trees, 13 shrubs, 4 sedges, 17 forbs, and 11 grass species). A complete list of the species is given in the Supplementary Information (Table S3.2). For trees, *Hymenocardia acida Tul.* (Phyllanthaceae) was hyperdominant, comprising 93.8% of the inventoried stems across all plots (Table S3.3 in Supplementary Information). There were 27 species common to both sites, 3 unique to Lefini, and 11 unique to Lesio Louna. The Sørensen index of dissimilarity between the two sites was 0.21, which indicates a 21% dissimilar species composition between sites. The most abundant grass species in all subplots was *Loudetia simplex* and *Hyparrhenia diplandra*. Poaceae was the dominant family across the plots, followed by Fabaceae and Cyperaceae. Fig. 3.3A summarizes the number of species per plot divided into vegetation types. Species richness was similar for all plots (LWR1 22, LWR2 25, LLR1 29, and LLR2 23), with a mean of 25 ± 3. There is a high presence of woody species with a geoxylic suffrutex growth form (Table S3.2), and the understory is more diverse.

The rarefied species accumulation curves (Fig. 3.3B) are comparable among the plots. The estimated sample completeness was for plot LWR1 96%, LWR2 99%, LLR1 93%, and LLR2 97%. When comparing diversity at the subplot level, NMDS ordination showed dissimilarity of the two sites in relation with the species composition of the subplots, but little difference between the two plots within each site (Fig. 3.4). Variation in species composition is best explained by the distance to forest, elevation, and tree and grass above-ground biomass (NMDS, $P < 0.05$).

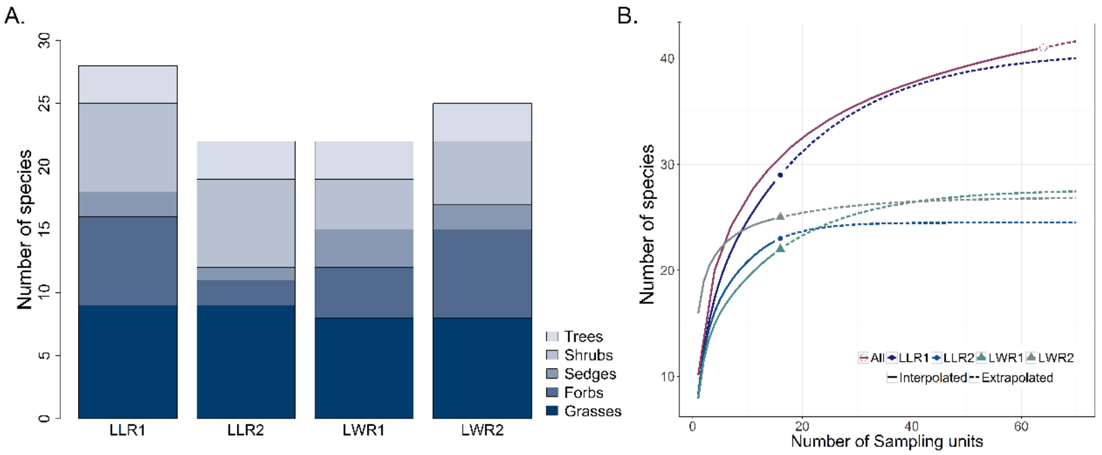

Figure 3.3. A. Number of species per plot by type (trees, shrubs, sedges, forbs or grasses) and total. B. Rarefied species richness showing the cumulative number of species observed and an extrapolated sampling curve (dashed line) of subplot species for all plots (n=16 subplots per plot), and for all combined (n=64).

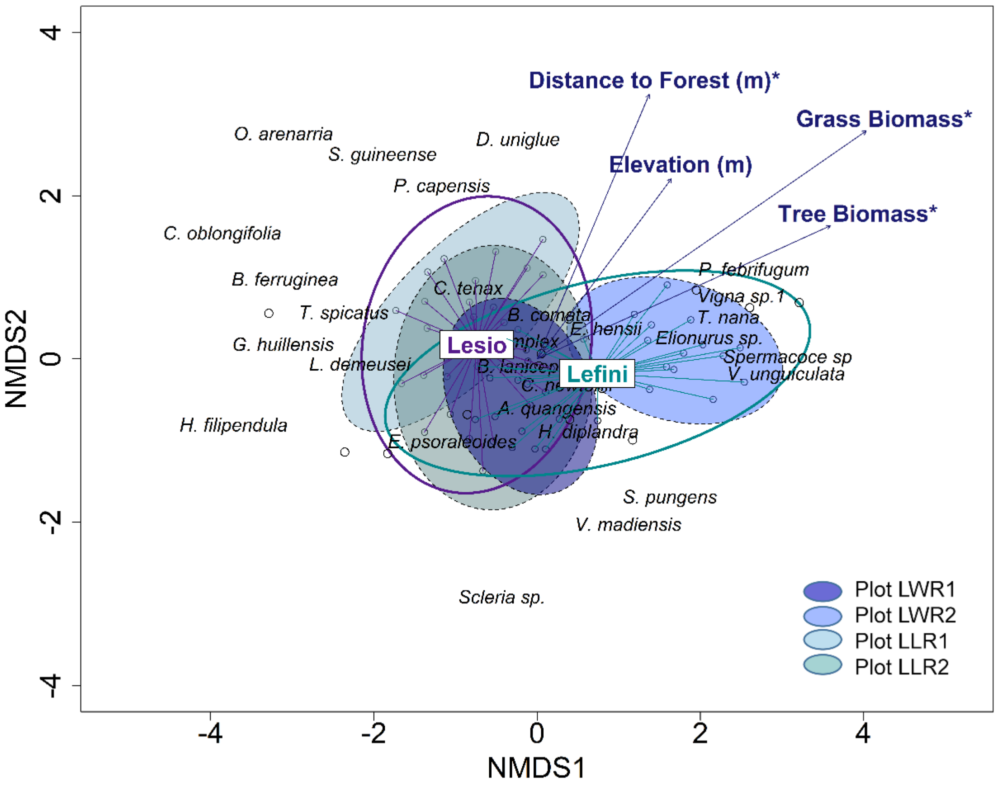

Figure 3.4. NMDS ordination for all the floristic data (grass and woody plants). Big circles grouping the sites (Lesio Louna (LL) and Lefini (LW)), Fill circles grouping the subplots (LWR1, LWR2, LLR1 and LLR2), with confidence limit for ellipses of 0.95. Floristic composition was correlated with environmental vectors, displayed as arrows (where $p < 0.05$, and * where $p < 0.01$). Elevation (m) = Elevation relative to lowest point in each plot.

3.5 - Discussion

3.5.1 Carbon stocks and comparison with other studies

At our two sites, the average total vegetation carbon stocks (above-ground and below-ground) was 6.5 MgC/ha, with the topsoil horizon (0–20 cm) holding over twice as much, 16.8 MgC/ha (Fig. 3.5, and considerably more carbon likely stored at deeper depths not investigated here).

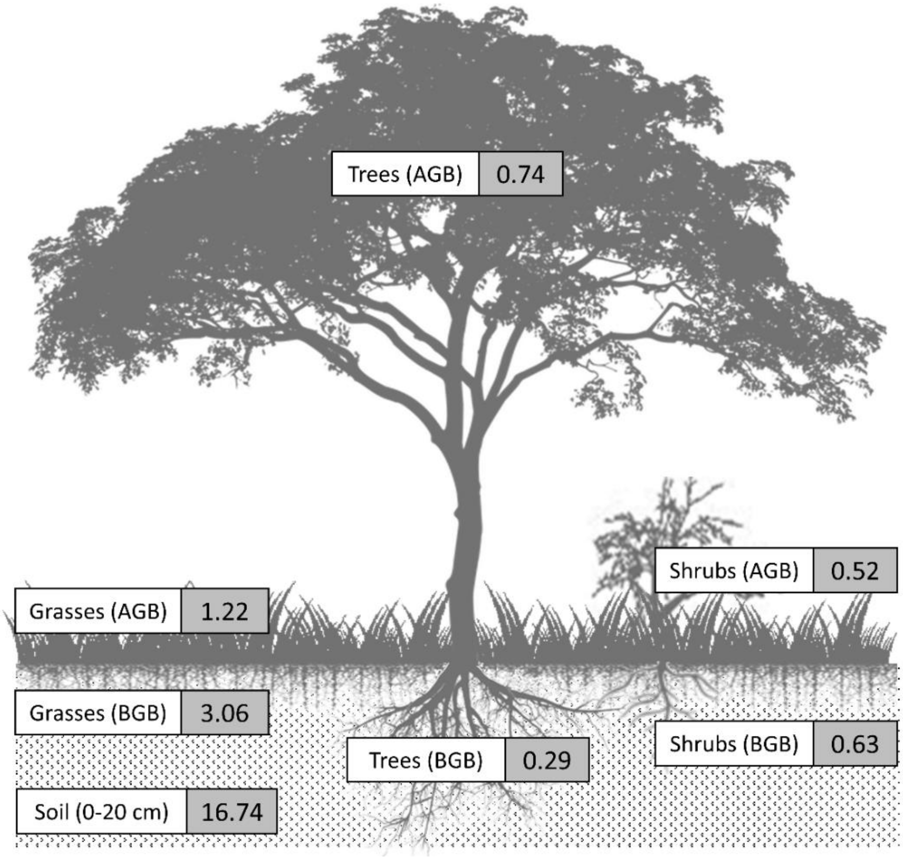

Figure 3.5. Representation of the average carbon stocks (MgC per hectare) for all the plots in the study sites. Soil is Organic Carbon (SOC) stock.

The climate of the Bateke Plateau, with annual rainfall of ~1600 mm and an intense 3–4-month dry season, would suggest a closed canopy forest in the absence of disturbances (Sankaran et al. 2005). Tree cover generally increases with rainfall, but fire is an important disturbance in areas with intermediate precipitation (Staver et al. 2011). On Kalahari sands, there is also a gradient of increasing woody cover and biomass with increasing precipitation, at least in the southern section (Scholes et al. 2002). Consequently, although we would expect the Bateke to have a high woody cover and tree density, the observed low biomass could be the product of frequent fires, which reduce woody cover and maintain the grasslands (Favier et al. 2004, Staver et al. 2011), and the sandy soils, which are poor in organic matter and nutrients (Yoka et al. 2010) and have a high percolation rate. The high precipitation favors grass productivity, providing more fuel for fires. Savannas with sandy nutrient-poor soils are more likely to favor woody over herbaceous cover (Scholes 1990, Sankaran et al. 2005, Bond 2008), although the edaphic conditions can also be a restriction for trees (Mills et al. 2013). Tree seedlings compete with grasses for water and nutrients below-ground (Scholes & Archer 1997), but disturbances are the main determinants for trees not attaining the maximum woody cover established by water availability (Mills et al. 2013).

Although these carbon stock values appear low for savannas, they are not unusual for the Bateke (Table 3.2). The tree biomass estimated in this study is between the values obtained by Apani (1990) for the Teke Plateau and by Gigaud (2012) for the DRC. Grass biomass is also similar to that calculated by Yoka et al. (2013) for the South of RoC and to Makany (1973), but is lower than some other studies (Apani 1990, Yoka et al. 2010). This could be due to the timing of the sample collection, which were later in the year than the likely time of maximal grass biomass, around May at the end of the main wet season (Apani 1990, Yoka et al. 2010). In the Kalahari sands, Scholes et al. (2002) found that grass biomass increased with higher precipitation up to 600 mm and then decreased due to competition with trees (up to 1000 mm). This does not appear to be the case in our two sites, but further research about tree–grass competition is needed to better understand this system.

Table 3.2. Allocation of carbon stocks (MgC/ha) in the Bateke Plateau savannas from different studies.

	GRASSES (MgC/ha)		**TREES (MgC/ha)**		**SOIL (MgC/ha)**	
	Roots	**Stems**	**Roots**	**Stems**		**Area**
Makany (1973)		1.39(1) - 1.71(2)				Plateaux Teke RoC
Apani (1990)	4.31	1.78		0.17*		Plateaux Teke RoC
Gigaud (2012)				1.66*		Bateke DRC
Lokegna (2015)			1.85*			Bateke(Mah) RoC
Yoka et al. (2010)		1.72(1) - 4.79(2)				Cuvette RoC
Yoka (2013)		1.18(1) - 2.63(2)				Cuvette RoC
Schwartz and Namri (2002)					15-20 (0-10 cm) 86-102 (0-100 cm)**	Bateke RoC
Ifo (2017)					13.28 (0-20 cm) 45.95 (0-100 cm)	Lesio Louna RoC
This study	3.06 ± 0.23	1.22 ± 0.09	0.29 ± 0.02	0.74 ± 0.06	16.74 ± 0.9 (0-20 cm)	Lefini/Lesio Louna RoC

Notes: (1) Loudetia simplex (2) Hyparhenia diplandra
** Trees and shrubs*
*** average of the Bateke land unit*

The biomass of saplings/shrubs was higher than might be expected from a visual assessment, which suggests a landscape dominated by grass and scattered trees. The density of shrubs in this landscape was very patchy, and the subplot density measurements have a non-normal, right-skewed distribution, with many plots not having any shrubs, and some containing high densities. Larger or more subplots would be required for a more robust shrub biomass estimation.

Few studies have quantified the BGB in the Bateke, but our results are similar to those obtained by Apani (1990) for grasses and Lokegna (2015) for trees. These values (mean) are low compared to reported general tropical savannas root biomass, such as the 6.48 MgC/ha reported by Jackson et al. (1996) for tropical grassland savannas. Tree, shrub, and grass BGB were estimated with ratios found in the literature, and therefore, having local allometric equations would provide better estimates. Moreover, we might have underestimated by using the mean root-to-shoot ratio described by Ryan et al. (2011), as this ratio varied from 0.27 to 0.58. The BGB of the geoxylic suffrutex species will have been underestimated as they contain disproportionately large underground structures.

Our savanna plots were characterized by a very low tree stem density (averaging 41.2 stems per ha) and low biomass, consistent with systems with high disturbance. This result indicates the importance of using large (>10 ha) plot areas for the inventory of this biome, as savannas are highly heterogeneous. However, in order to capture all landscape variability, larger scales of sampling would be needed (Staver 2017).

The topsoil contributes the most to the carbon pool in our plots (16.7 MgC/ha, 53% of the total), in concordance with other studies of savannas (Scurlock & Hall 1998, Ciais et al. 2011), and the low carbon density of these soils is similar to other studies in Kalahari sands (Bird et al. 2004). Soil carbon stocks are similar to those found in other studies of the Bateke Plateau (Table 3.2), such as Ifo (2017), and slightly lower than Schwartz and Namri (2002). Additionally, these values are much lower than in miombo woodlands, where the median soil C stocks (0–30 cm) were 35.9 tC/ha, but supporting a much higher above-ground woody biomass of 28.7 tC/ha (Ryan et al. 2016). Carbon content estimations were very similar in both profiles, being slightly higher in the h0 profile than in h1. These carbon stock estimations are important for further studies, to inform conservation measures and in the design of more effective data collection protocols.

3.5.2 Species diversity and community composition

The floristic inventory results are in concordance with those of other authors for the Bateke (Duvigneaud (1953a), Makany (1973) and Nsongola et al. (2006)). Most of the tree species inventoried are typical of dry savannas (Duvigneaud 1949). Many authors in fact denominate this type of savanna of the Bateke as Hymenocardia savanna (Duvigneaud 1953a, Descoigns 1972, Makany 1973), dominated by *Hyparrhenia diplandra* or by *L. simplex* (e.g., Makany 1973, Walters et al. 2013). *H. acida*, is a deciduous, fire-tolerant (Trapnell 1959), small tree that occurs in tropical African savannas mainly on sandy, loamy, or clayey soils (Duvigneaud 1949). It reproduces asexually through production of resprouts, stimulated by frequent fires

(Walters 2012). Koechlin (1960) described that he never saw a *H. acida* seedling in the area, which implies the importance of vegetative reproduction (Walters 2007). Boaler and Sciwale (1966) found for miombo woodlands that H. acida was one of the fastest growing trees, therefore potentially making them grow quickly enough to escape mortality by fire in places given enough precipitation, like in the Bateke. These characteristics of *H. acida* could explain its hyperdominance in this system.

In our inventory, we found six shrubs and trees with a geoxylic suffrutex growth form (Table 3.S1), indicating a pyrophytic component of the flora and potentially an established savanna in a climate suitable for forests (White 1977, Walters et al. 2006, Maurin et al. 2014). We have also found some Cyperaceae species, which often occupy recently burned grasslands, and some pyrophytes, including *H. acida*, *A. senegalensis*, *Bridelia ferruginea*, *Psorospermum febrifugum*, and *Maprounea africana* (Walters et al. 2006), which highlights the importance of fire in maintaining these ecosystems. Fire is likely responsible for maintaining the forest–savanna mosaic with abrupt boundaries between forest and savanna areas. We did not find savanna–forest transition species found in similar habitats, like Walters et al. (2006) in Gabon, perhaps indicating the savanna at our sites has been stable for some time.

The species diversity we found is quite low compared to other African savannas, for example in South Africa (Fynn et al. 2004, Smith et al. 2016) and for miombo woodlands (Masocha et al. 2011). The species richness is more comparable to values obtained for natural grasslands in South Africa, and greater than those for any secondary grasslands (Zaloumis & Bond 2016), suggesting these savannas are not new and probably have existed as a mosaic for long time. We also did not find any endemic species in our inventory, with most of them having wider distributions in Africa. However, we only subsampled 100 ha of savanna, from two sites located only 86 km apart, so our conclusions about plant diversity cannot be assumed to apply to the whole plateau. In Gabon, Wieringa and Sosef (2011) found for the Bateke Plateau National Park a relatively unique flora with a limited spatial extent, and Walters et al. (2006) encountered more endemism in forests than in savannas. Although the Bateke belongs to the Guineo-Congolian regional center of endemism (White 1983), some studies had found species distributions similar to other regions. Walters et al. (2006) concluded in their analysis about floristics in the Gabon's Bateke Plateau that over 50 percent of the species were classified as Guineo-Congolian, but 20 percent had extended distributions into the Zambezian or Sudanian phytochoria, and that sites on Kalahari sands in Gabon shared floristic affinities with Lefini. Similarly, Koechlin (1960) determined for the Kalahari sand savannas in the south of RoC that 12% of the species were endemic and 55% had a Sudano- Angolan distribution (Walters et al. 2006). Duvigneaud (1953a) described the Kalahari plateau in the DRC (Kwango) as an intermediate zone, with a Guineo-Congolaise climate but with Zambezian elements due to the edaphic conditions. Additionally, Fayolle et al. (2018) concluded, using the data presented here, that Lefini and Lesio Louna have floristic similarities with Northern and Western African savannas and woodlands. The mixed floristic composition of the Bateke is likely due to its historical spatial geography. These savannas have been fairly isolated from other savanna formations, with only some exceptions. The floristic affinities with the south and east could be explained by a connection via a savanna corridor with the Angolan highlands (Fayolle et al. 2018) and by the Kalahari sands sheets, which could have provided a connection with southern species, although this hypothesis remains uncertain (Walters et al. 2006). The similarities with the northern savannas could be explained by the fragmentation of the Congo Basin forest during the Last Glacial Maximum (18000 years ago) (Maley 1991, Fayolle et al. 2018). Furthermore, the Sangha River Interval provided a large savanna corridor connecting the Sudanian savannas in the north to the Bateke savannas (Maley 2001, Maley & Willis 2010, Bostoen et al. 2015).

3.6 - Conclusion

Our results show that the Bateke savannas store only small quantities of carbon per hectare, with the largest pools in the soil and roots. Its species diversity is low, and we found no evidence of endemism. The savanna ecosystem is clearly controlled by fire, with all plants showing adaption to regular burning. We have further shown the need to use large plots (>10 ha) to capture variations in carbon stocks and species diversity in this area. These data will thus inform future studies on optimal sampling methodologies and carbon dynamics in this ecosystem. Our results, although only representative of part of the Bateke, will further help in understanding the complex relationship between grasses, understory plants, trees, fire, and resources. However, more studies are needed in this ecosystem to inform conservation and restoration, particularly with regard to fire regime, and to understand future challenges from climate change.

3.7 - References

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3.8 - Supplementary information

Table 3-S 1. Soil characteristics of Lefini (LWR2) and Lesio Louna (LLR1) ± Standard error (n=16 per plot) for two horizons h0 (0-5 cm) and h1 (5-20 cm).

Horizons		**Organic Carbon Stock (Mg/ha)**	**C (%)**	**N (%)**	**Ratio C:N**
h0	LWR2	5.15 ± 0.27	0.71 ± 0.04	0.06 ± 0.003	12.47 ± 0.78
(0-5 cm)	LLR1	4.41 ± 0.31	0.62 ± 0.05	0.05 ± 0.003	11.70 ± 0.74
	AVERAGE	**4.78 ± 0.41**			
h1	LWR2	12.40 ± 0.38	0.55 ± 0.02	0.04 ± 0.002	12.56 ± 0.51
(5-20 cm)	LLR1	11.52 ± 0.72	0.53 ± 0.04	0.05 ± 0.05	11.74 ± 0.58
	AVERAGE	**11.96 ± 0.81**			
TOTAL	LWR2	17.55 ± 0.47			
(0-20 cm)	LLR1	15.93 ± 0.78			
	AVERAGE	**16.74 ± 0.91**			

Table 3.S 2. Species composition list (presence/absence data) for all subplots. (G.S. indicates geoxylic suffrutex species)

	FAMILY	SPECIES	G.S.
GRASSES	POACEAE	*Andropogon schirensis*	
		Brachiaria comata (A.Rich.) Stapf	
		Ctenium newtonii Hack.	
		Digitaria diagonalis (Nees) Stapf	
		Elionurus hensii K. Schum.	
		Elionurus sp.	
		Hyparrhenia diplandra (Hack.) Stapf	
		Loudetia simplex (Nees) C.E. Hubb.	
		Loudetia demeusei (De Wild.) C.E.Hubb.	
		Melinis nervialumis (Franch.) Zizka	
		Trachypogon spicatus (L.f.) Kuntze	
FORBS	ASTERACEAE	*Aspilia africana (Pers.) C. D. Adams*	
	COMMELINACEAE	*Cyanotis longifolia Benth.*	
		Murdannia simplex (Vahl) Brenan	
	COMPOSITAE	*Vernonia potamophila Klatt*	
	LAMIACEAE	*Englerastrum adenophorum (Gürke) T.C.E.*	
	LEGUMINOSAE	*Chamaecrista mimosoides (L.) Greene*	
		Desmodium velutinum (Willd.) DC.	
		Eriosema glomeratum (Guill. & Perr.) Hook.	
		Eriosema psoraleoides (Lam.) G.Don	
		Eriosema erici-rosenii R.E.Fr.	
		Eriosema sp. 1	
		Tephrosia nana Kotschy ex Schweinf	
		Vigna sp.1	
		Vigna unguiculata (L.) Walp.	
	RUBIACEAE	*Spermacoce ruelliae DC.*	
		Spermacoce sp1	
		Spermacoce sp2	
SEDGES	CYPERACEAE	*Bulbostylis laniceps C.B.Clarke ex T.Durand*	
		Bulbostylis hispidula (Vahl) R.W.Haines	
		Cyperus tenax Boeckeler	
		Scleria sp.	
SHRUBS	ANISOPHYLLEACEAE	*Anisophyllea quangensis Engl. ex Henriq.*	*
	APOCYNACEAE	*Cryptolepis oblongifolia (Meisn.) Schltr.*	
		Landolphia lanceolata (K. Schum.) Pichon	
	CHRYSOBALANACEAE	*Chrysobalanus sp.*	
		Parinari capensis Harv.	*
	CLUSIACEAE	*Garcinia huillensis Welw.*	
	HYPERICACEAE	*Psorospermum febrifugum Spach*	
	LAMIACEAE	*Vitex madiensis Oliv.*	*
	LEGUMINOSAE	*Dichrostachys cinerea (L.) Wight & Arn.*	
	OCHNACEAE	*Brackenridgea arenaria (De Wild. & T.*	*
		Ochna arenaria De Wild. & T.Durand	
	PHYLLANTHACEAE	*Bridelia ferruginea Benth.*	
	SMILACACEAE	*Smilax anceps Willd.*	
TREES	ANNONACEAE	*Annona senegalensis Pers.-*	*
	LOGANIACEAE	*Strychnos pungens Soler.*	
	MYRTACEAE	*Syzygium guineense (Willd.) DC.*	*
	PHYLLANTHACEAE	*Hymenocardia acida Tul.*	

TABLE 3.S3. Stem species number per plot for all trees (DBH ≥ 10 cm).

Tree species	LWR1	LWR2	LLR1	LLR2
Albizia ferruginea (Mimosaceae)				1
Annona senegalensis (Annonaceae)			1	
Bridelia ferruginea Benth. (Phyllanthaceae)			5	
Hymenocardia acida Tul. (Phyllanthaceae)	725	1476	956	704
Maprounea Africana (Euphorbiaceae)		2	3	
Strychnos pungens Soler. (Loganiaceae)	1	2	11	2
Syzygium guineense (Willd.) DC. (Myrtaceae)			45	185
Vitex madiensis Oliv. (Lamiaceae)			1	

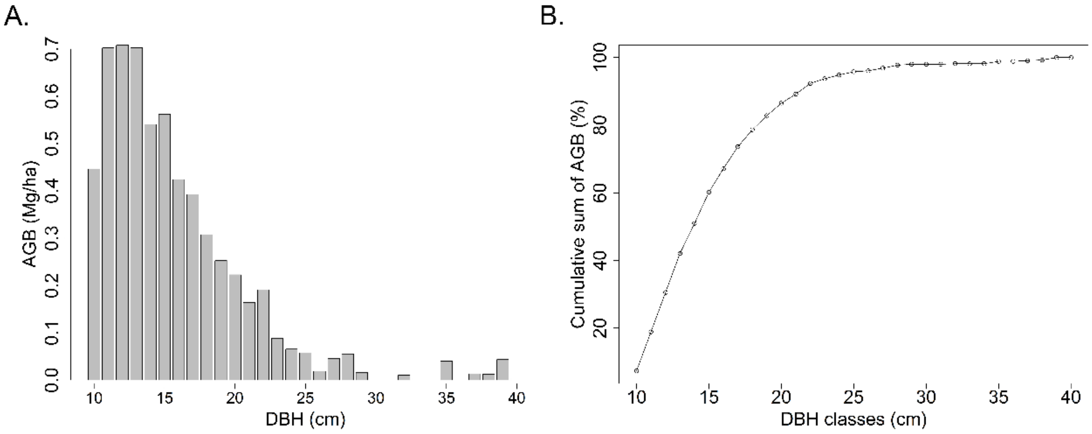

Figure 3S.1. AGB (A.) and cumulative sum of AGB (B.) vs. DBH classes for all plots for trees (DBH ≥ 10 cm).

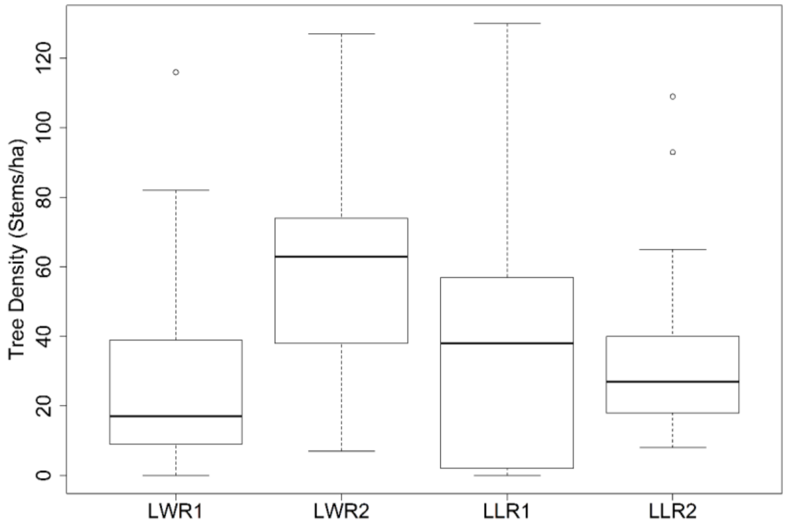

Figure 3S.2. Density of stems per hectare (DBH ≥ 10 cm) for all plots, with box and whisker data based on individual values for the 25 x 1 ha subplots within each 25 ha plot. Black lines represent the median of the data, boxes contain the middle 50 % of observations, and the whisker lines represent 90% of the data.

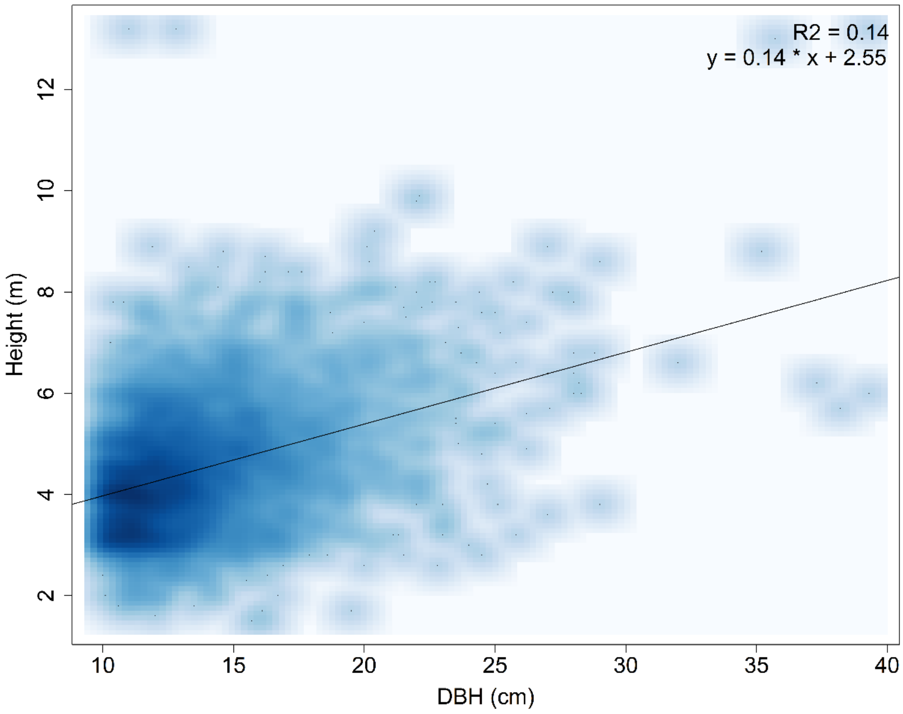

Figure 3S.3. DBH (cm) vs Height (m) for all trees in all plots, with point density. It shows a positive correlation between DBH and Height, with y= 0.14 * x + 2.55, and r2=0.14.

Chapter 4

The effect of fire seasonality and tree-tree competition in shaping the structure of a mesic savanna

Paula Nieto-Quintano, Casey M. Ryan, Edward T. A. Mitchard, Samuel Bowers

Hymenocardia acida (drawing by Paula Nieto)

This chapter is intended to be submitted to the journal New Phytologist for publication.

I collated and analysed the data, and wrote the manuscript, with advice and feedback from co-authors. I led the design of the experiment and re-measurements, with the collaboration of other participants as described in Chapter 2. The statistical model was adapted from the work of Samuel Bowers.

4.1 - Abstract

Understanding mesic savannas, their dynamics and the coexistence of trees and grasses, requires knowledge about tree demographics, and the identification of the key processes that regulate them, including fire and competition. Here we present data from a 3 year fire experiment using 25 ha plots in two mesic savannas in the Bateke Plateau with early season and late season fire treatments. These savannas have comparatively high precipitation (~1600 mm) and very low tree biomass (~0.7 MgC/ha). We used hierarchical models to relate tree growth and mortality rates to stem size, woody competition, fire seasonality, stem damage, and distance to closed canopy forest. Trees had low growth rates (averaging 1.21 ± ± 0.57 mm/yr), and mortality (3.24 ± 0.54 %/yr) across all plots. Late dry season fires significantly reduced tree growth (-0.08 mm/yr), but unexpectedly were also associated with reduced mortality. Stem damage was associated with a 0.15 ± 0.05 mm/yr reduction in diameter increment, and a higher probability of mortality, possibly related to relative vulnerability to fire. The best models of tree growth and mortality also indicate a potentially important role for tree-tree competition, though the effect is mixed with potential benefits from relative protection from fire. Results from this study can be used to improve knowledge of carbon cycle dynamics in mesic savannas, and to identify appropriate management strategies for the Bateke Plateau.

4.2 - Introduction

Savannas, characterised by the co-existence of woody vegetation with a continuous herbaceous layer, typically have a very heterogeneous spatial plant structure (Frost et al., 1986; Sankaran et al., 2005). Tree and grass biomass is variable over landscapes, from open grasslands to dense wooded vegetation, and tree populations range from spatially aggregated clusters to being widely dispersed (Scholes & Archer, 1997). Recent studies on savanna ecology highlight the importance of interactions between both bottom-up, resource limitation, and top-down, demographic restrictions from disturbances, as determinants of tree-grass coexistence (Sankaran et al., 2005; Bucini & Hanan, 2007; Bond, 2008; Staver et al., 2011; Lehmann et al., 2014; Staver, 2017). It is still unclear how the limiting mechanisms of tree and grass growth are related to competition and disturbances, and how their relative importance varies along environmental resource gradients (e.g. Scholes & Archer, 1997; Sankaran et al., 2004; Bond, 2008). The result is that savanna tree cover remains highly unpredictable (Staver, 2017). Mesic savannas, in particular, are highly dynamic and unstable systems, presenting strongly differentiated perhaps stable states of closed-canopy forest and open savannas (Sankaran et al., 2005; Staver et al., 2011). In these savannas, it is likely that fires or other disturbance events may be an important determinant of tree and grass coexistence and distribution, across a range of scales (Sankaran et al., 2005; Staver et al., 2011). In order to explain the dynamics of coexistence between trees and grasses, the presence of savannas in regions where climatic conditions may otherwise support closed canopy forests (Sankaran et al., 2005; Bond, 2008; Dohn et al., 2017), and the diversity of tree and grass densities at different spatial scales, we require an integrated knowledge of the processes that regulate these spatial patterns. This is particularly challenging in savanna ecosystems because the processes that act to structure plant populations operate across a range of scales, and these often interact so as to obscure the causal mechanisms promoting vegetation heterogeneity.

Savanna vegetation dynamics are underpinned by the tree demographic processes of growth, mortality and recruitment, which together determine tree cover, spatial structure and ecosystem function (Bond 2008). Understanding savanna demographic rates, and the processes that regulate them, is important for building accurate models of savanna dynamics (Holdo, 2006; Prior et al., 2006), as well as for their effective management. However, it is difficult to disentangle all the interacting processes that impact demographic rates and develop an integrated understanding of savanna systems. Whilst there have been a number of studies on savanna tree demographic rates in savannas (eg. Higgins et al., 2000; Holdo, 2005), the relative importance of the factors that shape them, and how they vary between regions, is still unclear, especially the role of fire and tree-tree competition (Sankaran et al., 2004; Holdo, 2005; Sea & Hanan, 2012).

Fire is an important factor in determining the composition and structure of mesic savannas (Bond & Van Wilgen, 1996; Bond & Keeley, 2005; Staver et al., 2011). Fires are very frequent in savanna ecosystems, occurring mainly during the dry season with median return intervals in Africa of 2–10 years (Archibald et al., 2010). They are largely the result of accidental or deliberate anthropogenic burning, though lightning ignition is known to occur occasionally (Archibald et al., 2009). In general in tropical savannas, woody cover increases with precipitation, but so does grass fuel loads, increasing fire frequency and intensity (Higgins et al., 2000; Bucini & Hanan, 2007; Lehmann et al., 2014).

Fire influences vegetation structure by top-killing and damaging trees, especially young trees or those intolerant of fire or otherwise damaged, and selects in favour of fire resistant and resprouting species (Higgins et al., 2000). Although most savanna trees are adapted to fire to some degree, fires are a common cause of whole-tree mortality and can top-kill in both mature and juvenile trees (Hoffmann & Solbrig, 2003). The growth rates of adult savanna trees may be suppressed by frequent or intense fires (Murphy et al., 2010). Fire also controls recruitment by maintaining, killing, or suppressing saplings; with very few seedlings surviving intense fires, even of fire-adapted species (Prior et al., 2006; Murphy et al., 2010). This so-called demographic bottleneck reduces woody biomass and woody plant density (Furley et al., 2008; Hoffmann et al., 2009), and unless there is a long enough time gap between fires so that stems can reach sufficient height or bark thickness to be resistant, trees are stuck in a “fire trap” (Bond & Van Wilgen, 1996; Hoffmann et al., 2009). As well as fire frequency, fire seasonality and intensity are crucial to predicting the impacts of fire on vegetation structures (Ryan & Williams, 2011). Late dry season fires are normally more intense and therefore more damaging, as the grasses that make up the majority of fuel are drier, than early dry season fires, which usually burn at low intensity and in patches (Trapnell, 1959; Holdo, 2005; Laris et al., 2016). Other factors such as the canopy cover, grass species, temperature, and moisture availability may impact fire intensity through influencing the grass fuel load, which can be quite variable year to year (Holdo, 2005; Lehmann et al., 2014).

The spatial structure of woody plants in savannas is irregular, normally showing dense patches or clusters of trees amongst more sparsely populated areas (Dohn et al., 2017, Staver et al., 2017). These clusters might result from facilitation (that is the process whereby tree growth and survival rates are increased by being near to other trees, possibly caused by increased nutrient availability), reduced herbivore pressure, and better protection from fire through the shading out of grasses, reducing local fuel loads (Mordelet & Menaut, 1995; Scholes & Archer, 1997). Fire frequency and annual rainfall have been suggested as the main factors supporting patchiness in savannas across multiple spatial scales, with patchiness of woody vegetation increasing with rainfall (Veldhuis et al., 2017). However, clustering of trees also results in the potential for tree-tree competition (Calabrese et al., 2010). Tree-tree competition in savannas mainly takes the form of belowground competition for water and nutrients (Smith & Grant, 1986). Competition between trees can limit their access to light, nutrients and water, inhibits seed germination and the growth of juvenile trees (Prior et al., 2009), and in extreme cases the combination will cause density-dependent mortality (Skarpe, 1991). The effect of tree clustering on growth and mortality are thus mixed (Skarpe, 1991; Shackleton, 2002; Holdo, 2006). Therefore, there may exist a trade-off between tree clustering, maintained by repeated fires and the mortality of isolated trees, and suppressed growth and density-dependent mortality due to tree-tree competition in clumps (Sea & Hanan, 2012; Svátek et al., 2018).

The spatial patterns of woody vegetation have been documented across many savannas and woodlands in Africa (Skarpe, 1991; Grundy et al., 1994; Couteron & Kokou, 1997; Jeltsch et al., 1999; Shackleton, 2002; Calabrese et al., 2010). However, few studies have quantified the spatial scale and intensity of woody vegetation competition and its effect on demographic rates (Smith & Grant, 1986; Calabrese et al., 2010; Dohn et al., 2017; Fensham et al., 2017). Although both tree-grass and tree-tree interactions are important in influencing savanna structure and function (Scholes & Archer, 1997), there are a limited number of studies on the latter (Scholes & Archer, 1997; Dohn et al., 2017). This might be due to the tree structure of savannas being extremely variable and therefore very challenging to sample, requiring either large plot sizes or long transect lengths to collect a sufficient sample size of trees experiencing the full range of tree-tree distances (Staver, 2017). Analysing the effect of fires is also challenging as fire experiments are rare, expensive and involve long-term management and mensuration in order to effectively capture the seasonality and variability of fires (Furley et al., 2008). Interactions between competition and fire have therefore mostly been assessed through modelling studies (Holdo, 2005; Martínez-García et al., 2013), which are themselves challenged by a lack of real-world field data for parameterisation.

There is, therefore, a need for experimental studies that control the fire regime and study the effect of tree growth and mortality related to local tree density using large plots such that many variations of tree density exist. These would lead to a better understanding of how fire, tree-tree facilitation, and tree-tree competition control spatial structures and demographic rates in savannas, and thus enable us to build models to understand their response to climate and land use change, and altered fire regimes (Midgley & Bond, 2015; Veldhuis et al., 2017). Given their socio-economic importance (Frost et al., 1986; Scholes & Archer, 1997), such understanding is vital. Long-term above-ground carbon uptake or release in savannas is mostly due to tree demographic dynamics, as grass carbon exchange is more ephemeral due to smaller below-ground and above-ground storage. However, the heterogeneity and dynamics of tree carbon storage is not well understood, and again needs experimental data to improve this situation (Staver, 2017). Understanding savanna dynamics is also globally important, as we currently understand little about how tropical savannas and woodlands impact the global carbon cycle, with estimates from different methods having large uncertainties (Ciais et al., 2011; Mitchard, 2018).

In this paper we present the results of such an experiment. We studied the dominant processes that regulate vegetation structure in the mesic savanna of the Bateke Plateau, a mosaic of savanna vegetation with forest patches, located in a region with an intermediate but strongly seasonal precipitation (1600 mm/year). This experiment was established in 2015 in two reserves in the Republic of Congo, using 25 ha plots subject to early and late burning treatments, and re-inventoried in 2016 and 2017. These data were used to analyse the diversity of vegetation structure and the rates of stem growth, mortality and recruitment, and relate them to fire treatment, woody competition, and other possible influencing factors.

Our research questions were:

- What are tree demographic rates (growth, recruitment and mortality) of the savannas of the Bateke Plateau?
- Does fire seasonality influence the demographic rates of this ecosystem?
- What is the tree spatial structure in this savanna? Are trees clustered, dispersed, or randomly distributed? Does tree-tree competition affect demographic rates?

We hypothesised that savannas of the Bateke Plateau have low mortality rates compared to other African savannas due to the dominant species being fire tolerant. We expect late dry season fires to be more intense and therefore have bigger effects on demographic rates, decreasing growth and increasing mortality rates. We expect to find spatial clustering of trees, but due to the sparse tree density, no resultant effect on demographic rates.

4.3 - Methods

4.3.1 Study area

This study was conducted in two protected areas located in the Bateke Plateau, the Lefini Wildlife Reserve (LWR) and the Lesio Louna Reserves (LLR) (Fig. 4.1). The Bateke Plateau is a savanna covered plateau located mainly in the southern Republic of Congo (RoC), extending into Gabon and Democratic Republic of Congo (DRC). The vegetation is dominated by an open canopy of *Hymenocardia acida* trees, with an understory of open *Loudetia* or *Hyparrhenia* grasses, and forests mainly associated with rivers and elevated areas (Duvigneaud, 1953). Soils are nutrient poor Kalahari sands (Schwartz & Namri 2002). This area has an average annual precipitation of 1600 mm and a mean annual temperature of approximately 25°C (see references, figures and discussion in Chapter 1, section 1.2.1). There is high seasonality, with a main dry season from June to September, and a short dry season in January and February. Fires are extremely frequent on the Bateke Plateau, mostly anthropogenic in origin and occurring mainly in the long dry season (Walters 2012). Herbivore densities are at present low due to hunting, and do not cause much disturbance (Vande Weghe et al., 2009; Walters, 2010).

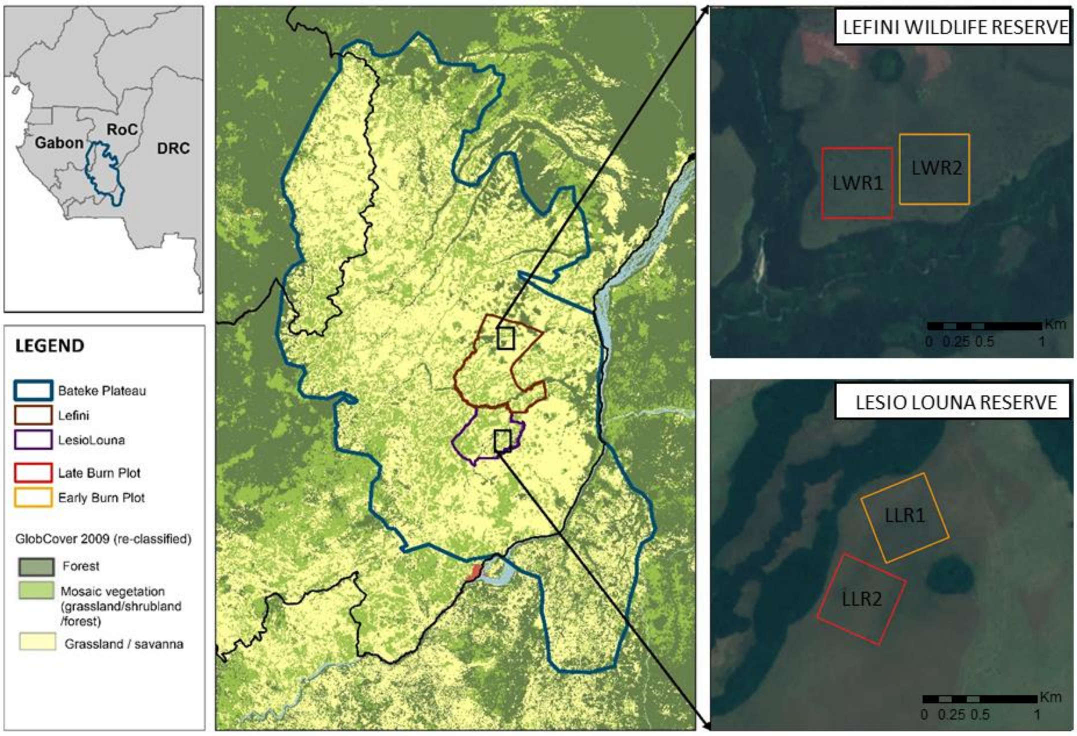

Figure 4.1. Map of the study area, the Bateke Plateau, located mainly in the Republic of Congo. The left hand map shows the extent of the Bateke Plateau (blue). The middle panel shows the location of the Lefini and Lesio Louna reserves, where the sampling plots were placed over a land use cover (GlobCover 2009, reclassified). The right hand panel shows the location of the sampling plots (Early Dry Season plot in orange and Late Dry Season plot in red) over Sentinel 2 imagery (Copernicus Sentinel-2 data 2018).

4.3.2 Fire experiment

Four 25 ha permanent sample plots (500 m × 500 m) were established in wooded savannas, two in each protected area (Plots LWR1 and LWR2 in Lefini and Plots LLR1 and LLR2 in Lesio Louna), in the year 2015. These were subject to different annual fire treatments, with one plot at each site burned at the beginning of the dry season (May/June for plots LWR2 and LLR1) and the other at the end of the dry season (September for plots LWR1 and LLR2) (Table 4.1). Plot area was considered sufficient to accurately represent the local tree layer of the wooded savanna. These plots were further divided into 25 1-ha quadrants each for analysis. In these plots we inventoried all trees with a Diameter at Breast Height (DBH, 1.3 m) greater than 10 cm, recording: species, DBH, height, status (alive/dead, standing/fallen, broken) and spatial location (with a handheld GPS). Each tree was tagged with a unique number for reidentification. DBH was measured at 1.3 m height above the ground, and if the tree forked below this, each stem was measured independently. Height was measured using a Nikon Forestry Pro laser, or directly measured for smaller stems. For the estimation of the Above-Ground Biomass (AGB) from these measurements, we used the generic pan-tropical allometric equation from Chave et al. (2014) with species specific wood density obtained from the Wood Density Database (Chave et al., 2009; Zanne et al., 2009) (further details in Chapter 3). Biomass was converted into carbon stocks using a conversion factor of 0.47 (Ryan et al. 2011). The plots were re-inventoried in 2016 and 2017. Measurements were taken immediately before applying the fire treatments, and at the same time of year to minimise any impact of seasonal variation in diameter. Where a stem was identified as dead, the probable cause of mortality was recorded (elephants, fire, human activity, other).

4.3.3 Demographic rates

Growth was estimated using the annual DBH increment (mm/yr) for each stem ≥ 10 cm that were recorded as alive in both 2017 and 2015 (n = 3576). We used DBH increment as a measure of growth as it can be self-scaling, where a unit of DBH increment represents more absolute biomass in a large tree than in a small trees, since large trees produce more biomass (Prior et al., 2004). Some DBH increments were negative, probably due to burning, loss of bark, shrinkage or changes in bark water content, or measurement error. Stem diameter increment estimates were omitted from the growth analysis if the point of measurement changed between inventories, or if there was an unrealistic growth (defined as any growth between <-1 cm or ≥ 1.5 cm/yr, based on outlying values in the frequency histogram of growth values). A total of 199 stems were omitted from the analysis due to unrealistic growth. Stem mortality was considered as a count for all stems recorded as alive in the first inventory (2015) and dead in the last inventory (2017). We define mortality as stem top-kill (complete death of the aerial biomass), assessed by visual interpretation, and acknowledge that our mortality rates may be overestimated due to stems that seem dead but might resprout in the future.

To estimate recruitment rates, we counted all new stems ≥ 10 cm, dead or alive, and expressed this as a percentage of total stems per year.

Growth and mortality rates were analysed using mixed-effects models, which account for the hierarchical nature of the data (Bates et al., 2015). We use linear mixed models for analysis of growth data, and logistic models for analysis of binary mortality data. Stem growth increment and mortality rate were the dependant variables. Site, plot and species were specified as random effects, with each plot nested within site. Recruitment rates were not modelled, as we did not have enough data to perform suitable analysis and account for fire seasonality effects.

We chose the following variables (all centred and scaled) as fixed effects in the models, as they have all been previously shown to affect tree growth and mortality rates in savannas (Holdo, 2005; Prior et al., 2006; Bowers, 2017):

- Initial Stem size: DBH measurement of each stem at the first inventory (2015).
- Competition: Woody competition can be inferred by analysing the spatial distribution of individual stems (Shackleton, 2002; Pillay & Ward, 2012). Stem competitive stress was assessed using a spatially explicit index of the DBH of neighbouring stems with their size and distance, the Hegyi competition index (Hegyi, 1974). It assumes that if competition between neighbouring plants is present, there would be a reduction in size of one or both of the competing neighbours, and this will be related to its size (Hegyi, 1974). For multi-stemmed trees the effective DBH of all stems was considered as a single tree, calculated from the sum total of basal area of all stems. For the calculations of the competition index we used edge correction (by expanding the point pattern through replication) and a size of 10 neighbours for each stem (Shackleton, 2002).
- Fire season: The fire treatment (Early or Late dry season burns) of each plot was included as a binary predictor.
- Stem Height (residuals): The residuals from a model of height-diameter were included to represent stems that were unusually tall or short. Height was not used directly as it was correlated with diameter (r^2 =0.15).

- Stem damage: Included as a binary predictor of tree health (undamaged/damaged). We considered a tree as damaged when there was any observation of leaning or fallen, broken stems, bark loss or bark scorched during the first inventory.
- Distance to forest: Elevation and distance to closed canopy (riverine) forest were strongly correlated, so only the latter was included, calculated from the centre of every 1-ha quadrat to the nearest forest patch edge.

Models were evaluated using full-subsets regression, in which all possible additive combinations of response variables are represented in the candidate model (Burnham & Anderson, 2002). Models were ranked and weighted using the Akaike's information criterion corrected for small samples (AICc), which identifies the models most strongly supported by the data based on the bias corrected, maximised log-likelihood of the fitted model and penalises the addition of parameters with poor explanatory power (Burnham & Anderson, 2002).

AICc weights (w_i) were calculated for all 64 models in the candidate set, by using maximum likelihood, to determine the relative importance of the fixed effects in each analysis. For each fixed effect, the weight of evidence (w+) was calculated as the sum of the AICc weights for all the models in which the effect appeared. Model averaged parameters and standard deviations were calculated from models weighted by their w_i, a method that reduces the uncertainty of selecting a single best model (Burnham and Anderson, 2002).

Model performance was assessed using a pseudo-R^2 measure, which approximates the variance explained by both fixed and random effects (R^2 conditional), and by the fixed effects alone (R^2 marginal), as described in (Nakagawa & Schielzeth, 2013). In addition, model residuals for the selected models were inspected visually for normality and homogeneity.

4.3.4 Spatial Analysis

We used second-order spatial statistics to determine the spatial correlation patterns of woody plants (Perry et al., 2002). To evaluate the spatial patterning of tree AGB we used Moran's I index of spatial autocorrelation, and correlograms. Moran's I coefficient measures the spatial correlation of a variable as a function of spatial location, and usually varies between -1 (negative spatial autocorrelation or no clustering) and 1 (positive spatial autocorrelation), with values close to zero indicating no spatial autocorrelation (Legendre & Legendre 1998). We also calculated Ripley's K and L functions to analyse tree spatial patterns (Besag, 1977; Ripley, 1977) (Supplementary information, Section 4.8). Ripley's K-test determines whether trees are significantly dispersed, clustered, or randomly distributed throughout the study area, over a range of distances. This method is similar to the Moran's I function but is able to describe point patterns at multiple user defined scales. These methods have been widely used in savanna ecosystems ((Perry et al., 2002; Perry et al., 2006; Ferreira et al., 2007; Schleicher et al., 2011; Pillay & Ward, 2012; Moustakas, 2015) and many others).

All data analysis was performed in R (R Core Team, 2015). For the spatial analysis we used the spatstat package (Baddeley & Turner, 2005). For the growth and mortality models we also used lme4 (Bates et al., 2014), MuMIn (Barton, 2015), and siplab (García, 2014) packages.

4.4 - Results

In total 4094 live stems ≥ 10 cm DBH were inventoried and measured in 2015, 92 % of which were *Hymenocardia acida* (Table 4.1). AGB varied between plots, reflecting the heterogeneity of the landscape. Carbon stocks were low, averaging 0.71 ± 0.06 MgC/ha across all plots (Fig. 4.2). There was almost no net mean carbon stocks change (-0.01 MgC/ha/yr), and no differences in carbon stock change associated with different fire treatments.

Table 4.1. Vegetation structure summary for all plots. Mean values per plot (±SE of the mean (for tree AGB is the SE of the mean of each quadrat). H.a. (%) is the percentage of stems belonging to the species *Hymenocardia acida*. Dead stems correspond to stems recorded as dead at the end of the period 2015 – 2017, mortality and recruitment are the average over 2015-17; all other columns give data from the 2015 inventory only.

Plot	Fire	Live stems	Density (stems/ ha)	H.a. (%)	Damage (%)	Tree AGB (MgC/ha)	Growth (mm /yr)	Dead stems	Mort. (%)	Recruit (%/ plot)
LWR1	Late	726	29.04	100	0.83	0.42 ± 0.09	1.75 ± 0.02	13	1.79 ± 0.49	5.65 ± 0.86
LWR2	Early	1459	59.20	99	1.33	1.01 ± 0.11	2.84 ± 0.02	47	3.22 ± 0.46	4.80 ± 0.56
LLR1	Early	1021	40.88	93	4.39	0.77 ± 0.16	-0.01± 0.02	58	5.68 ± 0.72	1.86 ± 0.42
LLR2	Late	888	35.68	77	4.61	0.66 ± 0.07	0.24 ± 0.02	20	2.25 ± 0.50	2.82 ± 0.56

Table 4.2. Carbon stocks change per plot (MgC/ha/year).

AGB MgC/ha/year	**2015**	**2016**	**2017**
LWR1	0.42 ± 0.09	0.42 ± 0.09	0.46 ± 0.10
Change	-	0	0.04 ± 0.01
LWR2	1.01 ± 0.10	1.03 ± 0.11	1.05 ± 0.12
Change	-	0.02 ± 0.01	0.03 ± 0.01
LLR1	0.77 ± 0.16	0.75 ± 0.15	0.67 ± 0.14
Change	-	-0.02 ± 0.005	-0.08 ± 0.01
LLR2	0.66 ± 0.09	0.67 ± 0.10	0.58 ± 0.09
Change	-	0	-0.09 ± 0.01

Mean tree density was 41.2 ± 33.2 stems per ha (Table 4.1), but with substantial variation (densities per 1 ha quadrat ranged from 0 to 130 stems/ha). Only 2.79 % of all stems were recorded as damaged in the first inventory, with higher rates of damage recorded in Lesio Louna than Lefini.

4.4.1 Tree demographic rates

Demographic rates differed between plots and sites (Table 4.1). Tree growth increment averaged 1.21 ± 0.57 mm/yr across all plots, but there was almost no growth in Lesio Louna. Rates of stem mortality also varied between plots, with mortality rates averaging 3.24 ± 0.54

%/yr. Early burned plots had higher mortality than late burned plots. Recruitment averaged 3.78 ± 0.60 stems/yr per plot.

The top ranked models of stem growth included damage, competition, fire seasonality and height residuals as predictors (Table 4.3, Fig. 4.2). The predictors for stem mortality top ranked models included the same variables, but also the initial stem size (DBH).

Table 4.3. Growth and mortality models, detailing the two best ranked models. Model parameters are: D- Initial stem damage, DBH- Initial stem size, F- Fire (seasonality: Early/Late), C- Competition index, H- Stem height (residuals). Models are ranked by AIC and the weight of evidence (w_i). Model fit is assessed with pseudo-R^2 measures, approximating variance explained fixed (marginal) and both fixed and random (conditional) effects.

Response variable	Model paramenters	AICc	ΔAIC	w_i	R^2 marginal / R^2 conditional
Growth	D+F+C+H	2999.53		0.18	0.016 / 0.276
	D+F+H	2999.79	0.26	0.16	0.015 / 0.265
Mortality	D+DBH+F+C+H	1147.00		0.17	0.079 / 0.089
	D+F+C+H	1148.03	1.04	0.10	0.075 / 0.087

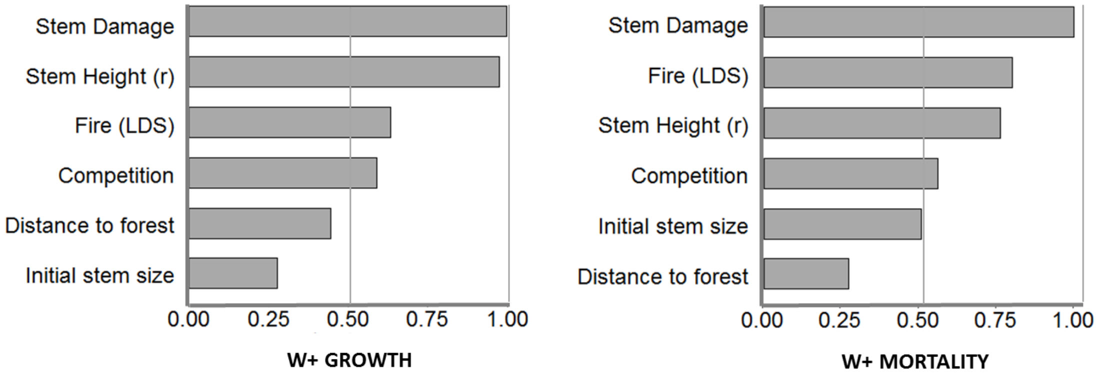

Figure 4.2. Weight of evidence (w+) for growth and mortality model parameters (equivalent to the probability that the parameter is present in the best model).

Observations of stem damage were a strong predictor of growth and mortality rates, associated with a 0.15 ± 0.05 mm/yr reduction in diameter increment, and a higher probability of mortality. Fire seasonality impacted both growth and mortality rates, with late dry season fires associated with a small reduction in growth rate (-0.08 ± 0.02 mm/yr), but also, surprisingly, a decrease in mortality. Competition between tree stems was included in both the highest ranked models, although it predicted a very small reduction in growth rate, with a large standard error, and a small increase in mortality. Height residual was also a strong predictor, with disproportionally taller stems having a marginally greater growth rate (0.03 ± 0.01 mm/yr per m of height). There was no evidence that initial stem size or distance to forest had any effect on growth rate or mortality.

The marginal and conditional R^2 were low for all models, suggesting large differences exist in the stem growth and mortality rates that are not captured by these variables (Table 4.2). The marginal R^2 were lower than the conditional R^2 for the growth models, highlighting the variability that exists between Lefini and Lesio Louna (with Lesio Louna exhibiting almost no growth).

Table 4.4. Model averaged coefficients (all standardised), using the conditional average (± 1 standard error of the mean). Mortality is expressed as log odds. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Variable	Estimated growth (mm/yr)	Estimated mortality (/yr)
Intercept	0.317 ± 0.115 **	-3.340 ± 0.245 ***
Damage	-0.146 ± 0.047 **	2.077 ± 0.301 ***
Stem Height (residuals)	0.028 ± 0.007 ***	0.179 ± 0.084 *
Fire (Late Dry Season)	-0.082 ± 0.022 **	-0.747 ± 0.231 **
Competition	-0.012 ± 0.008 .	0.148 ± 0.081 .
Distance to forest	-0.001± 0.009	-0.028 ± 0.099
Initial stem size	0.003 ± 0.007	0.118 ± 0.080 .

4.4.2 Spatial Structure

Trees were not randomly distributed in space (Fig. 4.3, statistical tests described below). Moran's I correlograms indicate significant spatial autocorrelation of tree AGB in all four plots (Section 4.8 Supplementary information, Fig. 4.S1), but with different strengths of autocorrelation for distances up to about 240 meters (plot LLR2), about the maximum distance to which we are sensitive with our 500 m x 500 m plots. Ripley's K and L functions indicate that trees were not randomly distributed, but were clustered in all plots (Fig 4.S1 and 4.S2).

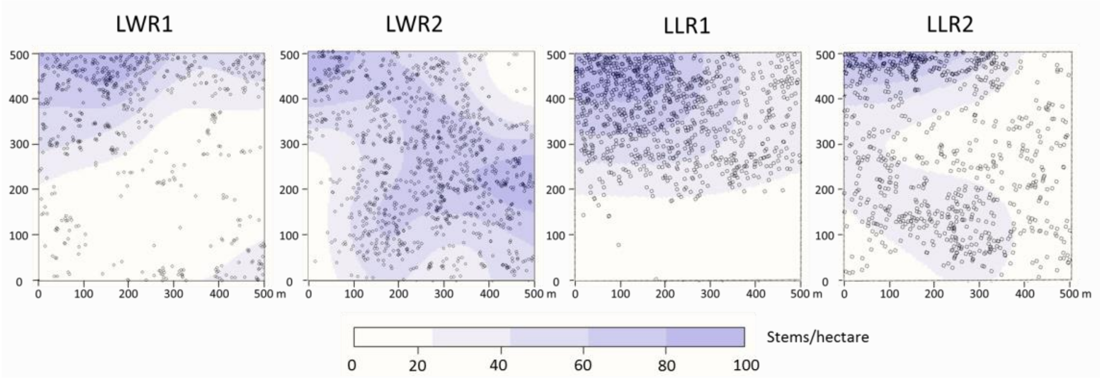

Figure 4.3. Spatial distribution pattern of the inventoried trees in the plots in Lefini (LWR1 and LWR2) and Lesio Louna (LLR1 and LLR2) with kernel smoother point density. Forest edge is at the bottom for all plots.

4.5 - Discussion

4.5.1 Demographic rates of wooded savanna in the Bateke Plateau

Over our three years of treatment there was almost no net change in woody biomass across all fire treatments, as increases were balanced by loss through stem mortality. We found a mean stem diameter increment of 1.21 ± 0.57 mm/yr for the period 2015-2017, considering all surviving trees. In the plots located in Lesio Louna there was almost no growth, maybe due to shrinkage because of dryer than normal years, as reported in other studies in savannas, or possibly a different and more intense past fire history, indicated also by the lower recruitment rates. Tree growth rates were highly variable and difficult to predict; the fixed effects of our models accounted for only a small, but significant, proportion of the variance. This high growth variability is common in savannas, determined by local environmental variability (Chides 1984), with growth models often providing poor fits to data, even in longer term studies (Frost et al., 1986; Holdo, 2006). Variability is also caused by measurement noise of the DBH and other variables, differences in the actual fire intensity experienced by trees which is highly dependent on local grass biomass and whether the grass actually burned (only about 70 % of the plot area typically burned in the early season burns), or by other small scale variations in resources not detected here, which reduce the predictive power of the model.

The low diameter growth rate in the present study compared with those of several other studies suggest that the woody plant species in the Bateke grow slower than in other African savannas. The low growth rate found here (1.21 mm/yr) is possibly explained by the nutrient poor sandy soils with high percolation rates, extreme seasonality of rainfall, high fire frequency and high evaporation rates, or the peculiarity of the main species *H. acida*. In South African savannas, Scogings (2011) found a diameter growth of 1.84-3.36 mm/yr, and Gaugris et al. (2008) of 2.78 mm/yr. In Kalahari sands, south of the Bateke but on the same geological formation, growth estimates were also higher, with growth varying as a function of size (Childes & Walker, 1987; Holdo, 2006). For miombo woodlands, however, they are similar to the plot-average growth rates by Bowers (2017) (1.55 mm/yr), Mugasha et al. (2017) (1.11-2.45 mm/yr) and Trouet et al., (2010) (1.05-1.88 mm/yr for *Brachystegia spiciformis*), although lower than the diameter increments found by Therrell et al., (2007) for another miombo species *Pterocarpus angolensis* (3.5 mm/yr). Here, we have only analysed growth in above-ground stems, while these species will have important underground structures, important for survival after fire (Prior et al., 2006), where much primary productivity might be stored. We have not found any published growth rates for *Hymenocardia acida*, the main tree species in these savannas, although it is described as a slow growth small tree (Trapnell, 1959), that quickly reaches a height of 2-4 m and then does not grow much more (Boaler, 1966). In our study, the effect of tree size on growth rates of adult trees were relatively small, maybe a sign that these trees have reached a peak size, as the correlation between diameter increment and size decreases with the age of the stems (Bowman et al., 2013), and they could be allocating resources to below-ground storage organs or reproduction. Previous studies in savannas have found negative, positive or neutral correlations between tree size and growth rates (Prior et al., 2006).

Mortality rates obtained here for stems with a DBH ≥ 10 cm averaged 3.24 ± 0.54 %/yr, notably lower than other African savanna systems, although mortality rates in savannas vary substantially among species and between size classes. For miombo woodlands, research in fire experiments found mortality rates of 5.4 %/yr (Ryan & Williams, 2011), 4.0 %/yr (Bowers, 2017) and 4.4 %/yr (Shackleton, 1997). In Kalahari sands, Childes and Walker (1987) also found higher mortality rates (about 4 % for adult trees). The low mortality rate here was expected, as all the stems measured were big (DBH ≥ 10 cm) and had escaped the fire trap.

Additionally, most of the stems are *H. acida*, a fire tolerant species. It should be noted that mortality in this study was top-killed mortality, with many trees likely maintaining the possibility of resprouting in the future.

Recruitment rates were 3.8 % of stems per year, notably lower than those observed in other savannas, but approximately matching mortality (Prior et al., 2009). Here, the low tree density and fire seasonality of these savannas could explain this low recruitment rate, as Prior et al. (2009) found that recruitment decreased with lower tree density and that fire seasonality had a bigger effect on recruitment than severity. Better data on recruitment and mortality rates will require the field experiment to run for more years, in order to have a longer time series of data for better estimates, as they both occur stochastically.

4.5.2 Does fire seasonality shape the demography of this ecosystem?

We found that late, and therefore presumably more intense, fires significantly reduced growth (as expected), but were also associated with reduced mortality, which we did not anticipate. In savannas, some studies have found a positive correlation between stem mortality and fire intensity (Shackleton, 1997; Ryan & Williams, 2011). Additionally, it has been suggested by some that frequency is more important than seasonality for tree growth (Murphy et al., 2010). In our plots, the late dry season fires burned the entire plots, but the early dry season fires were patchy and burned on average about 2/3 of the plots. As the grass biomass is relatively low in these sites (1.22 ± 0.09 MgC/ha, Chapter 3), neither type of fire was very intense, though late season fires were more intense than early season fires. Given the short duration of the study, this unexpected result could also be associated with random chance, and additional burns could reverse this finding. DBH did not have a significant effect on mortality, probably because stem mortality was only calculated for (relatively) big trees, and as shown by Ryan and Williams (2011) for stems with a DBH > 10 cm an increasing diameter did not provide further protection from fire induced mortality.

Trees showing some kind of damage in the original census subsequently grew less and were more likely to die. Similar results were obtained by Holdo (2006) for a mixture of miombo and Kalahari sand woodland savanna, and Bowers (2017) for miombo. This decrease of growth rates might suggest that damaged trees do not commit as much resource to woody production, or that visible damage is associated with reduced vigour. The effect on mortality at a plot scale was moderate, with damage noted in 13 % of dead stems, most of which was the result of fire (based on visual interpretation).

We limited the number of predictor variables in the demographic models to the ones likely to be associated with growth and mortality at our sites, and although we acknowledge some possible interactions between predictor variables, these were not included so as to reduce model complexity. Possible interactions term that could be included exist between DBH and competition and fire season, both which are expected to vary with stem size. The variance explained by all the models is significant, with the deterministic component to growth and mortality rates probably being reduced by the short time-period of the experiment, and the presence of unmeasured influences or stochastic events. These highlight the need of future lines of research, including long-term experimental studies measuring other biophysical and environmental variables.

4.5.3 Tree spatial structure and the effect of tree-tree competition on demographic processes

In this study the top ranked models indicate that competition results in a small reduction of growth and a small increase to mortality rates. Although only a small effect, this result is surprising, given the low tree density of these plots. It raises the question of whether tree-tree competition is important for structuring savannas. Holdo (2006) found small effects of competition on growth but positive correlations between distances between neighbouring stems and their combined basal area, suggesting that competition may be an important factor structuring this ecosystem. Dohn et al. (2017) found strong tree competition with neighbours up to 5 m in a semi-arid savanna in Kenya. Studies in savannas suggest that woody competition can have positive and negative effects on growth and mortality of neighbouring trees, and these will probably occur simultaneously, perhaps cancelling each other out. Various studies have used nearest neighbour methods and spatial pattern analysis to assess woody competition (Smith & Grant, 1986; Grundy et al., 1994; Shackleton, 2002), but their results were inconclusive or open to alternative interpretation (Sea & Hanan, 2012). Other studies used self-thinning concepts, suggesting that competition between trees, and between trees and grasses, limits growth (Sea & Hanan, 2012). All these studies bring to light that tree-tree competition might be an important, but largely overlooked, mechanism in savannas.

This savanna landscape of the Bateke Plateau has a sparse tree distribution, with tree stems clustered within the plots. This tree aggregation in clumps is typical of humid savannas, possibly as a result of past disturbance (Menaut et al., 1990), with patchiness typically increasing with increasing precipitation (Veldhuis et al., 2017). Fires in the Bateke Plateau are frequent, supporting aggregated patterns as fire exclusion in the centre of clumps favours the germination and establishment of seedling and saplings (Menaut et al., 1990), protecting recruits from fires and preferentially killing isolated trees. It is possible that clustering extends to longer scales than our plots. The non-uniform distribution found here provides a wide range of variation in potential tree-tree competition, and environmental stress. In order to capture all landscape heterogeneity, larger scales of sampling would be needed (Staver, 2017), and this could be done with remote sensing or with a set of plots along a transect arranged using cyclic sampling. Clumping reduces grass biomass under the canopy (Mordelet & Menaut, 1995) and increases protection from fire (Skarpe, 1991), although it also reduces growth rates due to competition from proximal neighbours (Menaut et al., 1990). As mentioned earlier, *H. acida* reproduces through resprouts stimulated by fires, and due to the low dispersal distance it might naturally end up aggregated in clumps. Indeed, while we treat individual nearby stems as individuals organisms in competition with each other, it is possible that nearby trees are clones, or even that they are connected underground and share nutrients and should be considered as one organism. In this context, the competition between stems we observe remains a true influence on growth rate, but could represent decisions made by the individual on allocation of carbon to different functions, rather than true competition. In these savannas, underground roots might me very extensive, maybe causing significant competition between near trees for water and nutrients. The low tree densities and small stature stems observed in the study sites, together with the slow growth rates and the short duration of the study, could make the effect of competition very difficult to assess.

4.6 - Conclusion

This study has provided estimates of demographic rates, and assessed the spatial pattern of a wooded mesic savanna in the Bateke Plateau. This is the first study providing demographic and woody spatial data for this region and thus it sets a baseline for future studies. Our demographic models coupled with the spatial analysis indicate that stem growth and mortality are influenced by fire seasonality. Tree-tree competition had a small effect on growth and mortality, and given the low tree density in these savannas, it might suggest that woody competition might be an important factor shaping savannas in Africa. These results suggest a balance between effects from competition between neighbouring trees under low water access and benefits among neighbours from fire protection. The results from the different fire frequencies indicate that early burning does not seem to reduce mortality, as might have been expected, but it increases tree growth, suggesting it could if maintained ultimately lead to higher biomass values. However, the low prediction power of the model reflects the short time period of this study. A longer time period for this experiment would be needed to better estimate the effect size. We have also shown the importance of large plots, which were needed to capture their spatial variation in this landscape with a sparse distribution of trees.

4.7 - References

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4.8 - Supplementary Information

4.8.1 Moran's I-Based Correlograms

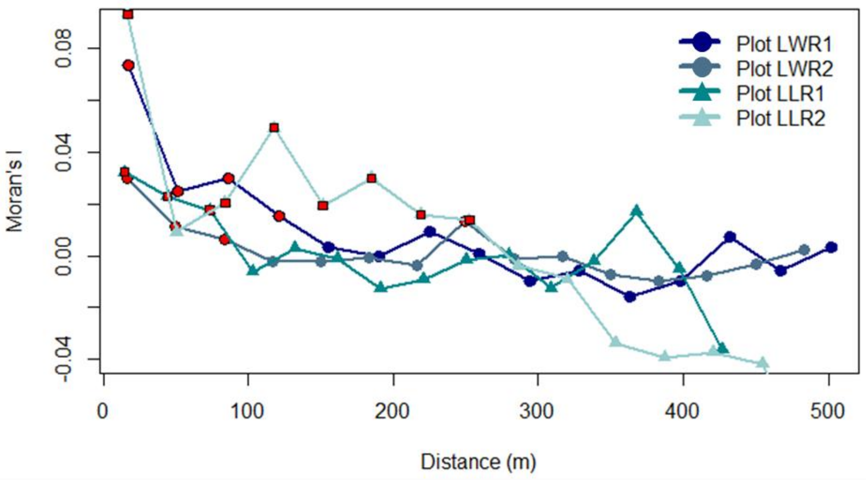

Figure 5S.1. Moran's I-based correlograms for tree AGB along distance classes for the four plots. Red dots indicate significant Moran's I values ($P < 0.05$) under the null hypothesis of no autocorrelation.

4.8.2 Ripley's K and L-Function

To describe tree spatial arrangements and analyse tree spatial patterns we used Ripley's K function and Ripley's K transformed to Besag's L-function (Besag, 1977; Ripley, 1977) with isotropic edge correction. Ripley's K-function is commonly used to characterize spatial patterns in ecology (Pillay & Ward, 2012).

Ripley's K-function uses point pattern spatial statistics, and measures the distances between all pairs of point observations (tree data) inside a circular search window to provide a measure of spatial patterns at various distances (t). Under the null-hypothesis of complete spatial randomness (CSR), with the uni-variate Ripley's K-function (Ripley, 1977):

$$K(t) = \pi t^2$$

L(t) function is a transformation of Ripley's K-function by subtracting the distance (Ripley, 1981; Diggle, 1983),

$$L(t) = (K(t)/\pi)^{½} - t$$

With complete spatial randomness (CSR), the value of L(t) is 0, negative values indicate a regular distribution and positive values indicate aggregation at scale t. To test the statistical significance of deviations of L(t) from zero under the null hypothesis of CSR, confidence intervals were generated by Monte-Carlo simulations (95% confidence limits, from 1000 simulations) (Besag & Diggle, 1977).

Results revealed significant clustering for all trees at several spatial scales.

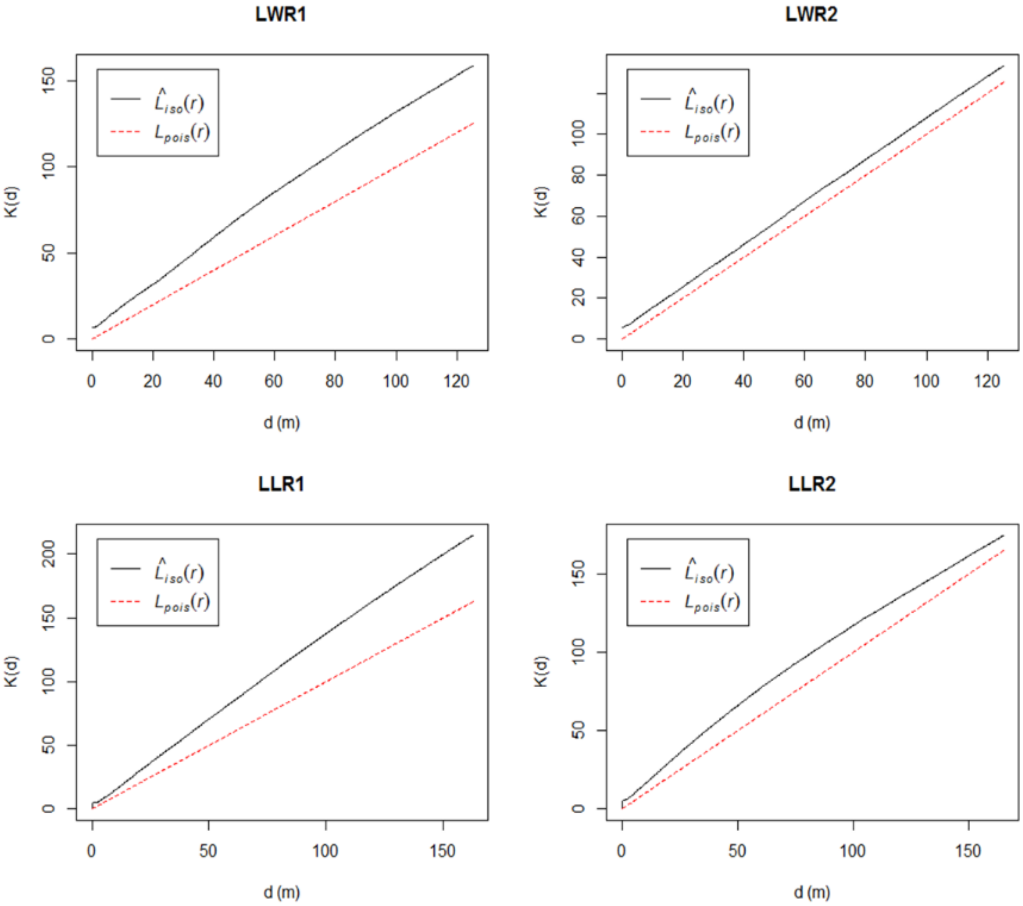

Figure 5S.2. Ripley's L functions for all plots. L(t) = 0 indicates that the spatial pattern at scale t is entirely random; L(t) < 0 indicates a regular pattern; L(t) > 0 indicates clumped pattern. Liso (r) indicates observed data, Lpois (r) shows CSR.

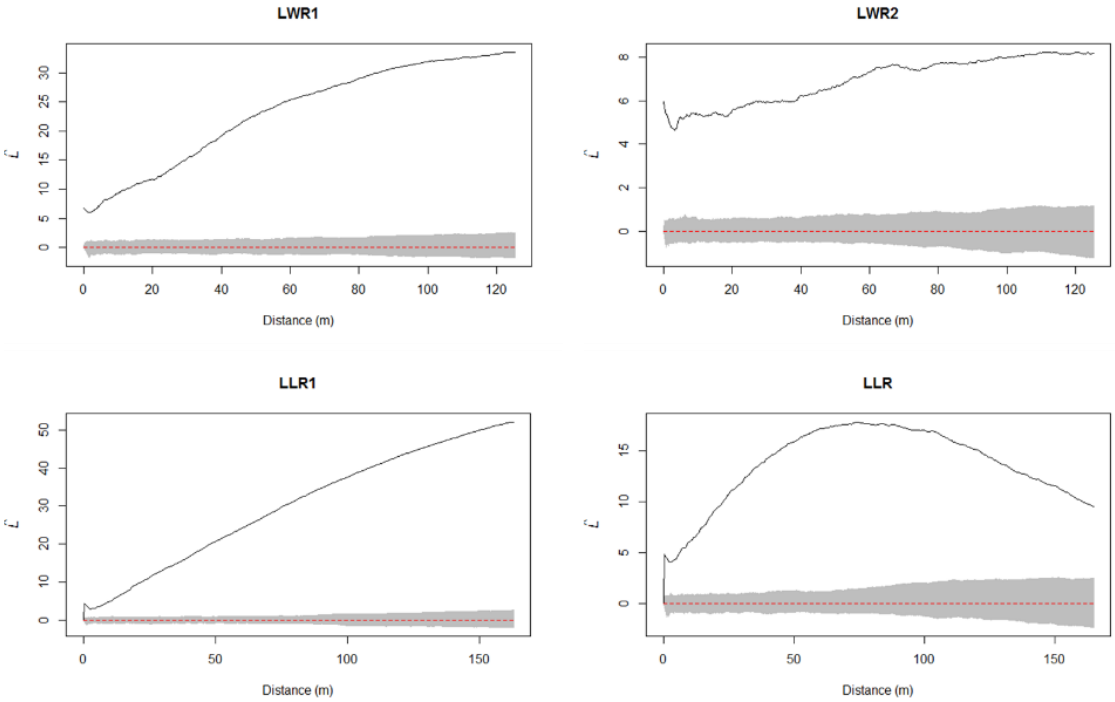

Figure 5S. 3. Ripley's L functions with Montecarlo envelopes. Thin lines correspond to 99% confidence intervals generated from 1000 Monte Carlo simulations under the null hypothesis of CSR.

Chapter 5 Environmental drivers of woody biomass variation across the Bateke Plateau

Paula Nieto-Quintano, Edward T. A. Mitchard, Casey M. Ryan

5.1 - Abstract

Savannas have a very irregular woody cover distribution, ranging from open grasslands to dense woodlands, influenced by many interacting biophysical and anthropogenic factors. This has major significance for carbon storage, and for many ecological processes. In mesic savannas, fire frequency and intensity, and soil characteristics, are thought to be the main determinants of vegetation cover. The objective of this paper is to test the relative strength of these and other environmental factors in determining the Above-Ground Woody Biomass (AGWB) of the mesic savannas of the Bateke plateau. We created a map of AGWB by combining field inventory and radar data from the ALOS-2 PALSAR-2 satellite, and we determined the fire regime of the landscape using a time series of MODIS satellite data. Additionally, we collated layers of the main potential biophysical (topography, climate and soils) and anthropogenic (fire, and distance to roads and towns) determinants of variation in AGWB. We observed that these savannas are subject to frequent fires, mainly occurring during the dry season. Fire frequency and soil sand content were the best explanatory variables for AGWB, with an increased fire frequency associated with lower AGWB stocks, and sandier soils supporting less AGWB across the landscape. However, surprisingly, an increased proportion of late dry season fires was associated with more AGWB. Slope angle was also an important predictor, with steeper slopes having more AGWB. This study is the first attempt to estimate large-scale variations in above-ground woody biomass in the Bateke Plateau.

5.2 - Introduction

Savannas are characterised by their heterogeneous cover of trees and grasses. The woody component is especially irregular, and its differences are of major significance for carbon storage (Furley, 2010), and for many ecological processes, having impacts on the fire regime, nutrient and water cycles, soil erosion and biodiversity (Sankaran et al., 2008; Lehmann et al., 2011). Woody cover in savannas ranges from open grasslands with scattered or no trees to dense woodlands, often varying between the two extremes within the same ecosystem, resulting in a complex landscape mosaic of patches of varying density and species composition. Above-ground biomass is therefore spatially and temporally variable in tropical savannas, influenced by many interacting biophysical (mainly edaphic, topographic, herbivores and precipitation) and anthropogenic (fires and other human-induced disturbances) factors (Bond, 2008; Furley et al., 2008). The relative influence of these factors is often difficult to unravel and lacks scientific consensus, due to a limited understanding of the processes underlying landscape heterogeneity (Bond, 2008; Staver, 2017).

At regional scales, the distribution of savanna and its maximum tree canopy cover is mainly determined by mean annual precipitation (Sankaran et al. 2005). Within a landscape, however, vegetation structure is strongly influenced by soil characteristics (e.g. texture and water holding capacity), topography and average precipitation, and interactions between these factors (Frost et al., 1986; Baldeck et al., 2014). Soil texture is associated with variation in AGB in areas with low soil organic matter content, affecting infiltration rates and soil moisture availability (Scholes & Walker, 1993; Colgan et al., 2012).

Sandy soils have a lower capacity to physically retain nutrients and organic matter (Baldock & Skjemstad, 1999). However, during drought episodes, sandy soils can prevent the reduction of deep moisture reserves as they limit capillary movements, providing deep water sources for plants, especially trees with their longer roots (Colgan et al., 2012). In tropical savannas with mesic rainfall levels (>650 mm/yr), precipitation is sufficient to support forest, and savannas are unstable systems in which disturbances, mainly fire and herbivores, determine the proportion of trees and grasses (Sankaran et al., 2005; Staver et al., 2011). Fire and herbivory reduce canopy cover and above-ground biomass both at regional and landscape scales (Baldeck et al., 2014). Fire frequency, intensity severity and seasonality are all important in determining vegetation structure (Bond & Keeley, 2005; Laris et al., 2016). Even though woody plants in savannas have developed traits to tolerate or resist fire, such as storage in below ground organs (White, 1977), rapid growth rates, re-sprouting abilities and thick bark (Higgins et al., 2000; Midgley et al., 2010), fire still limits recruitment of new saplings and is a leading cause of mortality (Midgley et al., 2010; Prior et al., 2010). Fires have significant effects in the African carbon cycle, and they occur mainly in savannas and woodlands (Valentini et al., 2014). Fire regime variability in savannas and woodlands is determined by climate (precipitation and seasonality), herbivory (influencing the tree/grass ratio) and human activity (as most fires are anthropogenic) (Archibald et al., 2010). A change in the fire return interval and seasonality of fires in mesic savannas can result in dramatic changes in the ecosystem's structure and composition, changing canopy cover and favouring grasses over trees (Laris et al., 2016). Fires in the late dry season tend to be more severe, causing more damage to trees, than fires early in the dry season (Louppe et al., 1995; Laris et al., 2016). It is intuitive that there will be an interaction between fire seasonality and fire intensity, with frequent late season fires having the greatest impact on trees, particularly tree recruitment, however there remains significant uncertainty about the impact of fire regime variability on vegetation structure over landscapes.

In general, there are two main methods used to investigate the effects of fire seasonality and frequency on savanna vegetation and carbon stocks, as well as other mechanisms that control tree cover. The first is field experiments, where fire frequency and seasonality can be controlled and replicated. Field plots provide the most reliable estimates of Above-Ground Woody (AGWB) carbon stocks, but due to limitations to time and resources they do not capture the full landscape variability, particularly in remote areas. The second approach is observational, where existing environmental variation is used to identify the dominant controls on AGWB. Remote sensing offers a tool to investigate this across wide areas and in different parts of the landscape, with a range environmental characteristics.

Remote sensing of above-ground biomass has developed rapidly over the past decades, with several relevant global-scale remote sensing data products now available without charge (e.g. Landsat, MODIS, ALOS mosaics). Most commonly, large-scale maps of AGB are based on optical data trained through field plots and spaceborne LiDAR footprints (e.g. (Baccini et al., 2008; Saatchi et al., 2011; Avitabile et al., 2016)), though these maps do not always agree well with each other and show large regional biases (Mitchard et al., 2013). Savanna ecosystems, such as the Bateke Plateau, are particularly challenging for remote sensing of AGB with optical data. As well as predominant cloud cover, optical remote sensing in savannas is impacted by vegetation heterogeneity over very small scales, the independent and difficult-to-separate phenological signals associated with trees and grasses, and significant inter-annual variation in rainfall and green-up. In many cases, Synthetic Aperture Radar (SAR) sensors can provide higher accuracy information on woody AGB stocks, with radar backscatter sensitive to the density of woody vegetation (Le Toan et al., 1992; Mitchard et al., 2011). Longer SAR wavelengths, for example L-band (15-30 cm), are less affected by soil conditions and grasses than shorter wavelengths, and are more strongly correlated with AGB in low and moderate biomass savannas than optical measurements (Mitchard et al., 2011; Bouvet et al., 2018). L-band SAR can be used for the estimation of AGB up to a signal-saturation point of between 50-100 tC/ha (Lucas et al., 2010), above which the backscatter intensity does not increase with AGB (Mitchard et al., 2011; Carreiras et al., 2013; Bouvet et al., 2018). L-band Synthetic Aperture Radar (SAR) data has been widely used for AGB estimation in savannas in Africa and Australia (Mitchard et al., 2009; Lucas et al., 2010; Mitchard et al., 2011; Ryan et al., 2012; Carreiras et al., 2013; Mermoz et al., 2014; Naidoo et al., 2016; Bouvet et al., 2018; McNicol et al., 2018) and many others). The retrieval of AGB by SAR systems is, however, impacted by soil moisture conditions, topography, soil roughness, and forest structure (Bouvet et al., 2018), so must be carefully processed and locally calibrated to provide reliable estimates of AGB.

In this study ALOS-2 PALSAR-2 L-band data were used to map the AGWB stocks in the Bateke Plateau at 100 m spatial resolution, benefiting from the use of large field plots for developing a relationship between the SAR backscatter and AGWB. This AGWB map is used together with biophysical and anthropogenic data, to identify the processes that are driving landscape-scale variation in AGWB across the Bateke landscape. The effect of fire can be studied by using remote sensing, with parameters such as fire frequency and seasonality easily calculated from daily fire products. The MODIS satellites, for example, are routinely processed to detect the thermal anomalies associated with biomass burning (active fires), and the sudden drop in greenness caused by fires passing through (burned area). We also analysed the effect of soil properties, by using sand content and soil organic carbon, estimating they are the main edaphic limiting factors in this savannas.

This information on vegetation cover patterns and the main drivers on heterogeneity is important for ecological science and effective conservation, and to understand what changes in the fire regime or precipitation could provoke, in an area where detailed maps of vegetation structure are missing. It will contribute to provide better estimates to the overall carbon budget, improve the knowledge for management and decision-making and will support conservation and management under the context of the Reducing Emissions from Deforestation and forest Degradation (REDD+) programme.

The objective of this paper is to quantify AGWB in a low biomass savanna on the Bateke plateau by combining field inventory data with remote sensing. We additionally aim to understand the determinants of variation in AGWB, enabling the modelling of carbon stocks by analysis the underlying biophysical (topography, climate and soils) and anthropogenic processes (fire, and distance to roads and towns). This study also examines the fire regime in this landscape and to what extent environmental variation influences the patterns in AGWB. This study is the first attempt to estimate large-scale variations in above-ground woody biomass in the Bateke Plateau.

The main research questions are:

- RQ1: Is L-band SAR able to estimate AGWB in low biomass savannas? If so, what is the woody AGB estimated for the Bateke savannas and how is it distributed in the Bateke Plateau?
- RQ2: What is the fire regime (fire frequency/seasonality) in the Bateke Plateau?
- RQ3: What environmental factors can be used to model woody AGB distribution across the Bateke Plateau landscape?

5.3 - Data and Methods

5.3.1 Study area

This study is conducted in the Bateke Plateau, a savanna-forest mosaic located mainly in the Republic of Congo, comprising 89,800 km^2. It consists of grassy and woody savannas with forests associated mainly to rivers. It represents the most northern area of the Kalahari sands, and extends to the Congo forest basin, the second largest tropical rainforest in the world. This area has an average annual precipitation of 1600 mm, high enough for a potential forest cover, and a mean annual temperature of approximately 25°C (Nieto-Quintano et al., 2018 and Chapter 3). Fires are extremely frequent on the Bateke Plateau, mostly anthropogenic dry season fires. Here, we focus on mapping the above-ground woody biomass, consisting mainly of *Hymenocardia acida* trees (see Chapter 3).

5.3.2 Field data

Field inventories were conducted in 2015, and the same locations re-inventoried in 2016 and 2017 (see Chapters 3 and 4). Field sites were located in wooded savannas in two protected areas of the Bateke Plateau, in Republic of Congo. Two plots were placed in the Lefini Wildlife Reserve (plots LWR1 and LWR2) and two plots in the Lesio Louna Reserve (plots LLR1 and LLR2). The location and size of sample plots was chosen to encompass the majority of environmental variation. A plot size of 25 hectares was selected to ensure the presence of woody cover variation at different scales and to calibrate the remote sensing imagery.

All stems with diameter at breast height (DBH) >10 cm were measured for DBH, height and their species recorded. Field plot data were converted to AGB using generic pan-tropical allometric equation from (Chave et al., 2014) with species specific wood density obtained from the Wood Density Database (Chave et al., 2009; Zanne et al., 2009) (further details in Chapters 3 and 4). Biomass was converted into carbon stocks using a conversion factor of 0.47 (Ryan et al. 2011). Each of the four plots of 25 hectares was subdivided into 1 hectare subplots for the purposes of calibrating the relationship between satellite radar backscatter data and AGWB, giving 100 subplots in total.

5.3.3 Mapping Above-ground Woody Carbon stocks

Maps of AGWB stocks in MgC/ha were generated using Synthetic Aperture Radar (SAR) data obtained from the Phased Array L-Band Synthetic Aperture Radar (PALSAR-2) sensor on-board Japan’s Aerospace Exploration Agency (JAXA’s) Advanced Land Observation Satellite (ALOS-2, 2015-onwards). SAR is an active sensor that emits a beam of energy towards the Earth’s surface and then measures the intensity of the signal that returns to the sensor (the radar backscatter), with different polarisations of energy emitted and received (in this case horizontal send horizontal receive, HH, and horizontal send vertical receive, HV). The HV polarisation offers advantages for biomass estimation in savannas, with its backscatter being determined by elements that change the polarisation of the beam of energy, such as trees, and backscatter being less affected by soil moisture (Mitchard et al., 2011). The long-wavelength L-band PALSAR-2 sensor is appropriate for biomass mapping as its radiation will largely interact with trees and other canopy elements, and in general, more woody biomass should produce higher backscatter values.

Satellite radar data from the L-band ALOS-2 PALSAR-2 sensor in Fine Beam Dual (FBD, containing HH and HV) mode (Shimada et al., 2010) were acquired over all field sites for 2015, 2016 and 2017 (Table 5.1). The data were provided at a 6.25 m pixel spacing, processing level 2.1. (geometrically corrected), and were converted from digital number (DN) to backscatter (γ^0 in dB, as the ratio of the power returned to the sensor relative to the energy emitted) using the revised calibration coefficients (Shimada et al., 2009).

$$\gamma^0[\mathrm{dB}]=10*\log10(\mathrm{DN})^2+\mathrm{CF},$$

Where, γ^0 is backscattering coefficient and CF is the calibration factor (CF= −83 dB both for HH and HV images).

Table 5.1. List of images scene IDs and dates ALOS-2 PALSAR 2.1.

Acquisition date	***Season***	***Site***
20/01/2015	**Wet**	Lefini and Lesio Louna
22/04/2015	**Wet**	Lefini and Lesio Louna
06/05/2015	**Wet**	Lesio Louna
03/06/2015	**Dry**	Lefini and Lesio Louna
17/06/2015	**Dry**	Lefini and Lesio Louna
01/09/2015	**Dry**	Lefini and Lesio Louna
19/01/2016	**Wet**	Lefini and Lesio Louna
20/04/2016	**Wet**	Lefini and Lesio Louna
01/06/2016	**Dry**	Lesio Louna
30/08/2016	**Dry**	Lefini and Lesio Louna
22/03/2017	**Wet**	Lesio Louna
14/06/2017	**Dry**	Lefini and Lesio Louna
29/08/2017	**Dry**	Lefini and Lesio Louna

The HH and HV backscatter values for pixels covering each plot site were extracted, with pixels averaged in the power domain so the arithmetic, not geometric, means were used (Mitchard et al., 2009). Biomass estimates from all the subplots (100 plots of 1 ha) were used to calibrate a biomass-backscatter relationship by using ordinary least squares regressions. Woody AGB for each of the 3 years was regressed against the equivalent 1 ha subplot HH, HV and HH/HV backscatter (γ^0) (in natural units, not dB). HH, HV and HH/HV ratio were tested for correlation with AGWB, and the one presenting the highest correlation was selected for further analysis. In the regressions, the backscatter was weighted using the inverse of the standard deviation of the backscatter, to account for pixels with more than one value of AGWB for certain years (areas with more than one image available per year as shown in table 5.1). We derived different models for the wet and dry season in order to account for seasonal effects of soil and vegetation moisture (Bouvet et al., 2018), which we used to convert radar backscatter to maps of AGWB for the years 2015-2017. This was done by determining the exact date of each ALOS-2 PALSAR 2.1 image.

These models were used to up-scale AGB estimates across the entire Bateke Plateau using data from the ALOS-2 PALSAR-2 radiometrically and geometrically calibrated PALSAR mosaic datasets at 25 metre resolution 2015. This mosaic product was used as it is freely available and has a global coverage, providing images of the whole plateau area. The global dual polarisation (HH, HV) 25 m resolution ALOS PALSAR mosaic produced by JAXA were used in this study. The mosaic consists of a collage of Fine Beam Dual-polarisation (FBD) data strips acquired in ascending mode with HH and HV polarizations. For each pixel, the mosaic dataset also includes values of the local incidence angle and acquisition date. The FBD data have a swath width of about 70 km. To cover the Bateke Plateau, it was necessary to use sixteen of the 1 x 1 degree tiles which were mosaicked into a single image. The data have been processed by JAXA using the large-scale mosaicking algorithm described in Shimada and Ohtaki (2010), including ortho-rectification, slope correction and radiometric calibration between neighbouring strips. The digital numbers (DN) were converted into γ^0 values using the previous equation. These were used to estimate the AGWB in MgC/ha for all the Bateke Plateau, by using the coefficients obtained in the models for the wet and dry season as appropriate given the timing of the input data strips. We tested that the mosaics and the level 2.1 scenes had the same average backscatter over the field plots, and the level 2.1 scenes were used in order to get the most noise-free data possible to maximise the accuracy of the best fit line.

The resultant map had a resolution of 25 m, but was subsequently aggregated to 100 m (1 ha), the same resolution as the field plots used to create it. This reduced the impact of radar speckle and should negate any geolocation errors between the different layers used in the analysis. I created three AGWB maps for each year (2015, 2016 and 2017), although the 2015 was chosen for further analysis.

5.3.4 Fire Regime

The MODIS burned area product MCD64A1 v006 (Giglio, 2015) was used for the years 2001–2017. MCD64A1 burned area is derived from a hybrid algorithm that uses both active fires and the drop in greenness caused by fire scares, and using both Terra and Aqua MODIS satellites (Giglio et al., 2009). This product has reduced omission error in burned area detection, and is considered better at detecting small burns than its previous versions (Giglio et al., 2016). It is provided at a 500 m spatial resolution. From this product we generated burned area maps for all the Bateke Plateau to estimate the fire regime of the area. We generated four variables representing the fire regime:

i. Fire seasonality (average burn date): To explore the intra-annual variations of the burned area, the year was divided into three seasons: wet (1st May - 15th September), early dry (1st May - 8th July) and late dry (9th July - 15th September), according to the annual pattern of rainfall distribution;
ii. Fire frequency (the number of times a pixel burned): Monthly burned area layers were combined to calculate the number of times a pixel burned during the period 2001-2017;
iii. Total burned area by month: The total area burned in the whole Bateke Plateau per month for the period 2001-2017;
iv. Percentage of late season fires: The percentage of fires that occur in the late season over the total fires.

5.3.5 Environmental Datasets

To examine the relative influence of environmental and disturbance factors on woody AGWB, we selected several biophysical and anthropogenic variables which we hypothesised would have a deterministic effect on AGWB stocks in the Bateke Plateau. This selection was based on a literature review, field visits, and data availability at a sufficient resolution (Fig. 5.1 and

5.2, and Table 5.2). Some climatic factors were not included, such as mean annual temperature which was very uniform in the study area, ranging from 23-27°C (Bioclim variable 5), and based on visual inspection appeared to be closely linked to surface elevation. We also didn't include data about herbivores as no suitable data were available, but this is unlikely to be a problem for the analysis because the density of herbivores in the Bateke, even if high in the past, is now low (Vande Weghe et al., 2009).

BIOPHYSICAL VARIABLES:

- **Rainfall**: Annual rainfall was used as a measure of water availability, one of the main determinants of woody cover (Walter, 1971). Estimates of mean annual precipitation for 2015 were derived from TAMSAT (Tropical Applications of Meteorology using SATellite data and ground-based observations) monthly data at 4 km spatial resolution, based on high-resolution thermal-infrared observations (Maidment et al., 2017).
- **Topography:** Topographic characteristics are an indirect proxy for localised variations in soil moisture and soil textural properties (Woollen et al., 2012), and the roughness of the local terrain can further serve as natural barriers to fire spread and thereby directly influence vegetation (Archibald et al., 2009). Topographic information is based on the 90 m resolution SRTM data version 4.1 (Jarvis et al., 2008) from which we derived elevation (in m above sea level) and slope angle (°). Based on this DEM, the Topographic Position Index (TPI) was further calculated (Weiss, 2001; Jenness et al., 2013). TPI is the difference between a pixel's elevation value and the average elevation of those around it, given a user specified neighbourhood distance. Positive values correspond to areas that are on average higher than their surroundings, values close to zero are flatter areas, and negative values are given to areas that are lower than their surroundings. TPI was further processed into a slope classification raster based on the TPI and the slope of each cell, by dividing it by the neighbourhood standard deviation and classifying the landscape into six broad topographic positions (valleys, lowers slopes, gentle slopes, steep slopes, upper slopes and ridges). Units are in standard deviations, such that a Standardized Elevation value of 1 would mean that this particular cell is 1 standard deviation higher than the average elevation in the neighbourhood.
    - Valleys: TPI ≤ [SD=-1]
    - Lower Slopes: [SD=-1] < TPI ≤ [SD=-0.5]

  - Gentle Slopes: [SD=-0.5] < TPI ≤ [SD=0.5], Slope Angle < 1]°
  - Steep Slopes: [SD=-0.5] < TPI ≤ [SD=0.5], Slope Angle ≥ 1°
  - Upper Slopes: [SD=0.5] < TPI ≤ [SD=1]
  - Ridges: TPI > [SD=-1]

  TPI was calculated using the Topographic Position Index extension in ArcGIS (Jenness et al., 2013), and a circular neighbourhood size of 1000 m. This scale was selected as being the most appropriate for this analysis at landscape scales, after trying other ranges, as we are interested in topographic habitat characteristics of large, distinctive topographic features.

- **Fire**: Fire is considered the main disturbance in this system, affecting vegetation structure, cover and species composition of savanna ecosystems (Higgins et al., 2000; Bond & Keeley, 2005). The fire variables included were fire count and percentage of fires in the late dry season, calculated as explained in section 5.3.4, using the years 2001-2017.
- **Soil data**: Soil data was obtained from SoilGrids (Hengl et al., 2017). SoilGrids predictions are based on globally fitted models using soil profile and environmental covariate data, produced using automated soil mapping based on machine learning algorithms. This product uses environmental variables to predict soil properties, so had the potential to cause autocorrelation with our other predictors. However, due to the lack of better information for the Bateke Plateau, and because correlation with other predictor variables was <40%, we use this data product. The physical soil properties chosen were (all obtained for depths between 0-200 cm.):
  - Sand content (50–2000 µm) mass fraction in %, as a proxy of drainage conditions and soil fertility given;
  - Soil organic carbon content (fine earth fraction) in g per kg.
- **Distance to rivers and forest**: The Euclidian distance to rivers, calculated from the Rivers of Africa HydroSHEDS dataset (Lehner et al., 2006). This variable is closely associated with distance to forests, which are mostly located along rivers in this region.

ANTHROPOGENIC VARIABLES:

- **Distance to towns and roads**: It is expected that intense disturbance events, including fuelwood extraction, agriculture or charcoal production, will mostly occur in areas that are easy to access. To calculate the distance to roads and towns, rasters were prepared giving the Euclidean distance from settlements or roads in the GEONETWORK dataset provided by FAO (2015).

- **Protected areas**: The spatial extent of the protected areas situated in the Bateke Plateau was obtained from the World Database on Protected Areas (WDPA), a joint project between UN Environment and the International Union for Conservation of Nature (IUCN) (IUCN, 2018). We included National Parks and Protected areas with an IUCN category IV.

All data were converted from their raw format, and transformed where necessary to the WGS 84 co-ordinate system and the UTM 33S projection using a combination of ENVI 4.6 (ITT, Boulder, USA), R version 3.1.3 and ArcGIS 10.1 (ESRI, 2015).

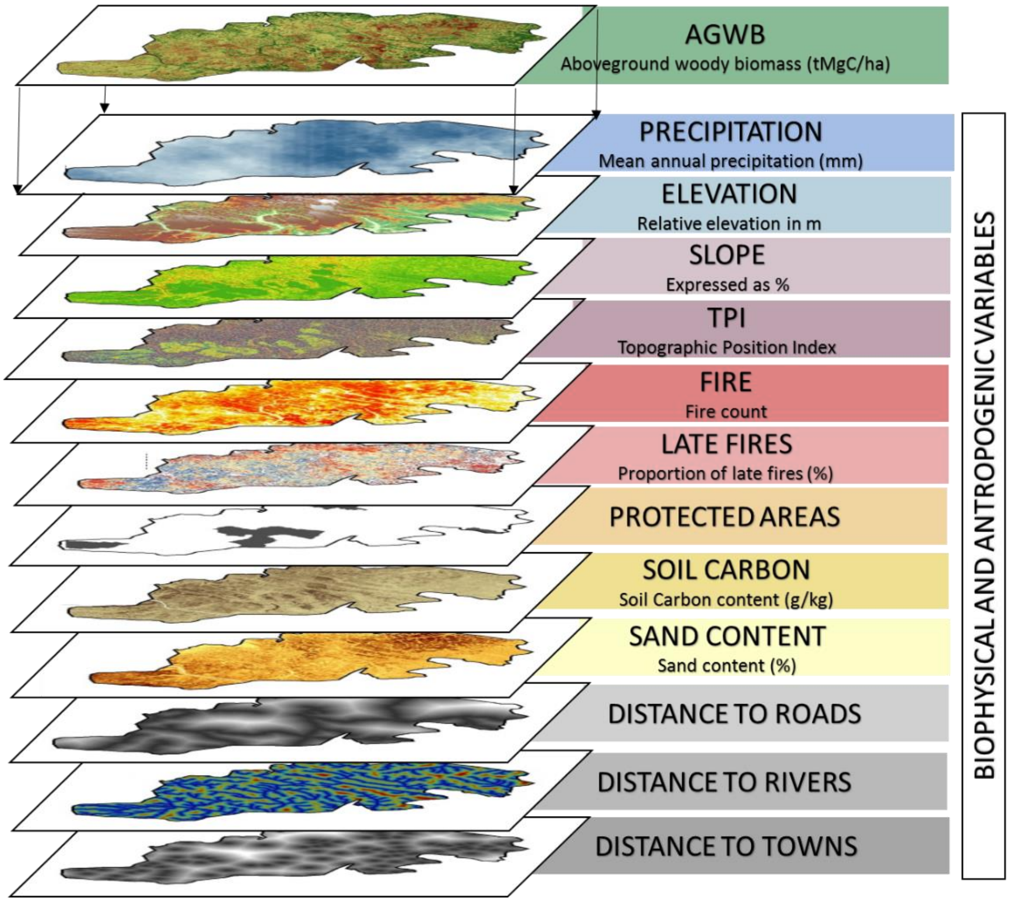

Figure 5.1. Schematic representation of the biophysical and anthropogenic data sets used in the analysis.

Table 5.2. Description of predictor and response variables used in the models.

Variable	*Description*	*Resolution*	*Range/Type*	*Derived from*	*Source*
Response					
Woody AGB	Woody biomass (in MgC/ha)	100 m	0-10 (continuous)	ALOS PALSAR	
Predictors					
Rainfall	Mean Annual Rainfall for 2015 (in mm)	4 km	823-1138 (continuous)	TAMSAT	Maidment et al. (2017)
Elevation	SRTM Digital Elevation (in m)	90 m	259-872 (continuous)	SRTM Digital Elevation, Version 4.1.	http://srtm.csi.cgiar.org
Slope	Slope in degrees	100 m	0-45 (continuous)	Calculated from DEM	
TPI	Topographic position Index	90 m	3-6 (discrete)	Elevation and slope	Jenness et al. (2013)
Fires	Fire count, number of fires per pixel in the period 2000-2015	500 m	0-31 (discrete)	Modis Burned area product	Giglio (2015)
Late Fires	Proportion of late dry season fires	500 m	0-100 (continuous)	Modis Burned area product	Giglio (2015)
Protected areas	Delimitation of protected areas	-	Binary 1/0 protected or not	World Database of Protected Areas	IUCN (2018)
Soil organic carbon	Soil organic carbon content (fine earth fraction) in g per kg	250 m	10-607 (continuous)	SoilGrids	Hengl et al. (2017)
Sand content	Sand content (50–2000 micro meter) mass fraction in %	250 m	35-93 (continuous)	SoilGrids	Hengl et al. (2017)
Distance to roads	Euclidian Distance to roads in m.	100 m	0-71169 (continuous)	Roads Of The World (VMAP0)	(FAO, 2015)
Distance to Rivers	Euclidian distance to rivers in m.	100 m	0-16000 (continuous)	Rivers of Africa HydroSHEDS	Lehner et al. (2006)
Distance to towns	Euclidian Distance to towns in m.	100 m	0-48975 (continuous)	Towns of DRC, RoC and Gabon	FAO, 2015

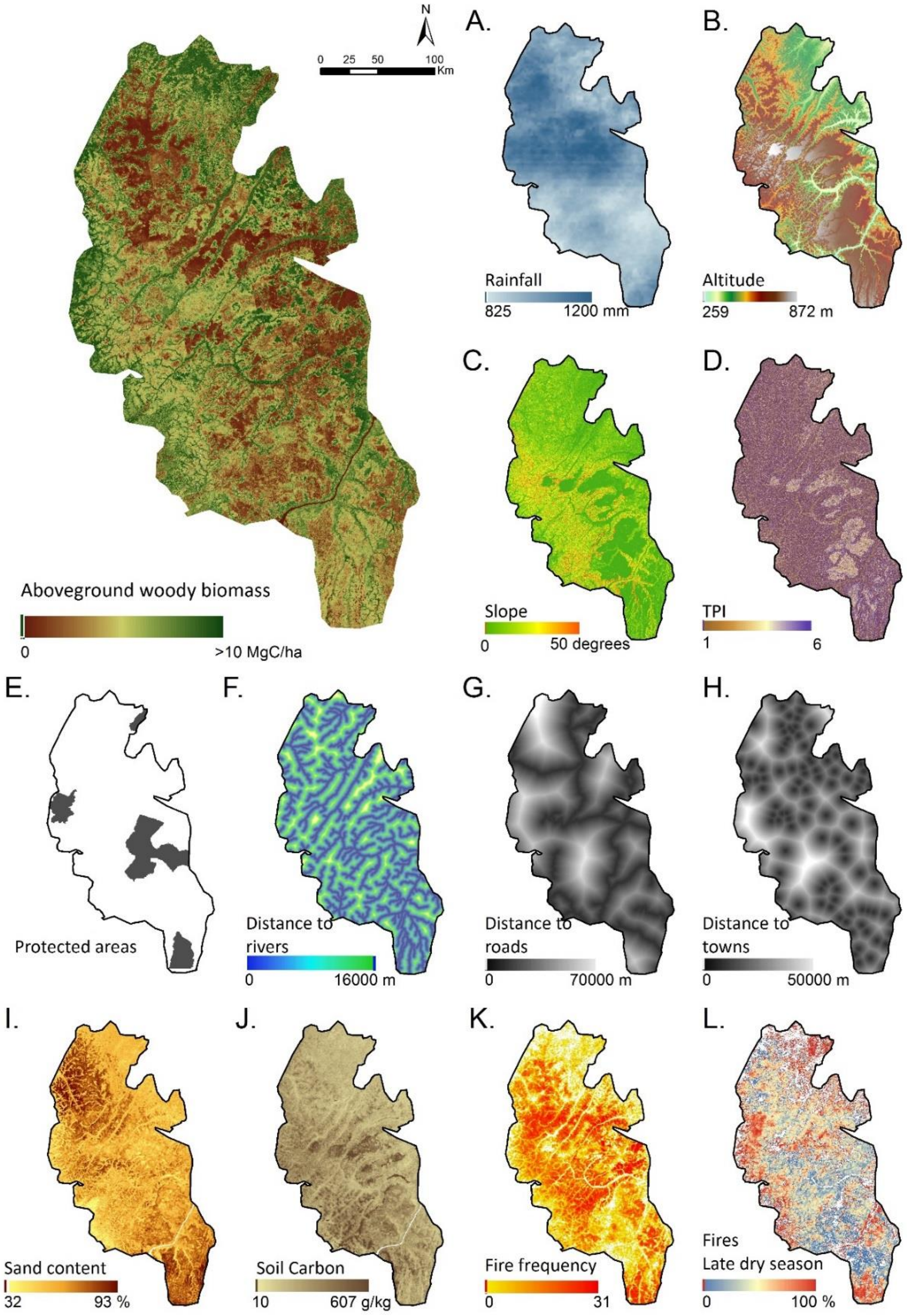

Figure 5.2. Data set for the AGB and the biophysical and anthropogenic variables used in this study as predictors of AGWB: (A) mean annual rainfall (mm), (B) altitude (m); (C) Slope (%), (D) TPI, (E) Protected areas, (F) distance to rivers (m), (G) distance to roads (m), (H) distance to towns (m), (I) Sand content (%), (J) Soil carbon (g/kg), (K) Fire frequency (number of fires), (L) Proportion of fires in the late dry season (%).

5.3.6 Statistical Analysis

Our field data only covered savanna areas, but in the AGWB map we created there are patches of substantially higher AGWB, associated mainly with dense forest adjacent to rivers (Chapter 3). We therefore needed to mask out these areas from our analysis. We attempted to use global landcover maps to do this masking, but none of the available maps were good for this landscape at small scales, so instead we applied a threshold to our AGWB map at 10 MgC/ha, a value selected by visual inspection. Further, anomalously large AGWB values were present in some small areas due to random noise in the imagery related to speckle and soil moisture and to the presence of structures with very high backscatter such as banana plantations. The masking procedure for closed canopy forest had a side effect of also masking out these areas.

AGWB estimated using the ALOS data consisted of positive values (corresponding to areas where woody vegetation was present) and zero or negative values (areas where there was no woody vegetation). First, we performed a linear model (Model 1) by masking all AGWB values equal or lower than zero. We opted for this method instead of converting all negative values to zero in order not to bias the data by zero-inflated values. Relationships between each of the continuous explanatory factors were tested for collinearity to ensure that there was no overlap in terms of explanatory power. This was performed using Spearman's rank correlation tests with a Variance Inflation Factor of <2 used to indicate variables that were not collinear. Model diagnostics were performed following (Zuur et al., 2010). Examination of the residual plots indicated that a log +1 transformation of AGWB was needed to ensure homogeneity of variance and the presence of normality in the residuals. The relative contribution of each explanatory variable was estimated by a partial R^2 and analysis of variance tests (ANOVA). In order to evaluate and compare the explanatory value of the predictors, we calculated partial pseudo-R^2.

5.3.7 Spatial dependency in the dataset

An exploratory analysis of the response variable and the residuals of the model revealed significant positive spatial autocorrelation (SAC) in the data (for AGWB: Moran's I = 1.00, P

<0.001; for model residuals: Moran's I = 0.995, P <0.001), as would be expected given similar vegetation types and combinations of environmental variables are always likely to cluster in space. As a result they cannot be considered as independent samples, with the residuals unlikely to be independently distributed. To account for this, we adopted a simple method of subsampling the dataset at a scale where small distance autocorrelation is no longer detected in order to reduce any spatial dependency in the data analysed. A fishnet of points was produced at 5 km to subsample the data (1782 points), and this was repeated multiple times with different starting points to test for stability in the results. This fishnet was used in both models. Semi-variograms were used to quantify the spatial dependence in the data and were produced. As the residuals of the model were still exhibiting a significant spatial autocorrelation (Moran's I-statistic = 0. 147, P <0.001), a generalized least squares (GLS) model was fitted to the data, to take the spatial correlation between individual observations into account (Cressie, 1993; Dormann et al., 2007) (Model 2). The GLS model incorporates spatial structure directly into model residuals by fitting semi-variogram functions. Five types of autocorrelation structure were tested using variograms (exponential, gaussian, spherical, linear, and rational quadratic) and the best one was selected using Akaike's Information Criterion (AIC). The exponential semi-variogram was selected and Variograms were used again to quantify the spatial structure of the data.

All statistical analyses were conducted in R (R Core Team, 2015) using the following packages: sp (Pebesma & Bivand, 2005), raster (Hijmans & van Etten, 2012), rgdal (Bivand et al., 2015), spdep (Bivand et al., 2015) for the Monran's I tests, nlme (Pinheiro J. et al., 2018) for the GLS, gstat (Pebesma, 2004) for the Semivariograms, asbio (Aho, 2011) for the partial rsquares. GIS analysis was conducted in ArcGIS.

5.4 - Results

5.4.1 AGB-Backscatter relationships

We found significant linear relationships between AGWB and HV backscatter (R^2 0.47 (dry season) - 0.39 (wet Season)) (Fig. 5.3). Relationships with the HH polarization and HH/HV ratio were less strong and therefore were not included in the model. The fitted model equations were:

$$AGWB_{dry} = 221.381 \times \gamma^0_{HV} + 0.856;\ R^2 = 0.48$$

$$AGWB_{wet} = 171.794 \times \gamma^0_{HV} + 0.135;\ R^2 = 0.37$$

Where: $AGWB_{dry}$ is the AGB of the dry season, $AGWB_{wet}$ is the biomass of the wet season, γ^0 is the HV radar backscatter.

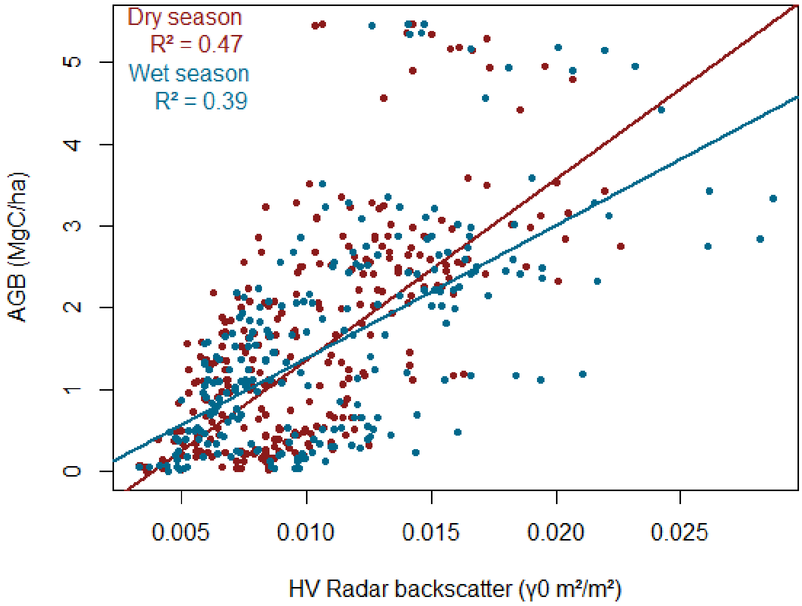

Figure 5.3. Biomass-backscatter relationship. HV radar backscatter (γ0) plotted against above-ground woody carbon stocks for all subplots in the two sites. Red Dry season. Blue wet season.

AGWB stocks maps (100 m resolution) were up-scaled to the whole Bateke landscape using the ALOS mosaic data (Fig. 5.5). Above-ground woody carbon stocks in savannas averaged 2.32 ± 2.15 (SD) MgC/ha across the Bateke Plateau, with 67.7 % of the study area categorised as woody savannas with AGWB <10 MgC/ha. Carbon stocks were highly spatially variable (Fig. 5.4), with forest areas bordering rivers and patches of savannas of different biomass values clustered across the landscape.

5.4.2 Fire regime

Approximately 76 % of the Bateke Plateau area was detected to burn annually (76.3% of area had 16 or more fires over the 2001-2017 year period). Fires were not detected during the study period in only 19.9 % of the Bateke Plateau, mainly corresponding to closed canopy forests along rivers. The spatial distribution of fires reveals that the area did not burn uniformly, with the incidence of fire varying from 1 fire to 31 fires, with a mean of 6 fires (Fig. 5.4). Fire seasonality in the Bateke Plateau peaked in late dry season (July–August) for all years (Fig. 5.4d and 5.5a), anti-correlated with the intra-annual rainfall distribution. There is an observable short dry season, with an associated smaller burning peak, during the months of January and February, confirming the existence of a bimodal precipitation distribution and fire season (Knoben et al., 2018). There is no evidence of an increasing or decreasing fire frequency with time (Fig 5.5b), and also no discernible relation between the precipitation of the previous year and the total burned area (Fig 5.5c).

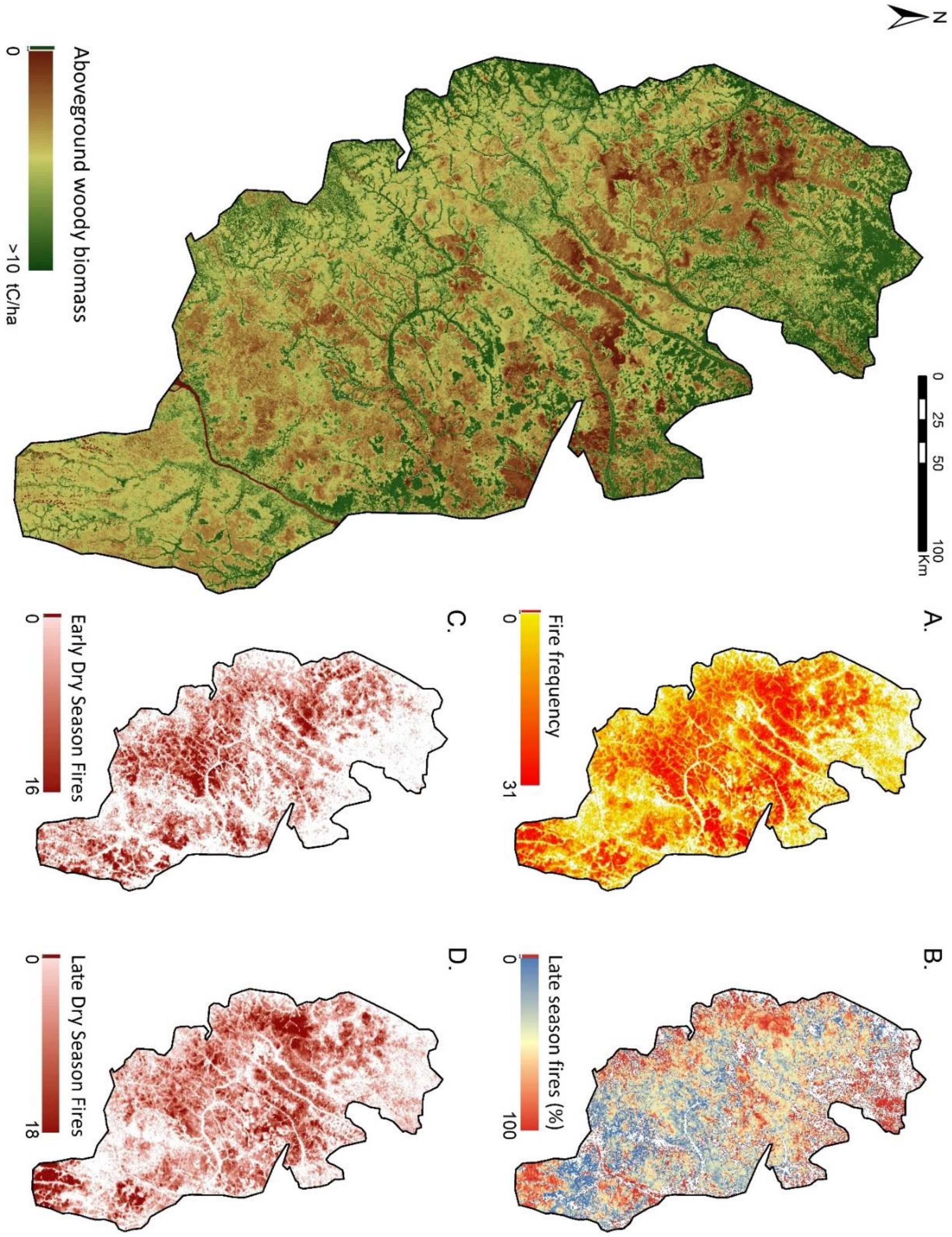

Figure 5.4. Left: Above-ground biomass map of the Bateke Plateau generated using radar backscatter data from ALOS PALSAR, calibrated using AGB estimates from field plots. Above-ground woody carbon stocks in savannas averaged 2.32 ± 2.15 (SD) MgC/ha across the Bateke. Right: Fire frequency for the Bateke Plateau for the period 2001-2017 calculated from MODIS Burned Area product: (A). Fire frequency; (B). Proportion of late dry season fires; (C). Total early dry season fires; (D). Total late dry season fires.

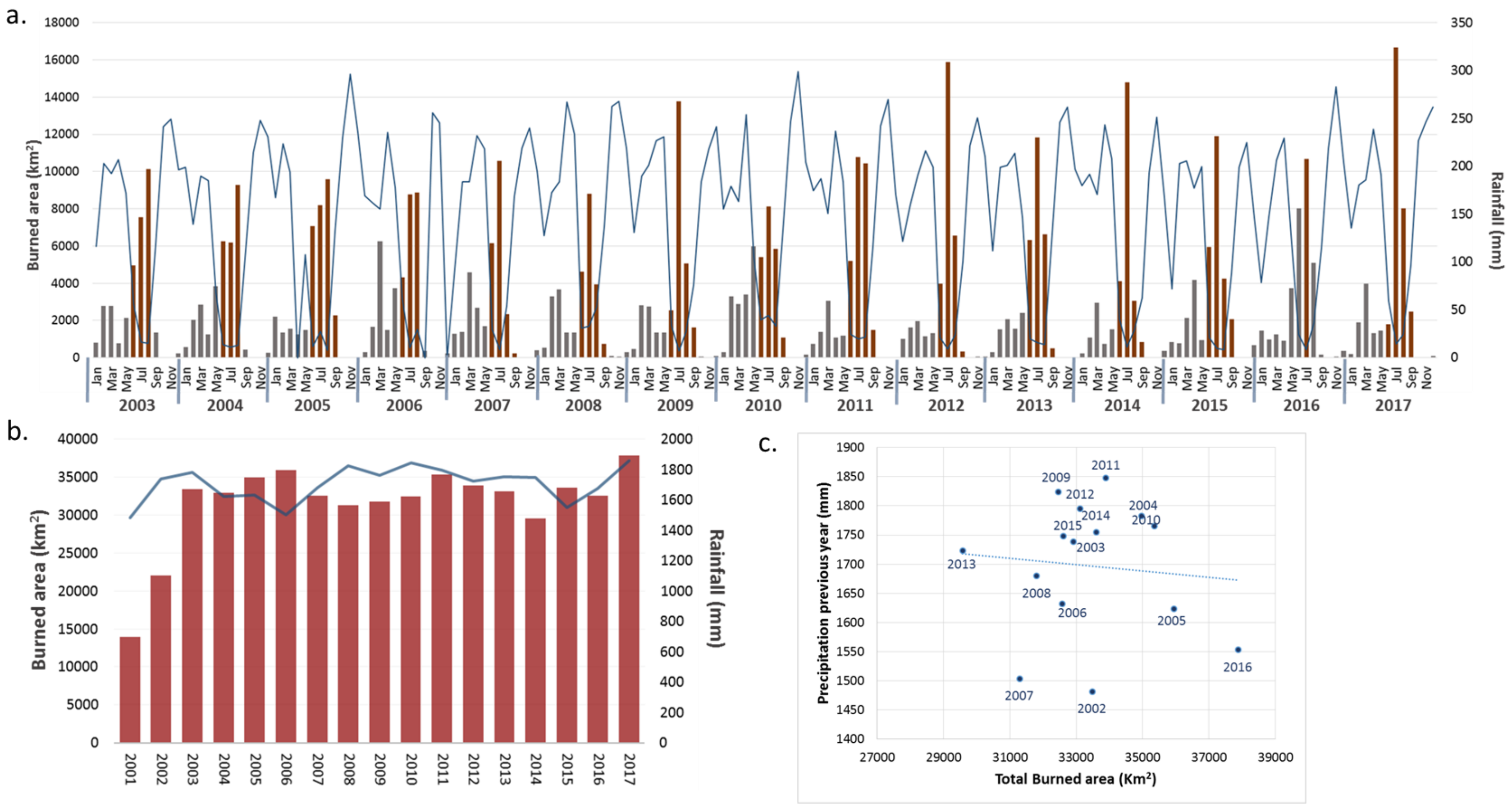

Figure 5.5. Top a.: Burned area (km²) per by month for the Bateke Plateau for the period 2003-2017, and mean rainfall (mm) per month (from TASMSAT). Bottom: b. Total Burned Area (km²) per year for the Bateke Plateau for the period 2003-2017, and mean annual rainfall (mm) per year (from TASMSAT). c. Total Burned Area (km²) per year for the Bateke Plateau for the period 2003-2017, and mean annual rainfall of the previous year (mm from TASMSAT). Years 2001 and 2002 were excluded from the analysis due to MODIS incomplete data (MODIS Aqua started in 2002).

5.4.3 Environmental determinants

There was a spatial correlation in the residuals of the model predicting AGWB, as indicated by the semi-variogram (Fig. 5.6a), and with the residual's Moran's I = 0.243, P <0.001. This suggests spatial correlation of other factors not accounted in the model. This was especially true at short scales. The spatial correlation was reduced at small distances using the GLS model with a fitted exponential semivariogram for the residuals (Model 2), which was chosen as it had the lowest Akaike's Information Criterion (AIC) (Fig. 5.6b).

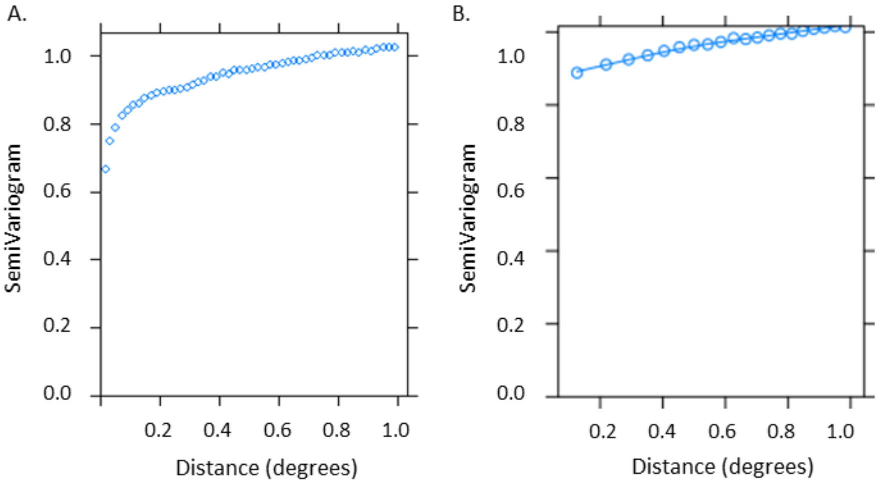

Figure 5.6. Semivariogram of A.) Fishnet every 2 km. B.) GLS model with fitted exponential semivariogram

In the statistical analysis we have considered how multiple environmental predictors determine AGWB across the Bateke Plateau. The two models have similar results, with both models indicating that the biophysical and anthropogenic variables had a weak explanatory power for AGWB (R^2=0.22 for the linear model, pseudo-R^2=0.28 for the GLS model), see Fig. 5.S2 in Supplementary Information for Regression plots). Partial R^2 values indicate that sand content and fire accounted for the largest part of the variation in AGWB in the models (Fig. 5.7). Model coefficients (Table 5.3) indicate that an increased fire frequency corresponds to lower AGWB stocks. However, the models also indicated that an increased proportion of late dry season fires was associated with more AGWB. The models show that more sandy soils tend to support less AGWB, and greater soil carbon content is associated with a small decrease in AGWB. Slope angle was also an important predictor, with steeper slopes having more AGWB. Protected areas, rainfall, topographic position index and distance to roads, towns and rivers are not significant predictors of AGWB.

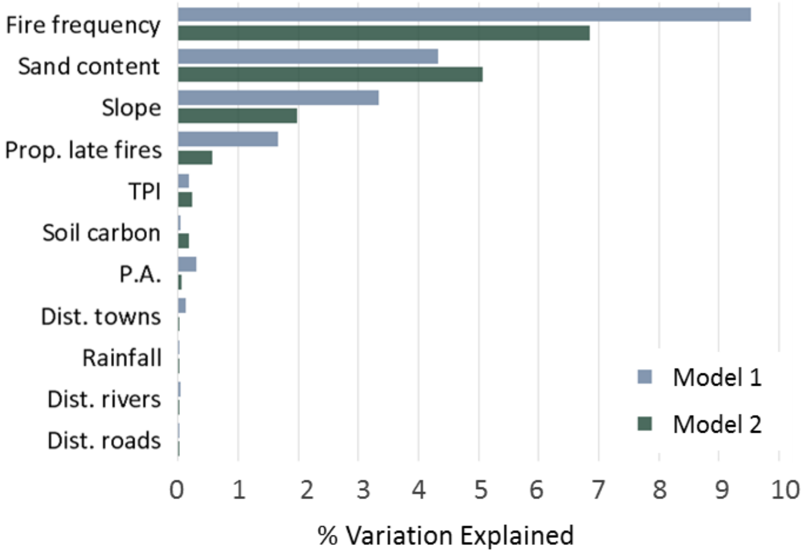

Figure 5.7. Relative Importance of the explanatory variables in % of the variation explained. Calculated using partial R-squares for the linear model, and partial pseudo R-squares for the GLS model.

Table 5.3. Model coefficients resulting from the non-spatial linear model (Model 1, fishnet 2km, Adjusted R-squared=0.221) and the GLS model dealing with spatial autocorrelation (Model 2, Pseudo R-squared= 0.283). Intercept is AGWB in log+1 units (in brackets STD error). ***P<0.0001, **P<0.001, *P<0.05, .P<0.1

Variable	Model 1	Model 2 (SAC)
Intercept	2.049 (0.224)***	2.540 (0.567)***
Rainfall	-3.190 e-5 (2.003 e-4)	2.913e-4 (5.690e-4)
Slope	0.026 (2.970 e-3)***	0.021 (3.098e-3)***
TPI	0.010 (5.722 e-3).	0.013 (5.410e-3).
Sand content	-0.018 (2.302 e-3)***	-0.0300 (2.782e-3)***
Soil organic carbon	-0.00074 (9.416 e-4)*	-0.0023 (1.076e-3)*
Protected areas	0.0796 (3.506 e-2)	0.0553912 (0.0522)
Fires	-0.03398 (2.509 e-3)***	-0.0344 (2.749e-3)***
Prop. late Fires	0.0216 (2.506 e-3)***	0.00143 (3.984e-4)***
Distance to Rivers	-6.132e-6 (4.29 e-6)	2.1e-6 (4.3 e-6)
Distance to roads	-3.599e-7 (1.18 e-6)	-3.99 e-7 (1.9 e-6)
Distance to towns	2.161e-6 (1.61 e-6)	1.00e-6 (2.2 e-6)

5.5 - Discussion

5.5.1 Woody AGB estimated using radar remote sensing for the Bateke savannas and its distribution

SAR remote sensing has been shown to be capable of estimating woody biomass in a tropical savanna landscape with very low above-ground carbon stocks. In this study, we tested using different SAR polarisations, HH (Horizontal-send Horizontal-receive), HV (Horizontal-send Vertical-receive) and the ratio of HV/HH backscatter data for measuring AGWB. The HV polarisation showed by far the greatest correlation with AGWB data. This is consistent with previous studies, which also found HV polarization to be more sensitive to biomass than HH (Mitchard et al., 2009; Lucas et al., 2010; Ryan et al., 2012; Carreiras et al., 2013; Mermoz et al., 2014; McNicol et al., 2018).

Estimates for the above-ground woody carbon stocks from the radar backscatter data across the plateau averaged 2.3 MgC/ha, higher than the estimates derived from the field plots (0.71 ± 0.06 MgC/ha).

The estimation of AGB using SAR backscatter is impacted by sources of error related to:

i. Woody cover structure and environmental characteristics, such as soil moisture,
ii. Uncertainties in radar data, (Mermoz et al., 2014; Bouvet et al., 2018).
iii. Estimation of the in situ AGWB, including field measurement errors, estimates of wood density and allometric models used.
iv. Errors in locations of the radar and in situ observation geometries.

We have used radar data (PALSAR-2 mosaic) acquired at different times of the year and this can include sources of error due to variations in environmental conditions (for example in soil moisture), as well as variations in the radar backscatter due to radar calibration and incidence angle variation varying across a scene. Seasonal effects were reduced by applying two different equations for the dry and the wet season, but of course this is only a binary distinction for a continuous value, and is not perfect. Here, AGB was only determined for stems > 10 cm DBH whereas the radar backscatter includes information on stems smaller than this.

Accuracy of our maps outside of the region of our field plots was not tested as we didn’t have any independent field data for the Bateke Plateau. However, the ecology and species composition of the savannas throughout the Bateke Plateau is similar (Duvigneaud, 1953), and our field subplots included both wooded and herbaceous savanna, including a wide range of AGWB values (Fig. 5.3).

5.5.2 Fire regime (fire frequency/seasonality) in the Bateke Plateau

This study has indicated the importance of fires in shaping the distribution of AGWB in the Bateke Plateau. Fire frequency is high, ranging from 0-31 fires in the 16 year period, with a mean of 6. A typical fire return interval in savannas is estimated to be 4 years (Laris & Wardell, 2006; Furley et al., 2008), but fire frequency in savanna woodlands in Africa varies widely, with the fire frequency we observe on the Bateke Plateau at the upper range of African fire return intervals (Archibald et al., 2010). Many of the savanna areas in the Bateke Plateau burn annually, while there were almost no fires detected in the forest areas. Fire frequency is related to the AGWB stocks, with more fires resulting in less biomass (Fig. 5.S1). The proportion of late dry season fires, however, is less strongly related to AGBW stocks. Fire is both a cause and consequence of low biomass (Archibald et al., 2009). The dynamic feedback of fire-grass-tree cover characterises the ecology of savannas, with fire reducing tree cover, allowing more grass biomass leading to greater flammability, which further reduces tree cover. Also, as tree cover increases, grass growth is suppressed reducing the available fuel for fires. This fire-vegetation feedback complicates the inference of cause and effect of fire in our model, maybe obscuring the effect of other variables.

Fire data used in this study was obtained from MODIS Burned area products. MODIS new Burned Product MCD64A1 v006 has been confirmed useful for the regional mapping of burned areas over tropical savanna areas (Alves et al., 2018). This product combines burned area and active fires, increasing the chances for a fire to be detected by the satellite overpass. The coarse resolution of MODIS data might have missed small and patchy fires, more frequent during the early dry season. Landsat provides an improved spatial resolution but due to its lower temporal resolution, images contained large cloud cover and couldn’t be used in this study. Recent satellites with open-access data policies, such as Landsat 8 (Roy et al., 2014; Schroeder et al., 2016) and Sentinel 2 (Drusch et al., 2012) will improve fire estimations in future work.

5.5.3 Biophysical and anthropogenic control of above-ground woody biomass in the Bateke Plateau

We hypothesised that AGWB stocks would vary across the landscape with greater AGWB stocks found in areas with higher precipitation, more elevated areas and with less sand content (Sankaran et al., 2005; Bucini & Hanan, 2007). We found that fire frequency and sand content were the main determinants in our model explaining variation in AGWB stocks. In contrast, rainfall is not significantly correlated with AGWB, and explained almost none of the variation. This is consistent with studies in many mesic savannas. Although water availability is a critical determinant of savanna structure (Sankaran et al., 2005; Bond, 2008), in mesic savannas like the Bateke Plateau, precipitation is considered sufficient to support closed canopy cover, and disturbances such as fire (Bond & Keeley, 2005; Sankaran et al., 2005), and edaphic conditions (Veenendaal et al., 2015) are considered to be the limiting factors.

Fire was the most prominent process regulating woody biomass in this landscape, with fire frequency being a more important predictor than fire seasonality. In our model, increased fire frequency was associated with decreased AGWB stocks across the landscape, likely because frequent fires reduce woody cover and reduce resprouting ability of seedlings and saplings (Higgins et al., 2000; Bond & Keeley, 2005). Fire seasonality was also an important though smaller predictor, with a larger proportion of late dry season fires associated in the model with a small increase in AGWB. One explanation could be that in areas with a greater proportion of late fires, the number of fires is low (as observed in Fig. 5.4), and this areas with more densely vegetation might have higher moisture and therefore are slower to burn. These areas will also take longer to dry out, and would only support fires later in the dry season. In the study area, fires peak in the long-dry season (June-September), which is the season of game hunting and plantation burning (Walters, 2012). There is a small secondary peak of fires in the short-dry season (January to February), when grasses are drier due to a reduced rainfall. Overall, there is a nearly continuous savanna burning in the Bateke Plateau, as the fire regime has changed in the last century and fire is now lit all year around (Walters, 2012). These fires outside the dry season could potentially have very damaging effects on the vegetation. Results from fire field experiments in savannas in the tropics show that the effect of seasonality is highly significant, with greater effects of late dry season fires compared to early dry season fires (Bond & Keeley, 2005; Veenendaal et al., 2018). However, these studies also suggest that fires very early in the dry season might have larger than average effects, as woody plants are not physiologically used to burning during the wet season. This could potentially be important in the Bateke Plateau during the short dry season in January-February, and would require further research.

Soils were important in explaining variation in AGWB stocks in our model. This was expected, as soils have been determined to be an important factor in shaping savanna vegetation structure at fine scales (Bond, 2008), and agrees with the findings of previous studies on the determinants of woody cover in the African savannas (Sankaran et al., 2008; Veenendaal et al., 2015). Sandier soils are associated in the Bateke with lower AGWB, possibly because they have lower nutrient availability and higher percolation rates. This is opposite to the results by Sankaran et al. (2008), who found, in their continental scale analysis, woody cover increasing as soil sand content increased due to their higher percolation rates below the rooting depth of grasses, reducing the competition of trees from the herbaceous layer. One possibility is that the water layer in these very deep sands of the Bateke is too low, and the sandy soils offers a limitation for trees as much as for grasses. Interestingly, soil organic carbon content didn’t explain much variation in AGWB, and greater soil organic carbon in our model was associated with a small reduction in AGWB. This has implications for management in these savannas, as soil texture and not organic carbon content seems to be the dominant factor.

Slope was a small but significant predictor, with more AGWB found in steeper areas. This might be explained by different edaphic conditions in these areas or by less disturbance by people. Topographic position index had a low explanatory power, with more AGWB found in valleys and in ridges. Protected areas was not a significant variable in the models, probably due to the large extent of these areas and the limited protection they have. Anthropogenic variables distance to towns and roads also were not important predictors in our model.

Overall, the predictor variables accounted for only 22 % of the variation in AGWB stocks. The reasons for this lack of explanatory power has a number of possible explanations, including the many complex and dynamic processes that act to shape savanna ecosystems, the importance of unmeasured variables, the presence of interacting effects between predictor variables, and uncertainty in the datasets used. The Bateke landscape is very large, and encompasses a large variability of environmental conditions. The large unexplained variation implies the importance of unmeasured variables in determining the spatial distribution of AWGB, potentially some other edaphic characteristics or soil conditions at small scales, which are not accounted for in the available datasets. Tree biomass in these savannas might not be deterministic, with the past ecological history maybe being a very important factor. The models suggest that the most important factor shaping this landscape is fire, and hence the past fire history would be very important, for which we lack data. Tree-tree competition could be a factor shaping the woody cover in these savannas, as discussed in Chapter 4, which may alter local vegetation dynamics without being strongly associated with environmental variation. Finally, our AGWB map itself is based on a relationship between AGWB and SAR backscatter with an R^2 of less than 0.5, and there may be errors in the other variables: together these random errors limit the maximum predictive power possible in the model to well below 50 %.

5.5.4 Changes in fire regime / precipitation

The observed effect of fire on AGWB could suggest that variations in the fire regime have the potential to result in changes to the biomass, although fire is both a driver of and a response to tree cover variation. This effect could be more intense in mesic savannas like the Bateke Plateau, where the precipitation is sufficient to support close canopy forests (Sankaran et al., 2005; Bucini & Hanan, 2007). Studies suggest that changes in fire intensity and frequency will result in significant changes in AGWB storage (Mitchard et al., 2011). Changes in the fire regime have recently been occurring due to changes in human intervention of fires (Walters, 2012), and this will probably have knock-on impacts on the landscape. Also, human population growth and better access to remote areas might increase the influence of people on fire regimes. Changing climatic conditions might also result in fires becoming more frequent and intense, due to an increase in temperatures, and in rainfall variation (Jolly et al., 2015; Serdeczny et al., 2017).

Using our model we can predict how potential changes in climate (precipitation), or fire regime (i.e. increase on the number of fires) will influence the AGWB in the future in the context of climate change and increased human disturbances. Our model indicates that a doubling of fire frequency in the savannas of the Bateke Plateau could be associated with a decrease in percentage of AGWB stocks of 29.68 %, while reducing the fire frequency by half will mean a potential increase of AGWB of 19.14 % (see Table 5.S1 in Supplementary Information for mean values, and 1st and 3rd quartiles). We note that these predictions can only approximate the impact of future changes, as there are likely to be multiple interacting factors that act to structure savanna ecosystems under global change. However, such predictions provide an important estimate of the magnitude of expected changes, and are important for effective management and for future fire management plans in the Bateke Plateau.

5.5.5 Biomass map comparisons

There are existing coarse resolution maps of the biomass of African savannas, but these do not agree with each other well (Hill et al., 2013; Mitchard et al., 2013; Avitabile et al., 2016). These pantropical carbon maps include the maps by Avitabile et al. (2016), Saatchi et al. (2011) and Baccini et al. (2012), which mostly reported large uncertainty at the pixel level. It can be observed in Table 6.1 and visually in Figure 6.1, that the Saatchi and Baccini maps significantly overestimate biomass in the Bateke landscape relative to the map produced in this thesis (Chapter 5). The Avitabile map is an improvement on the two older maps, but still appears to overestimate biomass on the Bateke Plateau. This result indicates the importance of having local biomass data in this region, and in other tropical landscapes that are presently underrepresented in forest plot databases.

Table 5.4. Biomass carbon stocks (mean and SD) calculated in this study (Chapter 5), compared to the biomass maps of Baccini et al. (2012), Saatchi et al. (2011), and Avitabile et al. (2016), all converted to MgC/ha.

	Mean biomass (MgC/ha)	**Standard deviation**
This thesis	2.32	2.15
Baccini et al. (2012)	25.45	13.76
Saatchi et al. (2011)	22.24	16.95
Avitabile et al. (2016)	6.00	8.84

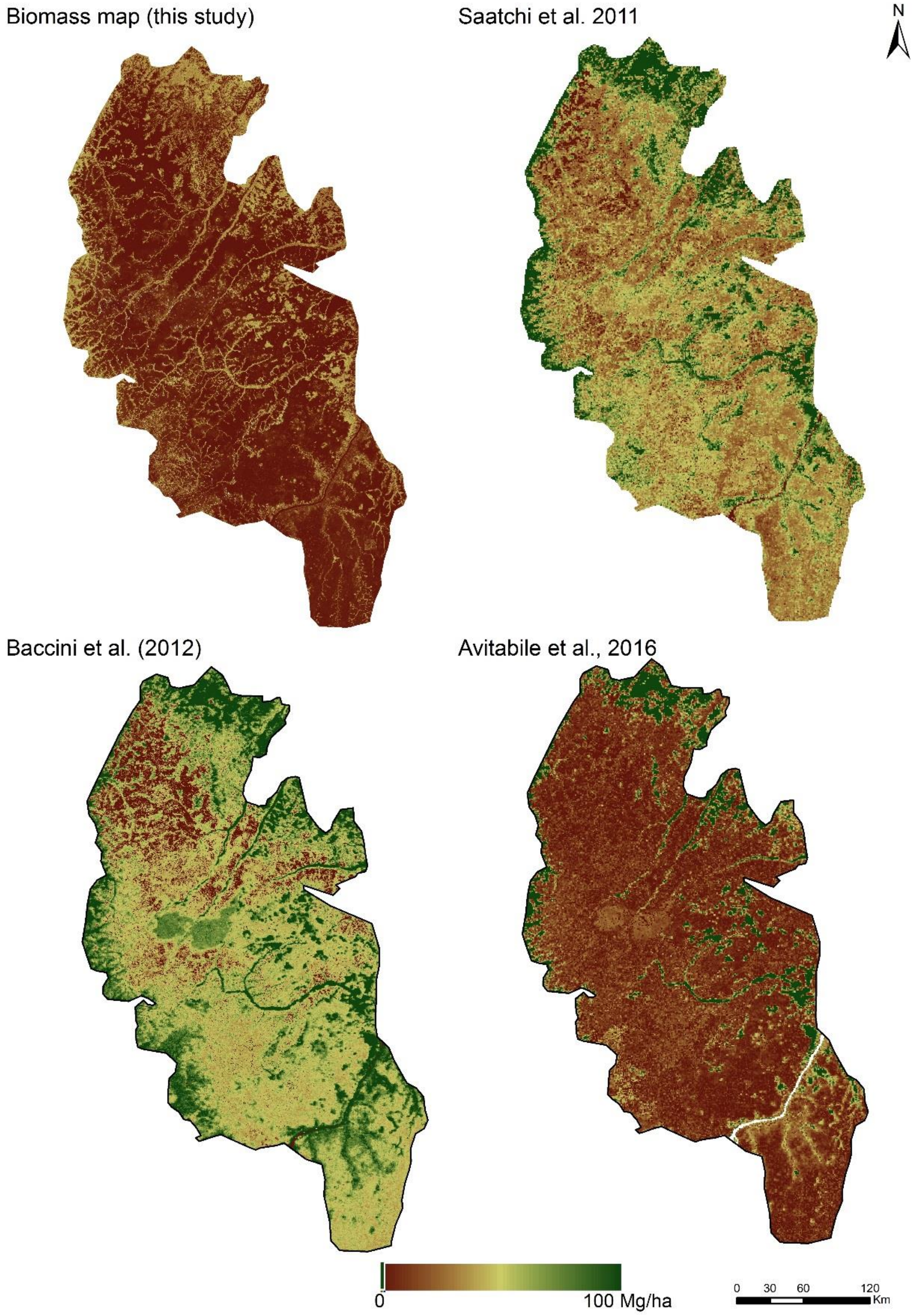

Figure 5.8. Maps of the Biomass stocks (mean and SD) calculated in this study (Chapter 5), compared to the biomass maps of Baccini et al. (2012), Saatchi et al. (2011), and Avitabile et al. (2016), all in Mg/ha.

5.6 - Conclusion

Above-ground woody carbon stocks have been estimated for the Bateke Plateau mesic savanna at a 100 m resolution. These maps offer the possibility of capturing small-scale patterns in AGWB stocks and improve our understanding on the main determinants of spatial variability in AGWB in the Bateke landscape. Fire frequency and sand content were the variables best related to AGWB variation. Our results are in concordance with several fire experiment studies in African savannas, which indicate that fire and soils are key process preventing woody biomass from reaching its climatic potential, especially in mesic savannas. Overall, our results indicated that multiple explanatory variables had a significant effect on AGWB and are probably interrelated to each other, and the existence of other unexplained factors affecting the low explanatory power of the model. This improved knowledge of the current environmental determinants of woody biomass is important for predicting how potential changes in climate (i.e. precipitation), or fire regime will influence these patterns in the future. This information is also very valuable for management and conservation of this landscape.

5.7 - References

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5.8 - Supplementary Information

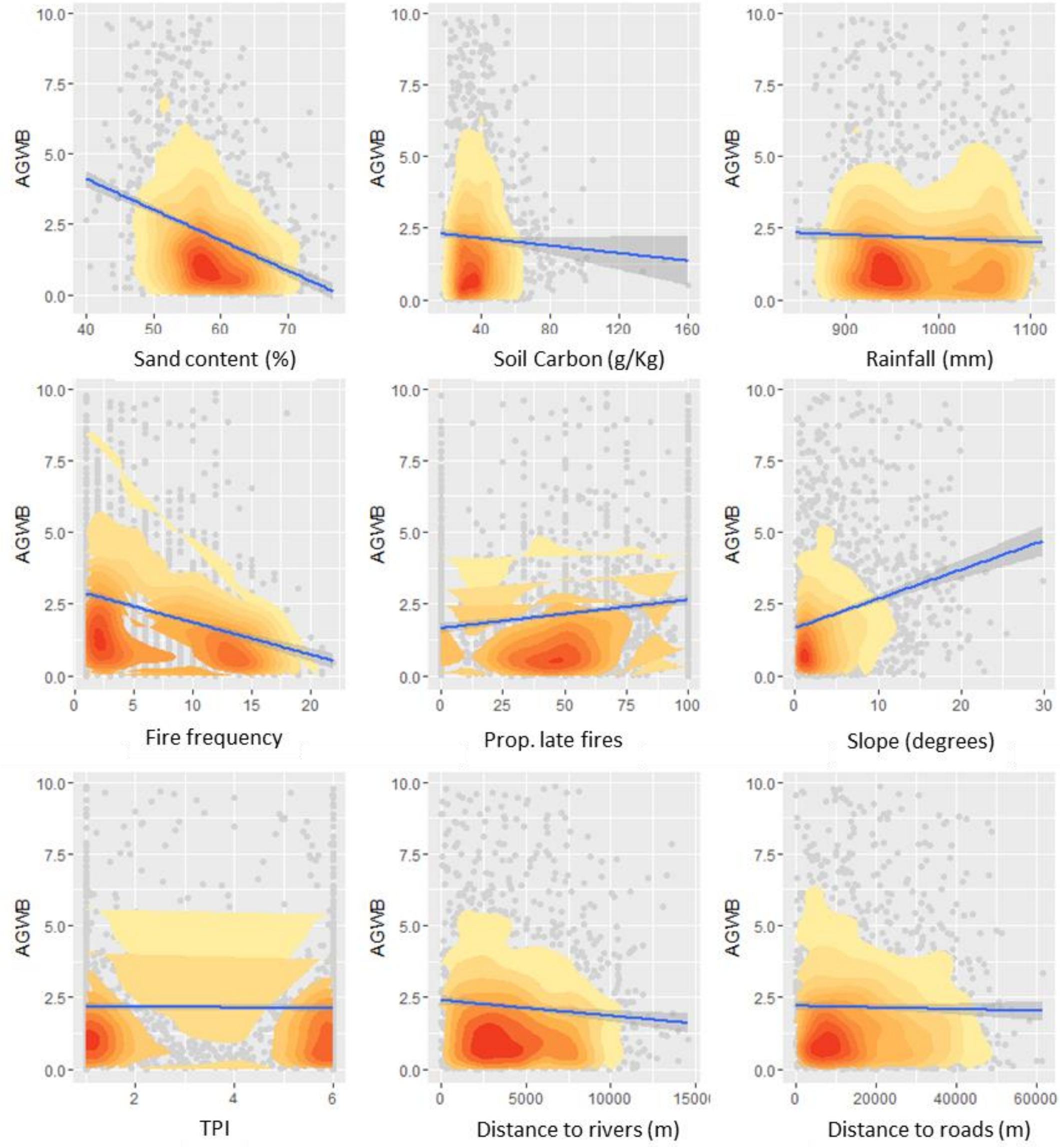


Figure 5.S1. Scatterplots with density estimations for the environmental raster datasets against AGWB (MgC/ha).

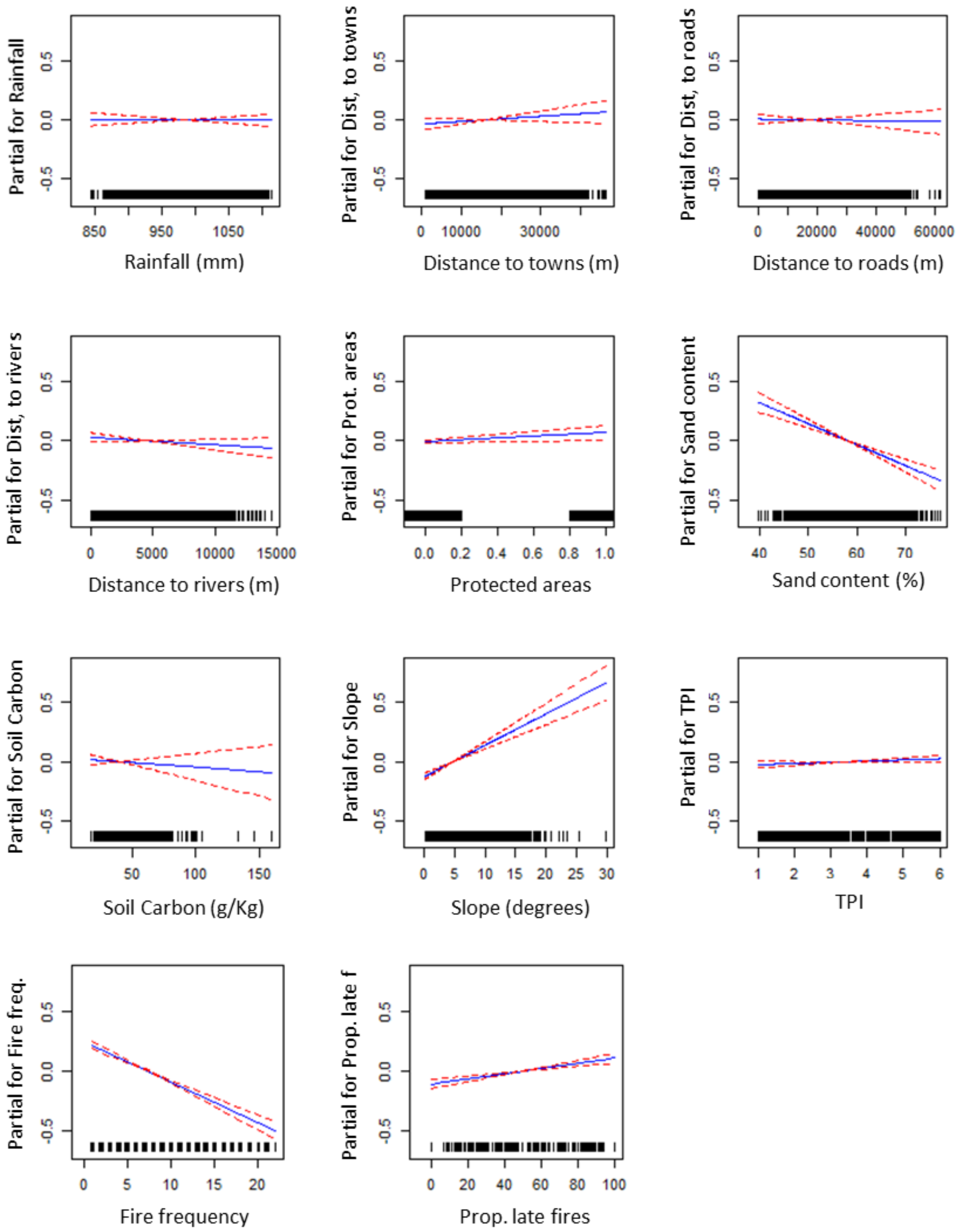
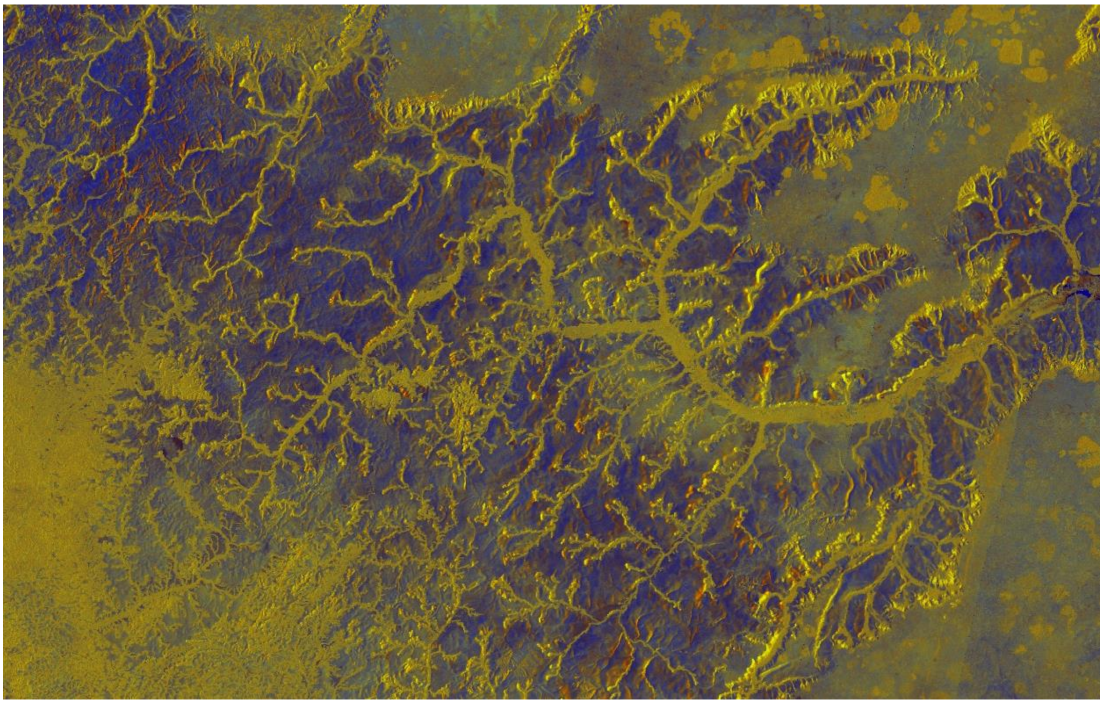


Figure 5.S2. Regression plots of AGWB against its predictors, with pointwise standard errors and a 1-d representation of the data (in black).

Table 5.S1. AGWB mean values predicted with the model when changing the fire frequency, with 1st and 3rd quartiles).

	AGWB (MgC/ha)	**1st and 3rd quartiles**
Model predicted	1.762	1.191-2.177
Double fire frequency	1.239	0.519-1.752
Half fire frequency	2.099	1.563-2.469

Chapter 6 Discussion and conclusion



Sentinel-1 backscatter (dB) (Red: VV, Green: VH, Blue: VV/VH ratio)

6.1 - Thesis summary

The objective of this thesis was to improve our understanding of the savannas of the Bateke Plateau, focussing on the dynamics of fire in this system. The Bateke Plateau is an understudied ecosystem, with few studies addressing its floristic composition and carbon stocks, and with the processes that underpin the savanna-forest mosaic not being well understood. This thesis represents a significant and unique dataset involving inventory plots covering 100 ha of the Bateke Plateau in Republic of Congo, an area an order of magnitude larger than any previous study in the region. The thousands of trees we have identified and measured, and hundreds of measurements of grass biomass, saplings and forbs, and the soil cores we collected, greatly increase the baseline knowledge of vegetation composition in the Bateke Plateau. Further, we have established a fire experiment and monitored it for 3 years, which if maintained will continue to enhance our knowledge; we have created a map of the above-ground woody biomass (AGWB) of the region; and we have compared this biomass map to other environmental layers in order to understand the large scale drivers of AGWB.

The main research questions of this thesis were:

i. What are the carbon stocks and floristic composition of a mesic savanna in the Bateke Plateau?
ii. What are the estimations of tree demographic rates under different fire seasonalities? What is the tree spatial structure and how important is tree-tree competition?
iii. What are the above-ground woody carbon stocks and fire regime of the Bateke Plateau, and the main determinants that regulate tree cover?

In this chapter I summarise the main results of each of the 3 research chapters, and review their application to the aims of this thesis. I will also discuss the fire experiment, fire management in savannas and recommendations for the Bateke, as well as identify key areas for further research arising from the outcomes of this work.

6.2 - What are the carbon stocks and floristic composition of mesic savannas of the Bateke Plateau?

In Chapter 3 I assessed the biomass and floristic diversity of two wooded savannas in the Bateke Plateau in the Republic of Congo. Using 4 experimental plots (25 ha) in two protected areas, we inventoried 4120 live tree stems (DBH ≥ 10 cm) in 2015, and re-measured them in 2016 and 2017. This information, together with the literature review performed of all studies in the Bateke Plateau, could help others to better understand these savannas. Some of the ways in which our study can inform this issue are discussed below.

6.2.1 Species diversity

The species diversity of our plots was low, as assessed in Chapter 3, but greater than expected for secondary grasslands (Zaloumis & Bond, 2016), supporting the idea that these savannas have probably existed as a mosaic for long time. The plots contained both fire tolerant trees and species with a geoxylic suffrutex growth form, both of which indicate the importance of fire in shaping this system over a long period of time. The geoxylic suffrutices, or geoxyles species, were defined by White (1977) as the underground trees of Africa. They are plants that have develop huge underground woody structures, protecting them from surface fires, and with aerial shoots that are short in height and duration, minimizing their resource input into annual growth (White, 1977; Maurin et al., 2014). They occur almost exclusively in higher rainfall savannas with frequent fires and are also common in areas where environmental condition reduce growth rates, such as low-nutrient soils (White, 1979), as in the case of the Kalahari sands (Maurin et al., 2014). These savannas are dominated by one tree species, *Hymenocardia acida*, a fire tolerant species that reproduces mainly through resprouts. Although (Boaler & Sciwale, 1966) found for miombo woodlands that *H. acida* was one of the fastest growing trees, we found in chapter 4 slow growth rates for adult trees. This hyperdominance remains unexplained, and requires further research, although it might be due to the high fire frequency reducing growth rates and making other species unviable, or the seasonal water availability. There was a richer under-canopy species composition, with 49 identified plant species (4 tree species, 13 shrubs, 4 sedges, 17 forbs and 11 grass species). The average species richness was 23 species per 25 hectare plot. I didn't find any endemism, but this experiment was not designed as a floristic diversity experiment, and it is very likely that I have missed some species, especially forbs and grasses.

Additionally, I investigated if the Bateke Plateau is a recently created anthropogenic savanna or an ancient forest-savanna mosaic. Some authors have suggested an anthropogenic origin for the savannas of the Bateke Plateau, caused by the arrival of human populations and the effect of fire (Aubreville, 1949; Duvigneaud, 1953; Elenga et al., 1994). White (1983) also defined these savannas as mainly secondary grasslands, areas that were once forest but which have been destroyed by agriculture, and with most of their component species being widespread (White, 1983). From these, it could have been assumed that the flora of the area lacks interest, and this is may be why there are not many scientific studies on the Bateke Plateau. Recent research, however, suggests these savannas to be floristically important at national levels (Walters et al., 2006), and new species are being discovered (Stone et al., 2006; van der Maesen & Walters, 2011). There is accumulating evidence that supports an origin of these savannas caused by past arid events, not recent clearance for agriculture. The savanna biome probably originated in the late Miocene/Pliocene worldwide (Beerling & Osborne, 2006; Pennington & Hughes, 2014). The recent climatic history of the region is complex, but it seems that there were shifts from forest to savanna cover related to humid and arid climate events for at least the past 40,000 years, and that a savanna-forest mosaic existed in the area even during the most humid periods (Schwartz, 1988; Elenga et al., 1994; Schwartz et al., 1995). The arrival of human populations was coincident with a major arid event that occurred 3000 year BP, causing the expansion of grasslands (Schwartz, 1992). Hence, human populations might have contributed to the present structure of these savannas, but these savannas are probably ancient.

The Bateke Plateau is situated within the Guineo-Congolian centre of endemism (White, 1979). This contains approximately 8,000 species, of which 80 % are endemic (White, 1983), but few of its endemic species are found in savannas. I discussed in Chapter 1 that some authors found species distributions similar to the Zambezian or Sudano-Angolan regions (Koechlin, 1960; Walters et al., 2006; Fayolle et al., 2018). These floristic similarities with other regions are likely due to its historical spatial geography. The Bateke was fairly isolated from other savanna formations because of the surrounding rainforest, with only some exceptions. There were some corridors (with the Angolan highlands, the Kalahari sands and the Sangha River Interval) that could explain the floristic affinities with other areas (Maley, 1991, 2001; Walters et al., 2006; Maley & Willis, 2010; Bostoen et al., 2015; Fayolle et al., 2018; Maley et al., 2018).

6.2.2 Carbon stocks

I found that the biomass stocks were low, mainly dominated by the soil top layer, in concordance with other studies of the Bateke (Apani, 1990; Schwartz & Namri, 2002; Yoka et al., 2010; Gigaud, 2012; Yoka, Loumeto, Djego, et al., 2013; Yoka, Loumeto, Vouidibio, et al., 2013; Ifo et al., 2015; Ifo, 2017). The total plant carbon stocks (above-ground and below-ground) was 7.4 ± 0.3 MgC/ha, low for a mesic savanna, and I hypothised in Chapter 3 that this was probably due to the poor sandy soils and a high fire frequency. This was further supported in Chapter 5, where both of these factors were the main explanatory variables in the model (i.e. areas with the least sandy soils, and lowest fire frequency, had the highest biomass values). The sandy soils are poor in organic matter and nutrients (Yoka et al., 2010) providing less growing capacity to plants. These soils also have a high percolation rate, with a potential rapid infiltration of water to deeper soil layers (Williams et al., 1996; Sankaran et al., 2008), where trees roots can reach but probably not grasses. This suggests that the hydrology may substantially modify the dynamics of tree−grass competition, maybe promoting faster growth rates of trees with deeper roots, although temporal differences in water availability might also play a role. This might be the case in areas where the sand deposits are not very deep, although in other areas the sands can reach tens or hundreds meters down, and therefore trees won't have an advantage. Although these sandy soils are poor, and the woody biomass values reported here are lower than other savanna systems, the top soil contributes the most to the carbon pool in our plots (16.7 MgC/ha, 53% of the total). Estimated grass carbon stocks were similar to the sum of the tree, shrub, and sapling biomass combined.

It should be noted that in November 2018 a paper was published with a new allometric equation for the Bateke Plateau and a shoot-root ratio (Ifo et al., 2018). This equation was not available during this study, and therefore the pantropical allometric equation (Chave et al., 2014) was used. Ifo et al., 2018 estimated that the pantropical equation underestimated the above-ground woody biomass of trees in the region by about 50%. If this is also the case in Lefini and Lesio Louna, the biomass values estimated in this study may also be underestimated. However, a more destructive sampling in other sites of the Bateke might be needed to better quantify biomass. Additionally, and surprisingly, they obtained a shoot-root ratio of 0.272, substantially less than those used in this study and that those reported for woody savannas (Ryan et al., 2011; Mugasha et al., 2013), due to differences in tree species rooting and tree architecture.

6.3 - Woody demographic rates and spatial structure, and the regulation of fire and tree-tree competition

6.3.1 Demographic rates and fire seasonality

In Chapter 3, I provided estimates of demographic rates, showing that tree growth rates (averaging 1.21 mm/yr), and tree mortality rates (3.24 %/yr) were low across all plots. The growth rate was lower than those reported for other African savannas (Childes & Walker, 1987; Holdo, 2006; Gaugris et al., 2008; Scogings, 2011). The factors responsible for these low growth rates are probably low soil fertility, high rainfall seasonality and high fire frequency. Lefini and Lesio Louna reserves had different growth rates, maybe due to different fire histories, but this has not been investigated in detail at this stage. Stem mortality rates were also in general lower than other savannas, but all the stems measured were big trees (DBH ≥ 10 cm) that had escaped the fire trap height, when trees are most susceptible to mortality due to fire, and the majority of them were fire tolerant species, adapted to the fire frequencies of these savannas. Certainly most trees had fire scars and a tortuous growth form suggestive of survival from previous fires.

I also investigated how rates of savanna tree growth and mortality are influenced by fire, competition from other trees, stem damage, stem size and height, and distance to closed canopy forest by using hierarchical models. Stem damage had a large impact on demographic rates, with having any damage reducing growth by 0.15 ± 0.05 mm/yr, and increasing the probability of mortality. We believe that most damage is caused by fire, and thus this finding points to the significance of delayed fire impacts, including on large trees. Some damage may also be caused by herbivores: elephants are the most likely cause here, and although we saw little direct evidence of elephant damage, they are present at the sites at low densities.

Regarding fire seasonality, in the experiment I found that a fire being late in the dry season caused a small reduction of tree growth compared to it being early (-0.08 mm/yr), but unexpectedly such fires were also associated with reduced mortality rates. However, the latter unexpected result is backed up with the whole Plateau dataset, where we find higher AGWB carbon stocks associated with areas with a higher proportion of late fires (not a greater absolute number) compared to early fires (Chapter 5), suggesting this is not an error in the dataset.

There are suggestions in the literature as to why we might have found the contradictory growth vs mortality findings. The faster growth in the trees in the early season burns is easy to describe without needing an explanation related to reduced tree death or damage: it has been found previously that early dry season fires can slightly improve growth in adult trees, either in response to nutrients released from the burnt ground vegetation layer, or reduced competition from grasses (Holdo, 2006). The reduced mortality rates in the late burn plots could be due to the fact that these are adult fire resistant trees, tolerant to late dry season fires. In the fire experiments, although late dry season fires burned all the plot in comparison with early fires which were patchy, none of the fires had were of very high intensity. The high fire frequency, as observed in chapter 5, might have created a dominance of adult trees with stem diameters greater than 10 cm, which I describe in Chapter 3. These trees have probably reached a peak growth, as the effect of tree size on growth rates of adult trees was relatively small and there were not many big trees, probably allocating resources to below-ground storage organs or reproduction. Fire and tree death both occur stochastically, so ultimately to obtain reliable data on the impact of fire seasonality on recruitment and mortality rates we will need the field experiment to run for several more years, as we used only three years of data. Additionally, we are missing information about the past fire frequency and intensity.

Recruitment rates were low in the plots (3.8 % of stems per year). It is thought that recruitment of saplings into an adult size class occurs only if the sapling experiences a sufficient period without fire, allowing it to grow above the fire-trap height and avoiding mortality (Hoffmann et al., 2012). As shown in Chapter 5, the Bateke experiences very frequent fires, which therefore explains the low recruitment rates. Additionally, the sandy soils offer poor growing conditions, and this will affect juvenile trees most, reducing their growth rates and thus the probability of reaching a fire-proof height (Prior 2006). However, it was clear from our plots that saplings can escape even if a fire comes through the savanna, as the early season burns particularly left significant portions of the plot unburned. Therefore MODIS-based fire frequencies may be higher than the fire frequency actually experienced by some saplings.

Further, it has been shown that a regime of annual early fires, while maybe favouring adult trees, may reduce the growth and survival of saplings, with effects on recruitment rates (Prior et al., 2006), as early dry season fires occur when photosynthetic rates are higher (Prior et al., 2004). I couldn't investigate this here, and I didn't model the effects of fire on recruitment rates in Chapter 4, as the sampling strategy was not optimised for this, with too few subplots and too short a time. However, in the longer term strong data on recruitment will come from the main plots, as the rate of trees arriving at the 10 cm size class is tracked. It will be important to continue to investigate recruitment to understand the effect of fire on the system, as saplings and young trees are probably the most affected by fire seasonality/intensity.

6.3.2 Tree spatial structure

These savannas showed a sparse tree distribution with low tree density. I found that trees were spatially aggregated in clusters, typical of humid savannas (Veldhuis et al., 2017). These clusters may offer more protection from fire, but also potential for tree-tree competition (Menaut et al., 1990; Calabrese et al., 2010; Sea & Hanan, 2012; Svátek et al., 2018). In the model I found that, indeed, competition results in a small reduction of growth and a small increase in mortality rates, although with only a small effect. This result was surprising, given the low tree density of these plots, which suggests that competition may be an important factor structuring these savannas. I discussed in Chapter 5 how other studies have found evidence of tree-tree competition being an important factor structuring savannas (eg. Holdo (2006), Dohn et al. (2017) (Smith & Grant, 1986; Grundy et al., 1994; Shackleton, 2002), but these studies are scarce and inconclusive. The data shows evidence of two competing processes: the clustering of trees which might offer fire protection, or an increase mortality of isolated trees in the past, but also trees being close to other trees reduces growth and increases mortality due to competition. This could be object of further research, by building a tree-based demographic model including fire that replicates this finding.

The models had a weak explanatory power, maybe due to the importance of unmeasured variables, or the fact that savannas are dynamic systems, with many and complex processes interacting shaping the savanna ecosystems, and the short time-period of the study, with a low signal to noise ratio.

6.4 - Estimation of the woody carbon stocks and fire regime in the Bateke Plateau, and the main determinants in tree cover

6.4.1 Causes of woody biomass levels

I estimated the Above-Ground Woody Carbon stocks (AGWB) for the Bateke Plateau at 100 m resolution by using ALOS PALSAR L-band data, and identified the fire regime in the area using the MODIS burned area product. I also analysed the effect of the main determinants of AGWB (fire, soil properties, topography and anthropogenic factors). Above-ground woody carbon stocks were highly spatially variable in the savannas, averaging 2.32 MgC/ha across the Bateke Plateau, with 67.7 % of the study area categorised as woody savannas. This value is higher than the estimates derived from the field plots (0.71 ± 0.06 MgC/ha). This is likely due to the field plots being in a region of the Bateke Plateau with lower AGWB that the average for the landscape, and not representing all fire or edaphic conditions.

The Bateke does not burn uniformly, with up to 31 fires occurring in a single pixel during a 16 year period, and as few as zero. There are general patterns though, with an average of 6 fires during the 16 years, and fires peaking during the main dry season, but also having a small peak during the short dry season in January and February. Rainfall was not significantly correlated with AGWB, consistent with studies in other mesic savannas where precipitation is considered sufficient to support closed canopy cover, and disturbance and edaphic conditions are the main limiting factors (Bond & Keeley, 2005; Sankaran et al., 2005).

Fires create a positive feedback, with the frequent fires maintaining an open canopy and reducing woody biomass (Trapnell, 1959; Bond & Keeley, 2005; Higgins et al., 2007). Studies and model predictions in global savannas found that more frequent fires led to decreases in tree cover (Higgins et al., 2000; Sankaran et al., 2008).

I also showed the importance of representing multiple biophysical and anthropogenic processes when modelling AGWB. Fire frequency and sand content explained the most variation for AGWB. More frequent fires were associated with lower AGWB stocks, but unexpectedly (though matching the results on mortality from the fire experiment), an increased proportion of late dry season fires corresponds with more AGWB. Beyond the explanations in 3.2.1, at this large scale this could simply be because areas with more biomass take longer for the grasses to dry out and become flammable, and therefore fires automatically occur later in the season.

As expected, sandier soils are associated with lower AGWB. However, greater soil carbon content was surprisingly also associated with a small decrease in AGWB. Slope was also an important predictor, with steeper slopes having more AGWB, probably related to less disturbance.

As stated above rainfall was not found to be important in explaining AGWB, but protected areas, topographic position index, and distance to rivers were also not found to be important. Some of the protected areas in the Bateke Plateau didn’t get full protection until recently, and not every part of their landscape is protected. Distance to rivers might be important in the first meters after the riverine forest, but in our plots it seemed that the savanna areas closer to the riverine forest had lower tree density, and these areas were also the lowest part of the plots. I can speculate that this could be because of the savanna area next to the riverine forest acting as a corridor for the fire and therefore experiencing higher fire frequencies.

6.4.2 The future under climate change and management

Under climate change, it is expected that over the coming decades rainfall variation will increase, temperatures will rise, and more common extreme events will occur, with the combination meaning that both fire frequency and fire intensity are likely to increase (Jolly et al., 2015; Serdeczny et al., 2017). This can result in an expansion of savannas (Delire et al., 2008). As it is important to understand how these changes will impact savanna vegetation, I used the model in Chapter 5 to predict how an increase in the frequency of fires will influence AGWB, although this is only an approximation as multiple interacting factors act in structuring these savannas. The model predicts that a doubling of fire frequency, while keeping everything else equal, resulted in a decrease in the AGWB stocks of the Bateke Plateau of 26 %. Of course there are larger carbon stocks below-ground (Chapter 3), and we do not have the spatial data nor mechanistic understanding to predict how they will change due to climate change: however the balance of probabilities estimate would be that under increased temperatures, increased fire frequencies, and lower AGWB, the soils would release carbon to the atmosphere.

As most fire is anthropogenic in these savannas, the climate related changes could be either mitigated or enhanced depending on management adopted. Taken together, results from Chapter 5 suggest that reducing fire frequency should increase carbon stocks. Preventing fire altogether in this landscape is very difficult, but our maintenance of the fire experiment shows that fire breaks can be effective, and the early burning of patches of fire can protect other areas from burning at all. The details of my management recommendations are explained in Section 6.5.2.

The picture on management for seasonality is more mixed, with early burning in the experiment being associated with increased tree growth rates and more patchy fires, but also higher tree mortality. Everything else being equal, across the landscape there is more AGWB found in areas where fires were found later rather than earlier. Ultimately, it may be that management for fire frequency is more important, which over large areas will probably involve a combination of early burns to set up fire breaks to protect some areas from burning, and some late burns to increase pyrodiversity, and because fire will inevitably escape or occur later in the season in the areas that have been protected from burning earlier in the season.

6.5 - Measurement of fire and fire management

6.5.1 Measurement of fire effects in savannas

In this thesis I have described the importance of fire in shaping the savanna vegetation of the Bateke Plateau. However, a limitation of savanna ecology is that much of our inference relies on observational studies, such as Chapter 5, where differences in fire regime are assumed to cause differences in vegetation, but where the causality could in fact be the other way round. This is an especially important problem with future climate change, as savannas will be pushed into climatic envelopes where they do not currently exist, so conclusions drawn from observational studies are even more limited. In this thesis, I have used both field experiments and remote sensing data to investigate the effect of fires on the savannas in the Bateke. These two methods provide a series of advantages and disadvantages, discussed in this section.

FIRE EXPERIMENT AND LIMITATIONS

The heterogeneity of savanna structure and the complexity of fire in savannas presents a challenge to experimental design. Long-term fire experiments in savannas are uncommon due to the difficulties and demands of their continued operation. They usually feature large variation in methodologies between sites, and insufficient replication within sites. Controlled fire experiments and observations of the effects of fire on vegetation in Africa started during colonial times (Furley et al., 2008), but most of these experiments have been little reported in the scientific literature. They also vary greatly in field protocols and are geographically constrained to some countries. Many of the first experiments were created with the objective of studying the effects of slash and burn agriculture, vegetation clearance, or grazing (Furley et al., 2008), and very few of them are long term experiments. Laris and Wardell (2006) provide a well-documented summary of fire experiments in the savanna, and a summary of fire experiments in the savannas around the world is included in Chapter 1 (Table 1S.1 Appendix 1). There have been several criticisms of burning experiments, mainly because of the lack of an initial rigorous protocol and design (Furley et al., 2008), and because experimental plots have often been relatively small in relation to the area represented, and conditions have been simplified. Despite these criticisms, much valuable information has been derived from past experiments, providing fundamental data on the fire ecology, the effects of burning and carbon cycling, that could not have been known from purely observational studies (Higgins et al., 2007; Van Wilgen et al., 2007; Furley et al., 2008). More fire experiments provide the data to improve vegetation and carbon dynamics models, which in some cases fail to simulate the conditions of the Bateke Plateau (for example, the model presented in (Delire et al., 2008) overestimates the tree cover in the Bateke, classifying most of it as deciduous or evergreen forest).

The fire experiment presented here was designed in order to study the effect of early versus late dry season fires and to obtain results within the timeframe of this PhD. I acknowledge that fire frequency is very important in savanna ecology, and this was investigated in the observational study in Chapter 5, but could not be rigorously investigated in a field manipulation experiment in the timeline of this PhD. The fire experiment started here could be extended to include plots of different burning frequencies. I have shown in Chapter 4 and 5 the need to use large plots to investigate tree demographic rates, capture variations in carbon stocks and the effect of fire on these. These large plots are also appropriate for calibrating remote sensing images. However, by using these large plots there were trade-offs for monitoring floristics: 400 x 0.25 ha plots spread across the whole Bateke would have covered the same land area (100 ha), but would like cover considerably more species diversity.

REMOTE SENSING AND LIMITATIONS

I have used field data at plot scales and linked these to landscape measurements of biomass and fire by using remote sensing.

The use of remote sensing has some limitations. In Chapter 5 I have used ALOS-2 to calculate an AGWB stocks map, which is affected by some bias due to variation in AGWB explained by things other than the radar backscatter. Also in Chapter 5, I used a 16 year time-series of burned areas identified by MODIS. MODIS has a coarse resolution, and it could have missed small and patchy fires, which is are common in savanna systems (Randerson et al., 2012), and probably in the Bateke Plateau. More recent satellites, like the optical Landsat 8 (Roy et al., 2014) and Sentinel 2 (Roy et al., 2014), or the C-Band Sentinel-1 (Mathieu et al., 2018), should improve the remote sensing detection of fires in future work, mitigating this issue. In this study I also faced some computational limitations, as in Chapter 5 I could not use all the pixels, and I had to use a selection of pixels every 5 km to model the determinants of AGWB, as shorter distances require too long to compute.

6.5.2 Fire management and recommendations for fire management in the Bateke Plateau

Tropical savannas are fire-adapted systems that require frequent fires to maintain the tree-grass co-existence. Without fire, much of the mesic savanna of Africa would probably become forest. The importance of fires in savanna ecosystems raises questions about their management, and whether to apply prescribed fires. This is particularly important as most of savanna fires in Africa anthropogenic in origin, and savannas have significant value to the local economy and national conservation.

Fire management was probably part of subsistence strategies used by local people over a long time period, both for hunting and protection (Laris, 2002). Extensive fire management in West Africa applied in colonial times was mostly interested in fire restriction to encourage forest encroachment (Laris & Wardell, 2006). However, fire exclusion might be undesirable in savannas, and also very difficult to accomplish. The results from long fire experiments, together with the change in ecological mentality, is improving the scientific knowledge needed for the better management of these areas, but there are still many issues being debated and fire management in savannas continues to be controversial. Some authors have debated the usefulness of fire management for the ecology of savannas (Parr & Andersen, 2006; Penman et al., 2011). One of the main fire management techniques applied currently is the patch mosaic burning approach, maintaining a variety of different fire treatments across a landscape to create landscape heterogeneity, which is meant to promote higher biodiversity, more grazing sites, and a more resilient system, and creates a barrier to more damaging large late fires (Bucini & Lambin, 2002; Laris, 2002). Early season fires also normally create patchiness on savannas, and so it is sometimes adopted as a management approach, however with criticism by some authors (Parr & Andersen, 2006). They argue that this is often used without the required empirical knowledge and understanding, and that a range of fire regimes have little effect on a resilient savanna ecosystem (Parr & Andersen, 2006; van Wilgen, 2009). Other authors have considered the risk of woody encroachment into savannas through the use of early season burns (Smit et al., 2016).

Overall, I believe that answers about fire management can only come from long-term fire experiments. We should continue to monitor existing fire experiments (see Table 1S.1 of Chapter 1 Supplementary Information for a list), and continue to perform metanalyses and learn from them. It is also imperative that we learn from the positive and negative experiences of fire management, which has been performed extensively and good records kept in many areas (for example in Lope National Park and Kruger National Park). There will definitely not be a one-size-fits-all management recommendation: it will vary by location and objective, and the optimum regime may even vary within a site (van Wilgen, 2009). Better monitoring of the outcomes of fire management practices, and an adjustment of them as understanding increases at a local as well as overall level, will improve the fire management of savannas.

In the Bateke Plateau, fire is not usually actively managed, although some protected areas are starting to consider fire management (for example the Bateke Plateaux National Park in Gabon). Fires are essential in the lives and culture of Bateke populations, and therefore close integration of local people and park staff in both planning and execution is needed for successful fire management. For this, Walters (2012) provides a study of the link between fire and society in the Bateke in Gabon, and recommendations on how to involve the communities in its management.

The results presented in this thesis show that early season fires were low intensity and didn’t burn all the plot area, creating a mosaic of burnt and unburnt areas. On the other hand, late dry season fires burnt all the plots, and were more intense. This was consistent with other studies on the seasonality of fires. This, however, didn’t result in very significant differences in the mortality or growth, indicating the importance of maintaining this experiment for longer periods to obtain conclusive results. Although early dry season burns creating patchiness in the landscape, its long-term sustainability and practicality is uncertain and needs further investigation. Late dry season fires don't seem to have a large effect on carbon stocks in these savannas relative to early dry season fires. As mentioned in section 6.4.2, it might be important to consider management of fire frequency, with a combination of semi-annual early burns and late burns creating patchiness in the landscape (Parr &

Andersen, 2006). In Chapter 5 I predicted an approximation of how doubling and halving fire frequencies will impact AGWB stocks. The model predicts that a doubling of fire frequency, while keeping everything else equal, resulted in a decrease in the AGWB stocks of the Bateke Plateau of 26 %. These fairly crude estimates provide the bounds of what management could potentially achieve, but without taking into account the practicality of imposing these fire regimes or the impacts of future climate change. The results from this thesis should be treated with caution if applied to management practices, as this fire experiment only ran for 3 years, and we don't have a good knowledge of the long term historic fire regime of the area. Because of this, we can't recommend a specific fire frequency as this will require further data from this and other fire experiments in the Bateke Plateau. Additionally, the determination of an optimal fire regime will require judgement of factors other than carbon storage, including detailed impacts on flora and fauna, continued provision of ecosystem services, and cultural heritage. Data from studies such as this one could inform how to address issues for potential future carbon management and REDD+ projects in this landscape. The results of the fire experiments here only represent the case of two protected areas in the center of the Bateke Plateau. These are additional to Walters (2012) results in the north-western Bateke in Gabon. Fire patterns, rainfall and cultural fire setting patterns of fire might differ in other areas of the landscape, and will require further studies in other areas to understand the wider context of fire-setting in the Bateke Plateau.

6.5.3 Recommendations for the continuation of the fire experiment and next steps

The fire experiment presented in this thesis has provided unique information of a largely understudied landscape. These experiments are very difficult to run, and need continuous monitoring and maintenance. However, its continuation has potential to provide improved and useful information about how fire structures these ecosystems, and how it should be managed in future. With this in mind, here I provide some recommendations for the continuation of a long-term fire experiment on the Bateke Plateau.

The three years of the fire experiment has shown the importance of continuous maintenance of the fire breaks throughout the year, especially at the beginning of the dry season, but preferably also throughout the year. This should consist of controlled burns performed by knowledgeable and well-equipped local teams who have participated in previous plot inventories. This activity would normally take less than one week to perform per site. For a better protection of the plots, it is also advisable to perform controlled burns at the north east of the plots in Lefini, and south east in Lesio Louna, to avoid the entrance of fires starting outside and advancing through these areas; the natural firebreaks of the gallery forest and river protect in the other directions. In-country support to the maintenance of all of the plots is essential for their continuation. This support could be provided by some form of collaboration between local village associations, the Université Marien Ngouabi, WCS, and local NGOs. WCS local staff have been trained to continue supporting the experiment (maintenance of fire breaks, annual measurements and fire treatment). Additional training of local staff in field protocols and methodology might be needed to continue support. A collaboration between WCS, as well as village associations, and assistants that aided in previous field work, and experts at the Université Marien Ngouabi, will be important in the long-term maintenance of the fire experiment, with a clarification of roles. Additionally, USFS is working with sensitisation and stakeholder engagement of the communities around Lefini (see Chapter 1 for more details). It is important to inform the community about the importance of a fire experiment in this area, and the improvements its conclusions could have in the management of the land they live on.

Next steps for the experimental plots include:

- Completing the inventory of the unburned plot LWR3. The data from the unburned plots (LWR3 and LLR3) could be used in the future, with a longer period of fire protection providing very useful information about the dynamics of this system;
- The establishment and payment of a local team to maintain fire protection over the long term;
- Continuous application of the fire treatments (May and September, preferably at the same time as the fires were performed in previous years) at plots LWR1, LWR2, LLR1 and LLR2, and where feasible the ongoing re-measurement of tree stems at these plots.

Where there is no possibility of performing all these tasks due to funding gaps, it would be advisable to, at minimum, maintain the fire breaks and the fire treatments, so that the periodicity of the fires is continued and the experiment can be taken up in the future. For strong results it is not necessary to inventory the plots annually; good results could still be collected from surveys every 2-3 years, and even if only inventoried every decade, useful and interesting results could result provided the fire treatments are maintained. Beyond 10 years we think re-inventory work would become very difficult, as the tree tags and subplot markers could become hard to find.

6.6 - Limitations and future work

This thesis generates many questions that would require future research. In this section I describe the limitations from this study, as well as lines for future work.

The fire experiment was designed for this research to study the impact of early vs late dry season fires, and therefore has some limitations. For a better understating it will be important to study the effects of fires outside the dry season and semi-annual fires, fires of lower than annual frequency. Semi-annual fires are rarely investigated, but as shown in Chapter 5, they occur in the Bateke Plateau, and will have important effects on woody cover. Similarly, the investigation of the fire free intervals will resolve questions about recruitment and tree establishment, but this is difficult as fire is stochastic, and few areas have a reliable and sufficiently old fire record to provide reasonable estimates of the long-term interval between fires. Ideally the fire regime would be known over the lifespan of the trees, which could be many hundreds of years.

It would also be valuable to see the effects of fire exclusion in the no burn plots over long term, to study recruitment under ‘ideal’ conditions, and see if forest encroachment occurs. A large number of experimental plots with different fire frequencies and seasonalities and over long periods would be required to reliably quantify the impacts of fire regime on savanna vegetation in a particular area, including the effect of infrequent extreme fires. This is very difficult to achieve, and would require knowledge of the long-term fire history of the plots. This is why controlled long-term fire experiments are very important, and this fire experiment contributes to the knowledge acquired by all fire experiments in savannas. It is important, however, to transfer of knowledge of fire experiments conclusion to scientific community and fire managers. A synthesis of fire studies in savannas in Africa could provide valuable information to understand fire vegetation dynamics for all Africa. The many studies that have been conducted over the past century have not been all reported in the peer reviewed literature, provide contrasting results, and lack information such as the weather at the time of study, the methodology used, and societal context.

In terms of fire ecology, to fully understand the effects of fire on the vegetation, it will be very important to understand the fire-ecology related to the species present here, especially the dominant tree species, *H. acida*, and the reasons for its hyper-dominance. To my knowledge, there have not been any studies on this, and this knowledge would be interesting in helping to model the response by the species to fire regimes. *H. acida* reproduces asexually through production of resprouts stimulated by frequent fires (Walters, 2012), although *H. acida* is not the only resprouting species in the Bateke. Resprouts will therefore grow faster than saplings from seeds, allowing the plants to escape the fire trap and reach sufficient height easier than species that reproduce sexually. Consequently, it would be important for future work to estimate growth rates in this area for shrubs of resprouts compared to seedlings with DBH < 10 cm, as they are expected to be higher.

More research is also needed into tree-tree competition, which I found in Chapter 4 to be a potential factor in shaping these low tree density savanna, and therefore might be a factor more important than previously thought in mesic savannas. The spatial clustering might offer higher survival, but also the tree-tree competition caused lower growth rates. Moreover, further investigating the tree-grass competition will help understand the factors leading to tree-grass co-existence in these savannas.

6.7 - Main contribution of this thesis to savanna science

This thesis adds to the state-of-art of knowledge about tropical savannas, especially of African mesic savannas. We have successfully met the objective of improving our understanding of the Bateke Plateau's savannas, focussing on the mechanisms that control tree carbon stocks, and the effects of fire seasonality and frequency on vegetation and biomass.

Savanna ecosystems have wide variations in ecosystem function, productivity, fire frequency and structure (Higgins et al., 2000, Sankaran et al. 2005). There are multiple factors and complex interactions determining savanna dynamics, making modelling their distribution and future extent under different climate change scenarios challenging (Sankaran et al., 2004 and Moncrieff et al., 2016). The Bateke Plateau is a unique savanna, with very low tree biomass despite its very high precipitation. The plots established as part of this thesis represent an extreme of high rainfall and low tree cover (Fig. 6.1), thus is an interesting case study of savanna dynamics. The plots are also located in a region that is very distant from other scientific savanna plots. For example, in the SEOSAW network (the largest plot network across the woodlands and savannas of southern Africa), the nearest inventory data to the Bateke is hundreds of kilometres away (Fig 6.2A). Additionally, in ForestPlots.net (Lopez-Gonzalez et al. 2009), the largest network of tropical forest plots, there is very limited data from savannas and no data collected for the Bateke Plateau (Fig 6.2B).

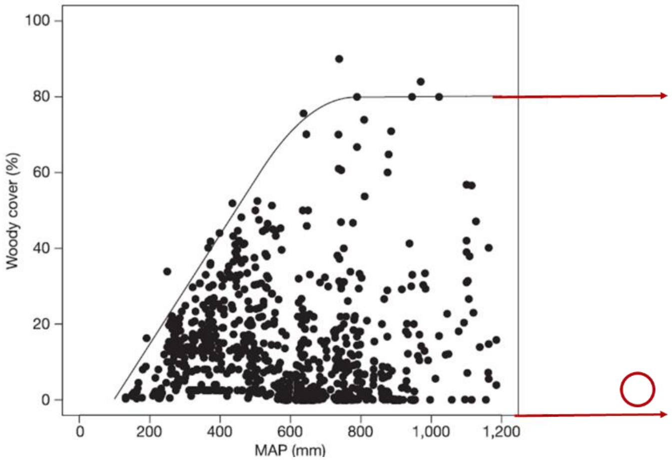


Figure 6.1. Change in woody cover of African savannas as a function of MAP (Sankaran et al., 2005). The Bateke plots (in red) are at an extreme of high precipitation and very low biomass.

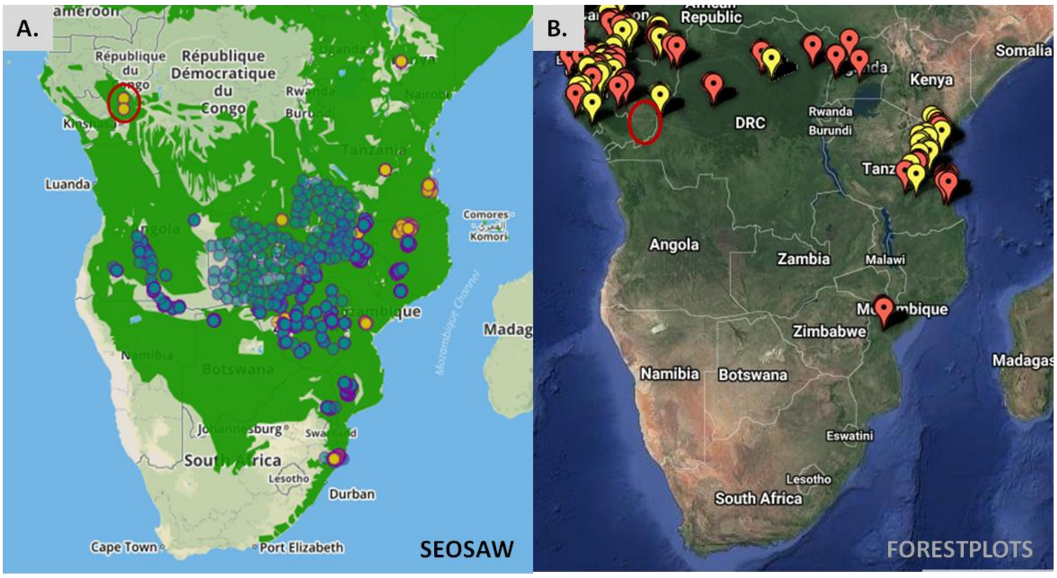


Figure 6.2. A. The SEOSAW plot network. The location of the plots presented in this thesis are circled in red. It can be seen that the nearest available plot data are hundreds of kilometres away. B. Forestplots.net., which largely contains plot data from closed-canopy forest. The Bateke Plateau is circled in red, and the data from this thesis will be added to the database shortly.

The plots sampled in this thesis will contribute to the field of savanna science, which has historically been poorly represented with experimental data, particularly in the high precipitation savannas of Central Africa. In chapter 3 I showed that the data presented in this thesis has important botanical value, as it contributes data to one of the areas least botanically known in the world and largely undersampled (Sosef et al. 2017). The data has already been used to show that the Bateke Plateau has floristic similarities with northern savannas, despite its relative isolation (Fayolle et al., 2018). The thesis also provides a literature review of past studies of the Bateke Plateau, mostly only published in French, thus a valuable resource for future researchers.

The experimental field data in this thesis is from very large plots (25 ha), by far the largest plots in the SEOSAW network. Data from large plots are particularly important for calibration of remote sensing data and for the study of spatial patterns in vegetation (e.g. Chapters 4 and 5). It provides guidance of the minimum size of plots required in this sparse savanna to effectively measure demographic rates, spatial variation, and for remote sensing studies. For example, in Chapter 5 these large-scale plots were used to measure carbon stocks in savannas in the Bateke Plateau, identifying that presently available pantropical biomass maps overestimate biomass in this landscape (Avitabile et al. (2016), Saatchi et al. (2011) and Baccini et al. (2012). The experimental design described here is designed as a long-term study, which will provide invaluable information for the study of changes in ecosystem structure, diversity, carbon storage, and tree demography. These plots are one of the few locations in African savanna that has been re-inventoried (dots in yellow in Fig 6.2A), contributing data required for demographic studies in savannas (e.g. Chapter 5).

Data from the Bateke Plateau fire experiment contributes to the knowledge acquired by previous fire experiments in savannas. I performed a unique and novel fire experiment, presenting and sharing an experimental protocol, including problems and caveats, which will benefit future experimental designs in savannas (Chapter 2).

6.8 - Concluding remarks

In this thesis, I investigated the main processes determining savanna vegetation dynamics in the Bateke Plateau. This ancient mesic savanna with high precipitation is climatically suitable for forest, but the nutrient poor sandy soils and high fire frequency maintain a low biomass state. This thesis has advanced our knowledge of species composition, patterns of vegetation heterogeneity, the determinants of woody demographics and cover, and carbon storage in the mesic savannas of the Bateke Plateau. The results are important for savanna ecology and for management in the Bateke Plateau, as well as driving forward basic scientific research in this understudied ecosystem. These results will also contribute to effectively model vegetation and carbon stocks savannas which will be important for predicting the impacts of future climate change.

6.9 - References

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