LATE HOLOCENE VEGETATION CHANGE IN NORTH-EAST NAMIBIA

Examining vegetation dynamics considering human land-use and environmental change

By Caitlin Dixon 2019

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Abstract

Local communities of north-east Namibia rely on natural resources for their livelihoods which has played and continues to play an influential role in the savanna ecosystem, although the degree to which people have impacted the regional vegetation is unknown. Long-term vegetation history can aid in conservation decisions by providing context to the current vegetation. Unfortunately, late-Holocene paleorecords of vegetation and climate change are virtually non-existent for north-east Namibia. Paleoecology proxies can determine long-term vegetation dynamics, particularly tree density, and determine the extent of natural and anthropogenic forcing on these changes. Three radiocarbon dated sediment cores were analysed using loss on ignition and mass spectrometry to determine organic and inorganic carbon content, and δ^{13} C values, respectively. A constrained hierarchical clustering (CONISS) was applied to these proxies to define distinct environmental periods. Two of the three cores suggest a more modern increase in tree density while the third core shows a rapid decline in tree density. Two of the cores suggest wetter periods between ca. 1000 - 500 BP and from ca. 300 BP. The oldest core spans the duration of the Holocene epoch and shows changes in hydrologic patterns and vegetation. There is evidence for two sites that past human resource harvesting has influenced the state of the modern ecosystems within the last 400 years, which has led to at least one of the sites showcasing typical 'bush encroachment' (i.e. invasion of woody plants). Additional proxies, such as pollen, fungal spores, and charcoal, would need to be taken into consideration in order to further explore the interaction between humans and vegetation in the region, and establish a comprehensive management plan for conserving vegetation in the region.

Introduction

Vegetation change has been extensively studied in African savanna biomes to determine the interacting roles of humans, herbivores, and climate on vegetation composition and structure. Most studies have focussed on recent (post 1950) change, though there are some paleoecological records (Burrough and Thomas, 2013). In spite of this, paleoecological data on north-east Namibia is almost non-existent in literature. One of the aims in paleoecological research is to establish long term trends in vegetation, fire, herbivory, climate, and land-use history, using proxies such as fossil pollen, stable isotopes, charcoal, and dung fungal spores.

Therefore, long-term trends can place the current state of the ecosystem into context and examine whether the ecosystem's current state falls within the range of expected variability, based on historic trends. Long-term data can aid in conservation management decisions by helping identify whether the current vegetation state is within natural variation, recovery, or degraded (Gillson, 2015). In order to create a comprehensive narrative of how the north-east Namibian savanna ecosystem has changed over time and which variables are responsible, reliance on savanna appropriate paleoecological proxy data is required to define trends and interpret changes.

North-east Namibia is an important conservation target given its centrality in the Kavango Zambezi – Transfrontier Conservation Area (KAZA-TFCA), the world's largest transfrontier conservation area which supports approximately half of Africa's African Elephant (*Loxodonta africana*) population (Lindsay *et al.*, 2017). Bwabwata National Park (BNP) is a protected area within the greater KAZA-TFCA with an additional role of supporting a population of approximately 5000 people, an atypical feature for a protected area which has resulted in BNP's management plan being celebrated for creating a space in which humans can co-exist with wildlife. BNP's current conservation management strategy is based on a survey of the flora, fauna, and people post-Namibian independence (1990). The timing of the survey came after the area had experienced rapid changes in land-use and fire regimes in a relatively short period of time.

The region has experienced four distinct land-use shifts: pre-1600 AD, natural resource harvesting (Khwe San communities); 1600 to 1940 AD, agro-pastoralism (Mbukushu, Lozi and Kololo empires, and colonial powers); 1940 to 1990 AD, military activity (South African National Defence Force); and 1990 AD to present, conservancies (Namibian independence to present). However, there is evidence that agro-pastoralists settled along the Okavango River from 1.5 to 2 ka (Mendelsohn, 2009). BNP has a complex pyrogeography (Humphrey, 2018) (i.e. interaction and feedback between society-culture, geophysical and biophysical aspects) and includes a shift from a past policy of fire suppression and prevention (1888 – 2005) to a policy of early burning from 2006 . Aside from institutionally mandated fire management, agro-pastoralism has also been linked to burning practices in Africa as a means of maintaining open grasslands and prohibiting bush encroachment (Sheuyange, Oba and Weladji, 2005).

North-east Namibia's vegetation is determined by numerous factors, such as topography, climate, substrate, fire, grazing and clearing (Burke, 2002). Burke (2002) suggests that except for clearing, these factors constitute natural determinants of savanna ecosystems; but the influence of humans on the region has made it increasingly difficult to differentiate between natural and human-altered ecosystems. As humans have existed in savannas for millennia savanna landscapes have been shaped through the interaction of both anthropogenic factors and natural determinants to create complex socio-ecological ecosystems (Marchant, 2010). Consequently, this region's vegetation is very dynamic, although there is a lack of understanding of the extent of these anthropogenic disturbances, such as changing fire regimes and land-use, and/or the degree to which climate has impacted the region (Sheuyange, Oba and Weladji, 2005). Furthermore, there has been a promotion for savanna conservation management to embrace flux over time and heterogeneity in space (Gillson and Duffin, 2007). A long-term perspective could greatly aid in understanding how the region's ecosystems have changed on a temporal and spatial scale while providing context to the modern ecological state.

Savanna biomes account for approximately c. 30% of terrestrial primary productivity (Grace et al., 2006) and are defined as mixed woodland-grassland ecosystems distinguished by sparsely dispersed trees resulting in open canopies and a continuous undergrowth, herbaceous layer consisting primarily of C₄ grasses. The ecological processes maintaining the dynamic relative abundance of trees and grasses are markedly complex (Bond, 2008). Fire frequency and intensity heavily regulate tree recruitment, which in turn influences the relative abundance of trees to grasses; and herbivory fulfils a similar and interacting role (Sankaran et al., 2005). These two mechanisms of disturbance are themselves further influenced by humans, who can manipulate both fire and herbivory, and environmental circumstances, for example changes in rainfall which will affect tree recruitment directly (February et al., 2013), and indirectly through its effects on biomass. Complex anthropogenic fire regimes are created through intentional burning and suppression of fire while natural fire regimes are influenced by environmental change such as temperature and rainfall (Bond, Midgley and Woodward, 2003). Herbivore abundance is influenced by humans through elimination by hunting and poaching, and the introduction of diseases (e.g. Rinderpest disease outbreak); as well as the introduction of livestock and establishment of protected areas. Climate can also regulate herbivore populations by influencing primary productivity of plants. Finally, another factor not to be overlooked is the influence of increasing CO₂ emissions, as some studies have

indicated that the phenomenon of "bush encroachment," the infringement of trees in areas that were once occupied by grasses, is linked to rising global CO₂ levels (Bond and Midgley, 2000). Given the ecological and historical complexity of savannas, a multi-proxy approach is required to identify which causal agent(s) is responsible for observed temporal changes, and to provide context for change over recent decades which may be due to the interacting effects of CO₂, climate and land-use change.

Sediment cores are useful geoarchives to reconstruct environmental and climatic change during the Holocene epoch and beyond (Dodd and Stanton, 1990). Coring involves the extraction of sediment from terrestrial, marine, lakes, or other wetland environments while maintaining the integral horizontal structure of the sediment. The logic behind this is that environmental material within the catchment zone gets transported through various processes, such as aerial or fluvial, and is deposited in sedimentary systems in sequential layers. The underlying assumption is that these layers reflect the state of the surrounding environment at the time in which they were deposited. Accumulation of these depositional layers allows the inference of the condition of the ecosystem at a given time. These sedimentary records can sometimes provide high-resolution proxy data, which can be sampled on a decadal scale, in order to interpret ecosystem condition alongside temporal related data such as land-use history and climate history. Fluvial deposits such as organic mud from perennial rivers, pan and lake sediments, and marine sediments have been noted for their potential to reconstruct the paleoclimate conditions in Namibia (Heine, 2005).

Studies have shown that changes in relative tree-grass abundance are a prominent feature of savanna biomes (Cuni-Sanchez *et al.*, 2016). Changes in relative tree-grass abundance have been customarily inferred from stable isotope analysis (McClaran and McPherson, 1995; Gillson, Waldron and Willis, 2004; Beerling and Osborne, 2006). Savanna grasses predominantly use the C₄ photosynthetic pathway (Sage, 2004) while trees and shrubs use C₃. The divergent nature of their carbon fixing mechanism makes it possible to use stable isotopes to infer changing relative abundances of C₃ and C₄ plants. In paleoecology, δ^{13} C values act as intrinsic tracers to determine changes in C₃ and C₄ relative plant abundances. δ^{13} C is an isotopic signature which is a measure of the ratio between ¹³C and ¹²C. ¹³C is an isotope constituting 1.1% of all naturally occurring carbon. The different photosynthetic pathways assimilate atmospheric ¹³C to different extents which results in C₄ plants having a δ^{13} C value between -16 and -10‰ and C₃ plants -33 and -24‰, relative to a standard. The

standard for δ^{13} C analyses is commonly the cretaceous marine fossil, *Belemnitella americana*, otherwise known as Pee Dee Belemnite. The sample had a high ¹³C:¹²C ratio which gave rise to the δ^{13} C value of zero (Brand *et al.*, 2014). Analysing δ^{13} C values across time functions as an appropriate proxy for changing tree-grass relative abundance in savanna systems.

Loss on ignition (LOI) is a widespread technique to determine total organic carbon content (TOC) and total inorganic carbon content (TIC). LOI involves the sequential heating of samples to specified temperatures for a specific duration in order to relate weight loss to specific fractions within the sample, specifically water content, organic carbon and inorganic carbon (carbonate). TOC can be used as a variable to measure the input flux of organic material with this being a potential indicator of moisture availability and levels of disturbance (Heiri, Lotter and Lemcke, 2001; Scott, Holmgren and Partridge, 2008). These events can also be documented by analysing the physical characteristics of the sediment core such as texture, grain size, and composition. LOI and lithology, the physical characteristics of the sediment, can be used as proxies to understand paleoclimate conditions and hydrologic changes on a temporal scale (Berglund, 1986).

Paleoecology proxies cannot be associated with the timing of events without the establishment of a robust chronology. Therefore, age-depth models are essential tools for associating proxies with time (Blaauw, 2010). There are several methods for constructing an age-depth model, although the different methods share a foundational assumption: that an increase in sediment depth is related to an increase in time, i.e. the deeper the sediment the longer ago the deposition took place. Input values for the age-depth model are established from dating elements within segments of the sediment core. The dating method is dependent on the type of environment the sample is extracted from and the age of the sample. The most common dating method for savanna systems is radiocarbon dating. Paleoclimate studies in Namibia and surrounding sites, with an emphasis on precipitation, often lack robust chronologies (Heine, 2005). This means that paleoclimate reconstructions do not examine that proxy records may represent either a general trend (millennia), a short period (decadal to centennial), or extreme events (days, weeks or months). Thus, constructing a reliable age-depth model allows for defining high time resolution which is essential for interpreting changes in paleoecological proxies and in comparing datasets between sites.

In order to achieve a long-term perspective of vegetation dynamics in north-east Namibia, terrestrial sediment cores will be sampled:

1) To reconstruct changes in tree density over time based on $\delta^{13}C$ and Accelerator mass spectrometry dates, and

2) To interpret the influence of environmental change, climate and/or land-use, based on sediment lithology and environmental history.

Methods



Description of study site and coring

Figure 1: Map of southern Africa (top) and the location of the three coring sites (bottom).

The study is situated in north-east Namibia with sites across the Kavango East and Zambezi Regions (Figure 1). Even though Namibia is the driest country in Sub-Saharan Africa, its north-east region experiences the highest mean annual rainfall for Namibia reaching > 600 mm.a⁻¹ (Heine, 2005), as well as less evaporation and warmer winters (Mendelsohn and Roberts, 1997c). This allows for the support of a range of ecosystems including: wetland systems, floodplains, and savanna-woodlands. The vegetation is characterised by broadleaf tree-shrub savanna biomes, encompassed within the southern limit of the Miombo ecoregion. Three permanent rivers flow through the region (from West to East): the Okavango River (with additional water supply from a confluence with the Cuito River), Kwando River, and Zambezi River. Each of these river systems arise in northern countries and belong to separate catchment areas - though, all these rivers can also connect to one another if water levels are sufficiently high (Mendelsohn and Roberts, 1997b).

Sites for coring were identified prior to extraction as wetland areas not connected to main river channels with suitable conditions for organic matter accumulation. Potential sites were probed to examine the consistency and depth of organic sediment, and the degree of sediment consolidation. Coring commenced if the sediment was predominantly dark, organic, clay rich mud and deeper than 50 cm. Coring did not occur if the material mainly consisted of gravel and/or river sand, as this medium does not preserve organic sediment to a great extent. Furthermore, paleoecological landforms relevant to the sites include isolated water basins adjacent to the perennial river systems in the floodplain zone (Kwando and Okavango), and lake sediments (Lake Liambezi). Coring was done during the dry season to ensure that the water bodies contained water perennially, which increases the likelihood of anoxic conditions for organic material accumulation over time. A Russian corer was used to extract the cores which were subsequently wrapped in aluminium foil and cling-film in order to limit microorganism growth by creating anaerobic conditions. Coring was carried out by Associate Professor Lindsey Gillson and Dr. Glynis Humphrey in October 2014. The cores (Table 1) were transported to the University of Cape Town and preserved in a refrigerator at ~4°C.

Table 1: List of sedimentary cores obtained from north-east Namibia, including details of the locality, core name, vegetation community and average annual rainfall (Mendelsohn and Roberts, 1997a), coordinates, sample depth, and estimated diameter of basin.

Location	Core name	Vegetation	Average	Latitude	Longitude	Depth	Estimated
(region)		community	annual			of	basin size
			rainfall			core	(m/diam)
			(mm)			(cm)	
Zambezi	Lake	Floodplain	600-650	-17.938461	24.376695	86	2000
	Liambezi						
Zambezi	Mukolo	Floodplain/	550-600	-17.877598	23.341643	87	80
		Riverine					
		woodland					
Kavango	Jackelberry	Floodplain/	550-600	-18.152061	21.712346	63	100
East		Riverine					
		woodland					

Lithology

Sediments of all three cores were described using an adapted Troels-Smith system by Kershaw (1997) and the Munsell Soil Colour Chart. The results were illustrated as a cross section of each core using the lithology plotting function of Tilia Software (Grimm, 1991) with the default Troels-Smith symbols.

Loss on ignition (LOI)

LOI was used to determine bulk density, dry weight, total carbon content (TOC), and total inorganic carbon content (TIC). Sampling was done by incrementally extracting approximately 2 cm³ of material from the sediment cores. Samples were placed in pre-weighed porcelain crucibles, weighed, dried overnight at 100°C, and weighed again. The samples were then heated to 550°C in a muffle furnace for four hours, left to cool, and weighed to determine TOC as a percentage of dry weight. Similarly, the samples were heated to 950°C for two hours to determine TIC as a percentage of dry weight (Heiri, Lotter and Lemcke, 2001). If material was too unconsolidated and collapsed when attempting to sample,

then these depths were not sampled which extends to the $\delta^{13}C$ analysis as these relied on LOI sub-samples.

Chronology

Chronologies were established using accelerator mass spectrometer radiocarbon dating. Two radiocarbon dates were determined for from Mukolo and Jackelberry, and three for the core from Lake Liambezi using organic sediment/gyttja material for dating. Samples were sent to Beta Analytic Inc, Miami, Florida. The basal radiocarbon dates for the cores from Mukolo and Jackelberry were analysed by Chrono, Queen's University Belfast, Northern Ireland in 2014. Uncalibrated dates were reported BP (before present) where the "present" is conventionally recorded as 1950 AD.

Age-depth models were constructed using the SHCal04 radiocarbon calibration curve (Hogg *et al.*, 2013) using the Bacon package in R (Blaauw, 2011). The SHCal04 radiocarbon calibration curve was used to account for the samples being in the southern hemisphere. Bacon utilises Bayesian statistics to calculate age-depth relationships.

An age-depth model for Lake Liambezi could not be constructed due to two dates (denoted by '*' in Table 3A) contradicting the underlying assumption that dates should appear in stratigraphic order. The age reversal is most likely the result of bioturbation of the sediments or high-intensity fluvial processes mixing younger and older sediments. The calibrated basal depth for the core from Lake Liambezi (Table 3A) was included to provide some context, and was established by Beta Analytic Inc. using a high probability density range method (Ramsey, 2009) and the SHCal04 radiocarbon calibration curve.

$\delta^{13}C$

Soil samples for δ^{13} C analysis were prepared following standard mass spectrometry methods. Samples were dried overnight at 40°C, rootlets removed to prevent influence of modern material on isotope analysis, and ground to homogeneity. A preliminary analysis was conducted by sub-sampling ten samples from the core from Mukolo to determine whether samples needed to be acid-washed in order to remove carbonates. The acid-washed subsamples were prepared by initially soaking the samples in 1 M HCl overnight and then following the standard protocol. The results indicated that there was no significant difference between δ^{13} C values of acid washed and non-acid washed samples. Subsequently, acidwashing was discontinued which was extended to the other cores as carbonate content, TIC from LOI, was similar across all three cores (Figure 1A).

Sediment samples were weighed in tin cups to an accuracy of 1 μ g using a Sartorius M2P electronic microbalance. The cups were compressed to enclose the sample. Samples were combusted in a FLASHTM 2000 organic element analyser and the gases passed to a DELTA VTM Plus isotope ratio mass spectrometer via a ConFlo IV gas control unit. All three items are made by Thermo Fisher Scientific Inc., Bremen, Germany. The in-house standards used were "Australian National University (ANU)" sucrose, Nastd (dried *Tropaeolum sp.* leaves), and Acacia (dried *Acacia saligna* leaves). Stable carbon isotope analyses were conducted at the Stable Light Isotope Laboratory at the Department of Archaeology, University of Cape Town.

Organic carbon content is known to decrease along the vertical sediment profile due to microbial activity, which results in δ^{13} C enrichment between -1.71‰ and -2.3‰. The degree of this enrichment can be modelled using the Rayleigh enrichment equation:

$$\delta^{13}C \ (modelled) = \ \delta^{13}C_s + \left(\ln\left(\frac{\partial C_1}{\partial C_s}\right)\right) * \epsilon$$

Where $\delta^{13}C_s$ is the δ^{13} C of the sample at 0 cm (surface), OC_1 is the TOC at depth 1, OC_s is the TOC at 0 cm (surface), and ϵ is the Rayleigh enrichment factor, which is -2‰ for this study as this is the accepted value for savanna-grassland systems (Wynn, Bird and Wong, 2005). Significant differences between modelled δ^{13} C and observed δ^{13} C can be interpreted as differences in C₄ and C₃ plant inputs as opposed to microbial breakdown of organic matter. To test whether the observed δ^{13} C values are a result of microbial enrichment and not a true isotopic signature of the environment, a paired t-test was conducted to establish whether there was a significant difference between modelled and observed δ^{13} C (Gillson, 2015).

Data analysis

The zones were determined by a hierarchical clustering stratigraphically constrained CONISS linkage method based on the TOC and δ^{13} C datasets using the Bray-Curtis distance method. The number of significant zones was determined by using the "broken stick" model. All analyses were performed using the 'vegan' (Oksanen *et al.*, 2019) and 'rioja' package (Juggins, 2019) available in RStudio (RStudio Team, 2019). The zones are numbered in ascending order down the length of the core.

Results

Chronology

Based on the nine radiocarbon ages, the sediments in north-east Namibia accumulated during the late Holocene. The Bacon age-depth model for Mukolo contained all the radiocarbon ages within the 95% confidence interval (Figure 2). The basal depth has a mean calibrated age of 836 BP (Figure 2; Table 1A). The Bacon age-depth model for Jackelberry contained all the radiocarbon ages within the 95% confidence interval (Figure 3). The basal depth has a mean calibrated age of calibrated age of 985 BP (Figure 3; Table 2A).

The calibrated ages for Mukolo and Jackelberry are clustered. The calibrated ages for the core from Mukolo are between ca. 800-500 BP (Table 1A), and ca. 1000-500 BP for the core from Jackelberry (Table 2A). Given that the radiocarbon age determinations were conducted on organically rich sediment (TOC in Figure 4 and 6) and are assumed to have been deposited under waterlogged conditions; Nash, Meadows and Gulliver (2006) interpret these age clusters as periods of increased moisture availability during which microbial activity increased and/or the duel effect of reduced microbial activity and decreased fire frequency or cooler dry season fires. If all of the above assumptions are met, this would potentially indicate a period of greater moisture availability from ca. 500-1000 BP.



Figure 2: Bayesian age-depth model for the core from Mukolo. Upper panel: (left) Markov Chain Monte Carlo iterations that calculate sedimentation rates, post-analysis (shaded curve) and prior (green line) estimates for sedimentation rates, and (right) post-analysis and prior estimates for auto-correlation of sedimentation rates. Bottom panel: age-depth model with 95% confidence intervals (broken lines), probability distribution of calibrated ¹⁴C ages (shaded grey), and the calibrated ¹⁴C ages used to construct the model (blue).



Figure 3: Bayesian age-depth model for the core from Jackelberry. Upper panel: (left) Markov Chain Monte Carlo iterations that calculate sedimentation rates, post-analysis (shaded curve) and prior (green line) estimates for sedimentation rates, and (right) post-analysis and prior estimates for auto-correlation of sedimentation rates. Bottom panel: age-depth model with 95% confidence intervals (broken lines), probability distribution of calibrated ¹⁴C ages (shaded grey), and the calibrated ¹⁴C ages used to construct the model (blue).

Mukolo core

The CONISS and broken stick model identified five significant zones for the core from Mukolo (Figure 4; Figure 3A). Zone 1 (0-7 cm; -64 to 147 BP), zone 2 (7-9 cm; 147-167 BP), zone 3 (9-13 cm; 167-207 BP), zone 4 (13-22 cm; 207-293 BP), and zone 5 (22-85 cm; 293-820 BP) (dates from Figure 2).

Mukolo is characterised by a layer of fine sand from 0-8 cm, and dark brown organic mud from 8-87 cm. The last layer, 63-87 cm, contained pockets of fine sand. Zone 1 contained the lowest TOC with 0.21% (3 cm) compared to the highest TOC in zone 3 with 18.15% (10 cm), a 17.94% difference. A 9.94% decrease in TOC was observed from 21-10 cm. The TOC of the remaining length from 21-87 cm fluctuated within a 4.16% range between 3.34-7.50%. The modelled Rayleigh enrichment δ^{13} C values and observed δ^{13} C values are significantly different for Mukolo (t = 3.667, df = 53, p-value < 0.001; Figure 2A). δ^{13} C values fluctuate between -20.48 and -22.51‰ across zones 5 to 3 (836-197 BP) with an average value of -21.67‰, indicating a stable predominantly C₃ system. Thereafter, δ^{13} C values decrease substantially to -25.15‰ in zone 1, a shift towards a dominant C₃ system, and then increase to -23.09‰ during a more modern period.



Figure 4: Lithology and stable isotopes diagram for the core from Mukolo. TOC is calculated as percentages of dry weight (%) of sediment samples from the LOI analysis. δ^{13} C is reported in parts per thousand (per mil, ‰). The results of the CONISS analysis (far right) are displayed as well as the ecological zones represented by the broken horizontal lines.

Lake Liambezi core

The CONISS and broken stick model identified five significant zones for the core from Lake Liambezi (Figure 5; Figure 4A). Zone 1 (3-18 cm), zone 2 (18-22 cm), zone 3 (22-59), zone 4 (59-65 cm), and zone 5 (65-84 cm).

Lake Liambezi is characterised by dark brown mud with some fine sand, which is absent from 59-79 cm. The top most layer from 0-4 cm contained fragments of gastropod shells. Bioturbation is evident from 60-70 cm due to distinctive marbling of the dark brown mud with lighter coloured silt and clay which is most likely the result of a flooding event. Additional evidence of this flooding event comes from the peak in TOC in zone 4. For the remainder of the core, TOC fluctuated from 3-59 cm within a 1.8% range between 4.1-5.9% and reached the lowest value from 75-83 cm between 3.5-3.9%.

The modelled Rayleigh enrichment δ^{13} C values and observed δ^{13} C values are significantly different for Lake Liambezi (t = 8.083, df = 51, p-value < 0.001; Figure 2A). δ^{13} C values fluctuate between -21.60 and -19.46‰ in zone 5. Zone 4 and 3's values fluctuate between - 19.44 and -17.63‰ with an average value of -18.69‰, indicating a stable predominantly C₄ system. A shift towards a more balanced C₃ and C₄ system starts in zone 2 with a decrease in δ^{13} C values. Finally, δ^{13} C values decline from zone 2 to 1 with values between -22.63 and -20.79‰.



Figure 5: Lithology and stable isotopes diagram for the core from Lake Liambezi. TOC is calculated as percentages of dry weight (%) of sediment samples from the LOI analysis. δ^{13} C is reported as parts per thousand (per mil, ‰). The results of the CONISS analysis (far right) are displayed as well as the ecological zones represented by the broken horizontal lines.

Jackelberry core

The CONISS and broken stick model identified five significant zones for the core from Jackelberry (Figure 6; Figure 5A). Zone 1 (3-13 cm; 126 to 307 BP), zone 2 (13-16 cm; 307-361 BP), zone 3 (16-17 cm; 361-379 BP), zone 4 (17-28 cm; 379-572 BP), zone 5 (28-44 cm; 572-750 BP), and zone 6 (44-62 cm; 750-971 BP) (dates from Figure 3). Jackelberry is characterised by lightly coloured layer of mud from 0-2.5 cm, dark brown mud from 2.5-27 cm, a high silt fraction layer from 27-44 cm, and dark brown mud with an increasing fine sand fraction and decreasing silt fraction from 44-63 cm. Plant material was present from 0-2.5 cm.

TOC remained between 3.5-5.6% 3-28 cm although there was a spike at 16 cm to 19% which could be the result of the oxidation of a large piece of modern plant material, such as roots. TOC increased from 28-56 cm to be between 6.5-11.8%.

The modelled Rayleigh enrichment δ^{13} C values and observed δ^{13} C values are significantly different for Jackelberry (t = 4.689, df = 39, p-value < 0.001; Figure 2A). The means for the observed and modelled δ^{13} C values were -20.1‰ and -18.8‰, respectively. δ^{13} C values gradually decline from zone 6 and 5 to zone 4 and 3. The transition from zone 2 to 1 is marked by a rapid shift towards a predominantly C₄ system.



Figure 6: Lithology and stable isotopes diagram for the core from Jackelberry. TOC is calculated as percentages of dry weight (%) of sediment samples from the LOI analysis. δ^{13} C is reported as parts per thousand (per mil, ‰). The results of the CONISS analysis (far right) are displayed as well as the ecological zones represented by the broken horizontal lines.

Discussion

Changes in woody vegetation cover

The core from Mukolo, located along the Kwando River outside of BNP, covers a period of 884 years. The coring site is located on the boundary of the Okavango-Kwando grassland and teak, *Baikiaea plurijuga*, shrubland vegetation units. The Okavango-Kwando grassland vegetation unit is characterised by lawns of the C₄ grass *Cynodon dactylon*, and clusters of *Echinochloa stagnina*, *Echinochloa pyramidalis* and *Vossia cuspidate*. Woody species are scarce except in areas with low grass percentage coverage (1-3%) and include *Rhus quartiniana*, *Acacia hebeclada*, and *Sesbania sp.*. The teak shrubland vegetation unit is the deforested state of the teak woodland vegetation unit. The stable isotope data from Mukolo suggest a gradual increase in C₃ plant representation from 1743 AD (207 BP) to the present after an extended period (613 years) of relatively stable δ^{13} C values between ca. -22 and -24‰.

The increase in C₃ representation indicated in the uppermost levels of the stable isotope record from 1753 AD could be a result of several anthropogenic factors. Teak shrubland is characterised by a dense layer of shrubs and small trees with only a few large Zambezi teak and camelthorn, Vachellia erioloba, trees. Zambezi teak has been extensively logged due to its status as a valuable hardwood resource for use in railway sleepers, construction and furniture. Mendelsohn and Roberts (1997a) noted that fires poses a threat to teak woodlands as a result of frequent fires burning young trees and sometimes damaging older trees leading to hardly any regeneration of Zambezi teak trees. They speculate that deforestation has opened teak woodlands sufficiently enough for anthropogenic and natural fires to influence the vegetation dynamics. This results in a shift from teak woodlands to teak shrubland which are characterised by a uniform layer of fire-resistant thicket species. Indeed, bush encroachment (i.e. the invasion of areas by woody species) is a widespread issue in north-east Namibia (Sheuyange, Oba and Weladji, 2005). Changes in fire regimes as a result of purposeful burning, such as stimulating the growth of fresh grass for grazing, and accidental fires probably became more frequent following the introduction of traditional agro-pastoralist systems ca. 1800 BP (Smith, 1992).

Given the current state of the teak shrubland, the increase in C₃ representation is appears to be consistent with bush encroachment. This may be due to agro-pastoralist activities as the establishment of the first Lozi Empire in the region, 1600s and 1700s, coincides with the increase in C₃ representation. The first Lozi Empire was followed by the Kololo Empire (1820s to 1864) and then the second Lozi Empire from 1864-1890. People from both empires practised subsistence agro-pastoralism (Colpaert, Matengu and Polojärvi, 2013). The precolonial period was characterised by traditional authorities making and enforcing laws that either prohibited or promoted forestry practices relating to the use of natural resources (Colpaert, Matengu and Polojärvi, 2013). Grazing intensity has been linked to bush encroachment (Weber, Moloney and Jeltsch, 2000). Thus, more frequent fires and intensified grazing probably contributed towards bush encroachment. Additionally, the theory of elevated CO₂ levels favouring C₃ woody species would contribute towards a more pronounced C₃ δ^{13} C value. Furthermore, the grass Cynodon dactylon is a valuable resource for thatching of houses, and accounts for up to 87% of homes using thatching for roofing (Central Statistics Office, 1994). Removal of this C₄ species would also decrease δ^{13} C values. Increases in tree density, despite teak deforestation, are consistent with the occurrence of bush encroachment which is corroborated by the establishment of additional people in the region.

The core for Jackelberry, located along the Kavango (Okavango) River inside a BNP core conservation area, covers a period of 1035 years. The coring site is located on the boundary of the Okavango-Kwando valley woodland and teak woodland vegetation units. Given that both vegetation units are predominantly composed of tree species, a decline in C_3 representation from 1643 AD (307 BP) from the stable isotope record is unexpected as it is inconsistent with the current vegetation.

Similarly to Mukolo, the timing suggests anthropogenic factors affected vegetation, but unlike Mukolo, there was a decline in C_3 representation. Deforestation of the teak woodland is most likely a contributing factor. Mendelsohn and Roberts (1997a) note that deforestation of teak woodlands can lead to not only teak shrubland but also open grassland. They do not explore the mechanisms that govern whether the removal of teak results in a grassland or teak shrubland. The Okavango-Kwando valley woodland vegetation unit is characterised by tall, diverse tree species and hosts some of the greatest diversity of animals and plants in the region (Mendelsohn and Roberts, 1997a). Yet, its vegetation is probably one of the most threatened vegetation units due to utilization by herbivores, both livestock and wildlife, as well as the loamy soils which present some of the best potential for growing crops in the region. Further upstream, one can find the degraded state of this vegetation unit which is the Okavango valley fields and shrubland vegetation unit. The degraded state is the result of heavy exploitation of vegetation within the Okavango River valley. This vegetation unit is composed of annual grasses, such as *Dactyloctenium giganteum* and *Urochloa brachyura*, as well as shrubs, weeds, and pioneer species. Given that most agro-pastoralists settled along the Okavango River course (Mendelsohn, 2009), a similar exploitation of woodland vegetation could have occurred resulting in predominantly C₄ grasses. The current vegetation shows a higher tree density, 16 to 30% cover teak, compared to grass, 1-5% cover *Cynodon dactylon*.

Increasing input from C₄ sedges may have contributed towards C₄ δ^{13} C values. Nash, Meadows and Gulliver (2006) conducted a Holocene paleoecology study along the Okavango River with coring sites ca. 30-80 km downstream of Jackelberry. They identified a distinct shift from grass to sedges within the last thousand years up to 200 BP. The most prominent sedges in the region of their study are C₄ sedges such as *Cyperus papyrus* and *Pycreus* nitidus. They hypothesised that this shift is most likely the result of increased grazing and/or burning, therefore anthropogenic. Sedges are not listed in the Okavango-Kwando valley woodland vegetation unit but are listed in the Okavango-Kwando grassland vegetation unit. This could potentially mean that the vegetation first shifted towards a state that resembles the Okavango-Kwando grassland vegetation unit after 1643 AD, and then subsequently shifted towards the modern state of Okavango-Kwando valley woodland. The vegetation composition before the sedge shift is also unknown. Nash, Meadows and Gulliver (2006) determined that the shift was from grass to sedge dominance. The timing of the final shift towards modern vegetation is unknown, as δ^{13} C values could not be determined for the uppermost layers due to difficulties when sampling unconsolidated material. Assuming that the results from Nash, Meadows and Gulliver's (2006) study extend to this region, a shift from Okavango-Kwando valley grassland to Okavango-Kwando valley woodland vegetation could be evidence of bush encroachment. Knowing when this shift towards the more woody vegetation unit occurred would be useful as this could be used alongside the stable isotope data of the core from Mukolo to interpret the drivers of bush encroachment as they share similar land-use histories and vegetation units (Mendelsohn and Roberts, 1997a).

The core from Lake Liambezi, located in the Zambezi region, covers a period from 18916 BP to the present. The coring site is located in the Chobe swamp grassland vegetation unit which is characterised by *Hyperthelia dissoluta*, *Hyparrhenia hirta*, *Setaria sphacelate*, and *Loudetia simplex*. Woody vegetation types are scarce, except for widespread, small knolls of *Diospyros lyciodes*. Additional vegetation includes, reed swamp species *Phragmites mauritianus* with patches of *Typha capensis*, both of which are C₃ photosynthetic species (Jones, 1988). The stable isotope data from Lake Liambezi suggests a gradual increase in C₃ representation after a period of predominantly C₄ plants. The timing of these shifts cannot be deduced because a chronology could not be developed for this sediment core, probably due to repeated inundation and drying of the site.

Lake Liambezi has experienced irregular water levels in recent history which has resulted in changes to land-use and subsequently vegetation. Currently, Lake Liambezi is classified as an open water system, yet maps prior to 1950 only show evidence of a swamp and not an open water body. The only other evidence that the lake contained water prior to this was in 1879 (Mendelsohn and Roberts, 1997b). Post 1950, an open water system was created for agricultural purposes through intensive burning of accumulated organic matter (Seaman et al., 1978). Timberlake (2000) concluded that the drying out of the lake in the early 1980s was attributed to climatic changes and not a result of anthropogenic factors. Decreased water levels and weaker flooding events resulted in utilisation of the area for grazing and cultivation (Mendelsohn and Roberts, 1997b; Colpaert, Matengu and Polojärvi, 2013). Removal of grass by these processes could have resulted in bush encroachment by species such as *Diospyros lycioides*, which could also be influenced by elevated CO₂ levels. Additionally, Lake Liambezi became invaded by Salvinia molesta in the late-1970s due to poor wastewater management resulting in eutrophic conditions (Schlettwein and Bethune, 1991). These processes could have acted synergistically to decrease grass abundance while increasing C₃ representation. However, due to the fact that an age-depth model could not be constructed, these theories are based on the assumption that the top layers of sediment reflect more recent periods in time.

Changes in climatic and hydrologic conditions

Several paleoecology studies have been focused on central southern Africa producing a comprehensive Holocene paleoenvironmental and paleoclimate dataset. Burrough and

Thomas (2013) analysed and reviewed 49 studies of which twelve are within the Mega-Kalahari sand sea, in which north-east Namibia is situated. The review concluded that present day and late-Holocene central southern African conditions are relatively stable compared to early- and mid-Holocene conditions and postulate that the onset started around 2 ka. Four studies from a group of eight that were closest to north-east Namibia indicated a period of wetter conditions from 2-1 ka. However, the eight studies closest to north-east Namibia do not have robust data from 1-0 ka, and therefore, the paleoclimatic conditions for north-east Namibia over the last 1000 years remain unknown.

The radiocarbon dates for the cores from Mukolo and Jackelberry suggest a period of wetter conditions from ca. 500 to 1000 BP. These results are in phase with the paleoenvironmental sequence from Drotsky's and Bone caves which indicates a wetter period between 1.6 to 0.5 kyr (Burney, Brook and Cowart, 1994). Chase et al. (2009) used sensitive paleoenvironmental proxies from the central Namib Desert to examine Holocene environmental change in the region. They found that after the end of the Little Ice Age (350-550 BP) a wetter period started around ca. 300 BP. The increase in TOC for the core from Mukolo, which suggests an increase in moisture availability, is in phase with this result as the increase starts at 293 BP. Hypothetically, if the results from the core from Jackelberry did indicate a shift towards C₄ sedges, then this could indicate a wetter period from 307 BP - as C4 sedges, such as Cyperaceae, require wetland conditions (Stock, Chuba and Verboom, 2004). However, the LOI results do not indicate an increase in moisture availability, as the TOC values remain relatively stable before and after the δ^{13} C shift. Interestingly, the Mbukushu leaders in the region were sought out by non-native people for their "rain making" abilities during the 1800s (Mendelsohn and el Obeid, 2003), as the area they inhabited was considered to receive more rainfall than surrounding regions. If there was an increase in moisture availability during this period it has not been preserved in the sediment. As stated previously, Nash, Meadows and Gulliver (2006) concluded that the shift to sedge dominance was probably not related to climatic changes. Although, the climate signals from Mukolo and the Chase et al. (2009) do suggest that ca. 300 BP is marked by a transition to a wetter period.

The LOI results of the core from Lake Liambezi suggest changes in the paleohydrology of the lake system. Reversals in the radiocarbon dates, and mixing of sediments identified from the physical description of the core suggest that bioturbation took place. The aftermath of the bioturbation event, most likely a flood suggested by the increase in TOC, led to a reduction in tree density as suggested by the stable isotope data. Flooding events and waterlogged soils restrict the growth of woody species due to their root systems intolerance for inundated soils. Consequently, floodplains associated with the rivers (Okavango, Kwando, Chobe etc.) are dominated by C₄ grasslands. The grass species is dependent on the frequency of flooding events (Mendelsohn and Roberts, 1997b).

Management implications

The soil erosion identified from the lithology of the core from Mukolo is of concern. Teak woodlands are not only useful for humans, they also protect fine Kalahari sands, *arenosols*, from soil degradation (Mudekwe, 2004). The presence of *arenosols* in the modern sediment layer suggests that soil erosion is prevalent. There could be another explanation for the deposition of fine sands. There are two types of soils found along rivers in the region. Firstly, sediments deposited during floods are called *fluvisols* which are a mixture of silt, clay, and fine sand. Secondly, *anthrosols* are a mixture of *fluvisols* and *arenosols* created through continuous ploughing of the soil (Mendelsohn and el Obeid, 2003). *Anthrosols* contain relatively low nutrients. Both scenarios indicate that soils have been degraded. Mendelsohn and Roberts (1997a) suggests that conservation resources should not be allocated to degraded teak woodlands, such as teak shrubland, due to the nutrient poor soil and bush encroachment.

Two common methods for managing bush encroachment include changing fire intensity and frequency (Archibald, 2016) and managing populations of large mammals, including domestic livestock and wild animals (Osborne *et al.*, 2018). Using fire to manage the bush encroachment around the Mukolo site sounds counterintuitive given that changes in the fire regime were hypothesised to result in the degraded teak woodland in the first place (teak shrubland) (Mendelsohn and Roberts, 1997a). A new method is creating 'firestorms', which are intense crown-fires (Archibald *et al.*, 2017). These have the capacity to clear heavily bush-encroached areas, if the goal is to re-establish the teak woodland - as removing the shrub layer might not be sufficient to allow for Zambezi teak recruitment (Piearce, 1985).

Teak woodlands have been degraded through extensive logging and human disturbance. The Zambian teak is currently listed as Near Threatened with threats to the species listed as logging and fire, which has resulted in the species being allocated protected status in Namibia (World Conservation Monitoring Centre, 1998). Management approaches for conserving teak

woodlands are split between natural and artificial regeneration (Piearce, 1985). Natural regeneration requires large mammals, such as elephants and buffalo, to trample and uproot shrub species while burying Zambian teak seeds and providing manure (Mitchell, 1961). The reduction in mammal populations has been identified as a possible driver in the decline of natural regeneration of Zambezi teak (Mitchell, 1961). Hunting but more significantly the rinderpest disease outbreak in 1886 have been established as the main drivers behind mammal reduction and subsequently reduced Zambezi teak regeneration (Wood, 1986). Therefore, shrub density has increased and Zambezi teak recruitment has declined. Artificial regeneration is a costly process and, due to the slow growth rate of Zambezi teak, requires 80 – 100 years to grow to a reasonable timber size of 30 cm (Piearce, 1985). This slow growth rate means that restoring teak woodlands would require a long-term management programme. In summary, restoring the teak woodland around this site presents staggering challenges and it is strategic to target existing teak woodlands.

The site for Jackelberry is currently a conservation priority due to the intact nature of the teak woodland. Intact teak woodland has been identified as a conservation target in north-east Namibia (Mendelsohn and Roberts, 1997a). The core from Jackelberry is located within the Buffalo Core Area a part of BNP. This core area is earmarked for additional conservation measures that control tourism and supplementary protection. The effect of CO₂ fertilisation as a driver of bush encroachment should be taken into account when monitoring this region. In order to maintain the teak woodland state within this region, it is important to identify the drivers and consequences of Zambezi teak reduction at the site surrounding Mukolo as indicators of additional, appropriate management intervention.

Further research

A multi-proxy approach would greatly benefit interpretation of changing tree density, climatic changes, and the regions sensitivity to human disturbance. Pollen would help to identify which families/genera are responsible for the observed changes in δ^{13} C. Pollen analysis could help identify whether C₄ sedge species have been present in the site from Jackelberry, which would have implications for the interpretation of vegetation change around the site. Macro- or microcharcoal can be used to reconstruct fire regimes and potentially link them to human activities. Charcoal and pollen proxies would be useful in further understanding how teak woodlands have been degraded over time. Furthermore, dung fungal spores can help understand the influence of herbivory on the vegetation, and extent and timing of agro-pastoralism in the region.

Concluding remarks

Contextualising current vegetation using long-term data helps facilitate the understanding of the drivers of change. The isotopic profiles and current vegetation for the sites suggests that bush encroachment is occurring throughout north-east Namibia. Bush encroachment has implications for conservation management decisions – as the biodiversity loss from homogenisation of vegetation communities impacts the provisioning of ecosystem services, both intrinsic and extrinsic. It is unclear whether these changes in tree density are purely from anthropogenic factors or climatic forcing, or an interaction between the two. This study's main objectives were exploratory; but the results suggest that management interventions are required to prevent further bush encroachment in the region. Further research using additional paleoecological proxies could aid in intervention strategies for bush encroachment.

Appendix

Lab no.	Depth (cm)	14 C Age $\pm 1\sigma$ yr (BP)	Mean calibrated age (BP)	Material
Beta - 525651	46	620 ± 30	525	Organic Sediment/Gyttja
Beta - 525652	60	590 ± 30	614	Organic Sediment/Gyttja
UBA - 30919	87	654 ± 28	836	Organic Sediment/Gyttja

Table 1A: Radiocarbon dates obtained for the core from Mukolo.

Lab no.	Depth (cm)	14 C Age $\pm 1\sigma$ yr (BP)	Mean calibrated age (BP)	Material
Beta - 525657	27	970 ± 30	559	Organic Sediment/Gyttja
Beta - 525656	54	890 ± 30	859	Organic Sediment/Gyttja
UBA - 30920	63	1090 ± 24	985	Organic Sediment/Gyttja

Table 2A: Radiocarbon dates obtained for the core from Jackelberry.

Table 3A: Radiocarbon dates obtained for the core from Lake Liambezi.

Lab no.	Depth (cm)	14 C Age $\pm 1\sigma$ yr (BP)	Mean calibrated age (BP)	Material
Beta - 525654	58.5*	16630 ± 50	-	Organic Sediment/Gyttja
Beta - 525655	70*	8860 ± 30	-	Organic Sediment/Gyttja
Beta - 525653	84.5	15720 ± 40	18916	Organic Sediment/Gyttja



Figure 1A: Total inorganic content (TIC) from the three cores: Mukolo (right), Lake Liambezi (centre), and Jackelberry (left). TIC is calculated as percentages of dry weight (%) of sediment samples from the LOI analysis.



Figure 2A: Measured δ^{13} C (red line) and modelled δ^{13} C using the Rayleigh enrichment equation (blue line) for the three cores from: Mukolo (right), Lake Liambezi (centre), and Jackelberry (left).



Figure 3A: Broken-stick model (red line) and CONISS cluster analysis (black line) for the core from Mukolo. The circle represents the significant number of clusters.



Figure 4A: Broken-stick model (red line) and CONISS cluster analysis (black line) for the core from Lake Liambezi. The circle represents the significant number of clusters.



Figure 5A: Broken-stick model (red line) and CONISS cluster analysis (black line) for the core from Jackelberry. The circle represents the significant number of clusters.

References

Archibald, S. (2016) 'Managing the human component of fire regimes: Lessons from Africa', *Philosophical Transactions of the Royal Society B: Biological Sciences*. Royal Society of London. doi: 10.1098/rstb.2015.0346.

Archibald, S. *et al.* (2017) 'Interactions between fire and ecosystem processes', in *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. Cambridge University Press, pp. 233–261. doi: 10.1017/9781139382793.015.

Beerling, D. J. and Osborne, C. P. (2006) 'The origin of the savanna biome', *Global Change Biology*, 12(11), pp. 2023–2031. doi: 10.1111/j.1365-2486.2006.01239.x.

Berglund, B. E. (1986) Handbook of Holocene palaeoecology and palaeohydrology. J. Wiley.

Blaauw, M. (2010) 'Methods and code for "classical" age-modelling of radiocarbon sequences', *Quaternary Geochronology*. Elsevier, 5(5), pp. 512–518. doi: 10.1016/J.QUAGEO.2010.01.002.

Blaauw, M. (2011) 'Flexible paleoclimate age-depth models using an autoregressive gamma process', *Bayesian Analysis*, 6(3), pp. 457–474. doi: 10.1214/11-BA618.

Bond, W. J. (2008) 'What Limits Trees in C 4 Grasslands and Savannas?', *Annual Review of Ecology, Evolution, and Systematics*. Annual Reviews, 39(1), pp. 641–659. doi: 10.1146/annurev.ecolsys.39.110707.173411.

Bond, W. J. and Midgley, G. F. (2000) 'A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas', *Global Change Biology*, 6(8), pp. 865–869. doi: 10.1046/j.1365-2486.2000.00365.x.

Bond, W. J., Midgley, G. F. and Woodward, F. I. (2003) 'What controls South African vegetationclimate or fire?', *South African Journal of Botany*, 69(1), pp. 79–91.

Brand, W. A. *et al.* (2014) 'Assessment of international reference materials for isotope-ratio analysis (IUPAC technical report)', *Pure and Applied Chemistry*. IUPAC Secretariat, 86(3), pp. 425–467. doi: 10.1515/pac-2013-1023.

Burke, A. (2002) 'Present vegetation in the Kavango region', *Namibian Scientific Society*, 50, pp. 133–145.

Burney, D. A., Brook, G. A. and Cowart, J. B. (1994) 'A Holocene pollen record for the Kalahari Desert of Botswana from a U-series dated speleothem', *Holocene*. SAGE Publications Ltd, 4(3), pp. 225–232. doi: 10.1177/095968369400400301.

Burrough, S. L. and Thomas, D. S. G. (2013) 'Central southern Africa at the time of the African

Humid Period: a new analysis of Holocene palaeoenvironmental and palaeoclimate data', *Quaternary Science Reviews*. Pergamon, 80, pp. 29–46. doi: 10.1016/J.QUASCIREV.2013.08.001.

Central Statistics Office (1994) 1991 Population and Housing Census. Windhoek.

Chase, B. M. *et al.* (2009) 'A record of rapid Holocene climate change preserved in hyrax middens from southwestern Africa', *Geology*, 37(8), pp. 703–706. doi: 10.1130/G30053A.1.

Colpaert, A., Matengu, K. and Polojärvi, K. (2013) 'Land use practices in Caprivi's changing political environment', *Journal for Studies in Humanities and Social Sciences*, 2(2), pp. 141–162.

Cuni-Sanchez, A. *et al.* (2016) 'African savanna-forest boundary dynamics: A 20-year study', *PLoS ONE*. Public Library of Science, 11(6). doi: 10.1371/journal.pone.0156934.

Dodd, J. R. and Stanton, R. J. (1990) *Paleoecology: Concepts and Applications*. Second. Toronto: John Wiley & Sons, Inc.

February, E. C. et al. (2013) Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses, Source: Ecology.

Gillson, L. (2015) 'Evidence of a tipping point in a southern African savanna?', *Ecological Complexity*. Elsevier, 21, pp. 78–86. doi: 10.1016/J.ECOCOM.2014.12.005.

Gillson, L. and Duffin, K. . (2007) 'Thresholds of potential concern as benchmarks in the management of African savannahs', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1478), pp. 309–319. doi: 10.1098/rstb.2006.1988.

Gillson, L., Waldron, S. and Willis, K. J. (2004) 'Interpretation of soil δ^{13} C as an indicator of vegetation change in African savannas', *Journal of Vegetation Science*. John Wiley & Sons, Ltd (10.1111), 15(3), pp. 339–350. doi: 10.1111/j.1654-1103.2004.tb02270.x.

Grace, J. *et al.* (2006) 'Productivity and carbon fluxes of tropical savannas', in *Journal of Biogeography*, pp. 387–400. doi: 10.1111/j.1365-2699.2005.01448.x.

Grimm, E. (1991) 'Tilia and Tiliagraph'. Springfield: Illinois State Museum.

Heine, K. (2005) *Holocene Climate of Namibia: A Review Based on Geoarchives, African Study Monographs.*

Heiri, O., Lotter, A. F. and Lemcke, G. (2001) 'Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results', *Journal of Paleolimnology*. Kluwer Academic Publishers, 25(1), pp. 101–110. doi: 10.1023/A:1008119611481.

Hogg, A. G. *et al.* (2013) 'SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP', *Radiocarbon*. Cambridge University Press (CUP), 55(4), pp. 1889–1903. doi:

10.2458/azu_js_rc.55.16783.

Humphrey, G. (2018) *The role of humans, climate and vegetation in the complex fire regimes of north-east Namibia.* University of Cape Town.

Jones, M. B. (1988) 'Photosynthetic Responses of C 3 and C 4 Wetland Species in a Tropical Swamp', *The Journal of Ecology*. JSTOR, 76(1), p. 253. doi: 10.2307/2260467.

Juggins, S. (2019) 'Analysis of Quaternary Science Data'. Available at: http://www.staff.ncl.ac.uk/stephen.juggins/ (Accessed: 30 September 2019).

Kershaw, A. P. (1997) 'A modification of the Troels-Smith system of sediment description and portrayal', *Quaternary Australasia*, 15(2), pp. 63–68.

Lindsay, K. *et al.* (2017) 'The shared nature of Africa's elephants', *Biological Conservation*. Elsevier Ltd, pp. 260–267. doi: 10.1016/j.biocon.2017.08.021.

Marchant, R. (2010) 'Understanding complexity in savannas: Climate, biodiversity and people', *Current Opinion in Environmental Sustainability*, pp. 101–108. doi: 10.1016/j.cosust.2010.03.001.

McClaran, M. P. and McPherson, G. R. (1995) 'Can soil organic carbon isotopes be used to describe grass-tree dynamics at a savanna-grassland ecotone and within the savanna?', *Journal of Vegetation Science*. Wiley, 6(6), pp. 857–862. doi: 10.2307/3236400.

Mendelsohn, J. (2009) Land Use in Kavango: Past, Present and Future.

Mendelsohn, J. and el Obeid, S. (2003) *Sand and Water - A profile of the Kavango Region*. Cape Town: Struik Publishers.

Mendelsohn, J. and Roberts, C. (1997a) 'Administration, governance and services; People of Caprivi; Soils and vegetation', in *An environmental profile and atlas of Caprivi*. Windhoek: Ministry of Environment and Tourism, pp. 8–24.

Mendelsohn, J. and Roberts, C. (1997b) 'Farming in Caprivi; Wild animal resources; Rivers, wetlands and water supply', in *An environmental profile and atlas of Caprivi*. Windhoek: Ministry of Environment and Tourism, pp. 26–39.

Mendelsohn, J. and Roberts, C. (1997c) 'Introduction; General description of Caprivi', in *An environmental profile and atlas of Caprivi*. Windhoek: Ministry of Environment and Tourism, pp. 1–6.

Mitchell, B. L. (1961) 'Ecological aspects of game control measures in African wilderness and forested areas', *Kirkia*, 1, pp. 120–128.

Mudekwe, J. (2004) 'Anthropogenic threats to the Baikiaea plurijunga (Zambezi teak) forests of

Southern Central Africa.'

Nash, D. J., Meadows, M. E. and Gulliver, V. L. (2006) 'Holocene environmental change in the Okavango Panhandle, northwest Botswana', *Quaternary Science Reviews*, 25(11–12), pp. 1302–1322. doi: 10.1016/j.quascirev.2005.11.004.

Oksanen, J. *et al.* (2019) 'Community Ecology Package'. Available at: https://github.com/vegandevs/vegan (Accessed: 16 October 2019).

Osborne, C. P. *et al.* (2018) 'Human impacts in African savannas are mediated by plant functional traits', *New Phytologist*. Blackwell Publishing Ltd, pp. 10–24. doi: 10.1111/nph.15236.

Piearce, G. D. (1985) 'How to save the Zambezi teak forests', in *Commonwealth Forestry Association*. Victoria.

Ramsey, C. B. (2009) 'Bayesian analysis of radiocarbon dates', *Radiocarbon*, 51(1), pp. 337–360. doi: 10.1017/S0033822200033865.

RStudio Team (2019). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Sage, R. F. (2004) 'The evolution of C4 photosynthesis', *New Phytologist*, pp. 341–370. doi: 10.1111/j.1469-8137.2004.00974.x.

Sankaran, M. *et al.* (2005) 'Determinants of woody cover in African savannas', *Nature*. Nature Publishing Group, 438(7069), pp. 846–849. doi: 10.1038/nature04070.

Schlettwein, C. H. . and Bethune, S. (1991) 'Wetlands Conservation Conference for Southern Africa', in Matiza, T. and Chabwela, H. N. (eds) *Aquatic weeds and their management in southern Africa: biological control of Salvinia molesta in the Eastern Caprivi*. Gaborone: IUCN, pp. 173–187.

Scott, L., Holmgren, K. and Partridge, T. C. (2008) 'Reconciliation of vegetation and climatic interpretations of pollen profiles and other regional records from the last 60 thousand years in the Savanna Biome of Southern Africa', *Palaeogeography, Palaeoclimatology, Palaeoecology*. Elsevier, 257(1–2), pp. 198–206. doi: 10.1016/J.PALAEO.2007.10.018.

Sheuyange, A., Oba, G. and Weladji, R. B. (2005) 'Effects of anthropogenic fire history on savanna vegetation in northeastern Namibia', *Journal of Environmental Management*, 75(3), pp. 189–198. doi: 10.1016/j.jenvman.2004.11.004.

Smith, A. B. (1992) Pastoralism in Africa: origins and development ecology., Pastoralism in Africa: origins and development ecology. London: Hurst & Company.

Stock, W. D., Chuba, D. K. and Verboom, G. A. (2004) 'Distribution of South African C3 and C4

species of Cyperaceae in relation to climate and phylogeny', *Austral Ecology*, 29(3), pp. 313–319. doi: 10.1111/j.1442-9993.2004.01368.x.

Timberlake, J. (2000) 'Biodiversity of the Zambezi Region', *Biodiversity Foundation for Africa: Occasional Publications in Biodiversity*, 9.

Weber, G. E., Moloney, K. and Jeltsch, F. (2000) *Simulated long-term vegetation response to alternative stocking strategies in savanna rangelands, Plant Ecology.*

Wood, A. P. (1986) 'Man's impact upon the mukusi forests of Zambia, with special reference to Sesheke District', in Piearce, G. D. (ed.) *Proceedings of the First International Conference on the Teak Forests of Southern Africa*. Livingstone: Zambia Forest Department, p. Chapter 3.

World Conservation Monitoring Centre (1998) Baikiaea plurijuga, The IUCN Red List of Threatened Species.

Wynn, J. G., Bird, M. I. and Wong, V. N. L. (2005) 'Rayleigh distillation and the depth profile of 13C/12C ratios of soil organic carbon from soils of disparate texture in Iron Range National Park, Far North Queensland, Australia', *Geochimica et Cosmochimica Acta*, 69(8), pp. 1961–1973. doi: 10.1016/j.gca.2004.09.003.