

**A study of carbon, nitrogen, and
biogenic silica concentrations in
Cyperus papyrus, the sedge
dominating the permanent swamp of
the Okavango Delta, Botswana, Africa**

Giulia Lodi

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Cover Picture: The Okavango River flowing in the permanent swamp surrounded by papyrus (<https://www.ormesulmondo.com/>).

English abstract

GIULIA LODI

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Abstract: The Okavango Delta is southern Africa's greatest wetland and is among one of the most pristine wetlands in the world. There is moderate information about how this system functions, however, the research on nutrient concentrations and cycles is especially limited. This study provides new knowledge on the Okavango Delta by analysing samples of *Cyperus papyrus*, one of the main aquatic plants in the area. Total nitrogen (TN), total organic carbon (TOC), and biogenic silica (BSi) concentrations in papyrus were measured and examined. Papyrus was harvested from three sites in the permanent swamps of the Okavango Delta, and divided in the different organs: umbel, culm, scales, roots, and rhizome. The two methods used in this study are elemental combustion analysis for TN and TOC and wet chemical digestion for BSi. I investigated if there were differences in TOC, TN, and BSi depending on the part of the plant, the age of the plant, the environment in which the plant was growing, and the flood period. The highest TN concentrations were found in umbels, rhizomes, and roots. Umbels function as both a photosynthetic organ and an inflorescence; rhizomes act as a storage for nutrients; and roots have been found to be colonized by N₂-fixing bacteria. Moreover, TN concentrations in juvenile organs were higher than in mature ones. This was associated active translocation and recycling of nutrients in the first stages of growth of papyrus from mature to juvenile plants which then might cause a higher productivity in juvenile plants. The environment in which papyrus grows does not seem to influence TN concentrations, however, during high flood periods there was a higher TN amount in papyrus. The results of the study showed TOC concentrations between 39-43%, the highest concentrations were found in umbels and rhizomes and the lowest in the roots. Statistical analyses on TOC concentrations comparing the growing sites and the flood periods did not give any significant results for any part of papyrus. Lastly, the highest BSi concentrations were found in mature organs since silica is accumulated inside the plant throughout its life. BSi was not uniformly distributed among the different organs, possibly because of a passive transport of dissolved silica through the transpiration system and deposited in regions mostly affected by water loss. The growing site does not seem to influence BSi concentrations in papyrus. However, BSi in rhizomes was twice as high during high flood periods than during flood recession.

Keywords: Okavango Delta, papyrus, total nitrogen, total organic carbon, biogenic silica

Supervisors: Daniel Conley, Karl Ljung, Johanna Stadmark

Subject: Biogeology

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Svensk abstract

GIULIA LODI

Lodi, G., 2022: Kol-, kväve- och kiselkoncentrationer i papyrus (*Cyperus papyrus*) i Okavangodeltat, Botswana, Afrika. *Examensarbeten i geologi vid Lunds Universitet*, Nr. 639, 35 sid. 45 hp.

Sammanfattning: Okavangodeltat är södra Afrikas största våtmark och en av världens minst påverkade våtmarker. Kunskapen om hur våtmarkssystemet fungerar är begränsad, särskilt vad gäller halter av näringsämnen och omsättning av näringsämnen i de dominerande våtmarksväxterna. I den här studien presenteras analyser av kol-, kväve- och kiselhalter i *Cyperus papyrus* som är den dominerande akvatiska växten i stora delar av deltat. Papyrus samlades in från tre platser i den permanenta våtmarken i deltat. Material samlades in från växter med olika ålder, från olika växtplatser och under hög- och lågvatten. Varje insamlad växt delades upp i: blomställningar, stammar, fjäll, rötter och jordstammar. Alla prover analyserades för halt av totalt kol, totalt kväve och kisel. Skillnader i koncentration av näringsämnen från de olika växtdelarna analyserades med avseende på ålder, växtmiljö och vattenstånd. De högsta kvävehalterna uppmättes i blomställningar, rötter och jordstammar. Detta förklaras av att blomställningar både är fotosyntetiserande och producerar blommor och frön, jordstammarna lagrar näring, och rötterna har ofta associerade kvävefixerande bakterier. Kvävehalten var också högre i juvenila växter, eftersom växter har mer aktiv näringstransport under den första tillväxtfasen. Kvävehalterna var generellt högre under högvattenfasen, medan växtplatsens avstånd till strömfåran i deltat inte påverkade kvävehalten. Koncentrationen av totalt kol låg mellan 39 och 43 procent med högst halter i blomställningar och jordstammar, och lägst i rötter. Halten totalt kol var inte korrelerad med växtmiljö eller vattenstånd. Andelen kisel var högst i äldre växter, vilket beror på att växterna ackumulerar kisel under sin livstid. Kiselinnehållet var inte jämnt fördelat mellan olika växtdelar, sannolikt eftersom kisel fälls ut i större utsträckning i de delar som är påverkade av vattenförlust. Kiselhalten var högre vid högvatten än vid lågvatten, medan växtmiljön inte påverkade kiselhalten.

Nyckelord: Okavangodeltat, papyrus, kväve, organiskt kol, biogeniskt kisel

Handledare: Daniel Conley, Karl Ljung, Johanna Stadmark

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1 Introduction

The Okavango Delta is located in northern Botswana and is southern Africa's greatest wetland. It is one of the world's largest Ramsar sites (wetland sites selected to be of international importance under the Ramsar convention) and it has been recently added to the UNESCO list of World Heritage Sites in 2014 (West et al., 2015). The Delta covers about 55000 km² in area and it is very important for the region. In fact, the Okavango Delta is one of the only two perennial sources of water in Botswana. Moreover, the Okavango Delta belongs to the most pristine wetlands in the world (McCarthy & Ellery, 1998). A first explanation for this is that the region has never been densely inhabited by humans, even though the first record of humans here dates back to more than 30000 years (Thomas & Shaw, 1991). A second reason is that water management projects never have impacted the region's hydrology (McCarthy & Ellery, 1998). A third cause is the presence of the malarian mosquito and the tsetse fly, which represent a problem for both humans and cattle (Stanistreet & McCarthy, 1993).

A more profound understanding of the Okavango Delta is necessary to preserve the value of this oasis of water and wildlife. Since there is moderate information about how this wetland system originated, how it functions, and which processes take place (Mendelsohn et al., 2010), this study provides new knowledge on the plant communities in the Okavango Delta. *C. papyrus* is one of the main aquatic plants both in the Panhandle and in the permanent swamp (Fig. 1; Struyf et al., 2015). It is known that

papyrus wetlands are some of the most productive systems on Earth (Saunders et al., 2013), but still, in the Okavango Delta, research on nutrient concentrations and cycles is limited (Mendelsohn et al., 2010). Moreover, little research has focused on wetland dissolved silicon (DSi) concentrations and cycling or on the cycling of DSi compared to nitrogen cycling (Struyf & Conley, 2009). Therefore, a detailed study on nutrient concentrations in *C. papyrus* wetlands is of major significance to better comprehend how this fascinating ecosystem operates.

1.1 Research questions

The aim of this MSc thesis project is to study TOC, TN, and BSi concentrations in *C. papyrus* plants. To do this, the analysis will consider different variables: the age of the plants (juvenile or mature), the sampling area (channel margin or backswamp), and the stages of the flood pulse (high flood or flood recession). These factors could control the nutrient concentrations in *papyrus* and in the Delta. The major hypotheses that are tested in this study are:

1. TN content in younger plants is higher than in more mature plants.
2. TN and TOC contents are higher during high flood than during flood recession.
3. TN and TOC contents are higher in plants harvested on channel margins compared to the backswamps.
4. BSi content is higher in mature plants as com-

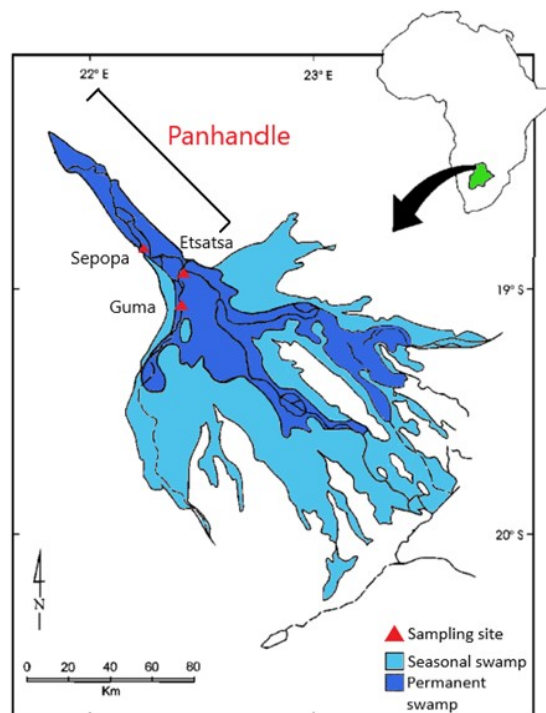


Figure 1. The Okavango Delta map, showing the permanent and seasonal swamps, and the three sampling sites (modified from Christison et al., 2005, fig. 1).

pared to juvenile plants.

To examine these hypotheses, three sites in the Panhandle region were chosen (Fig. 1) and 261 samples of different parts of the papyrus plant were harvested, namely umbel, culm, scales, roots, and rhizome. The sampling was executed in 2017 collecting samples of different age to compare juvenile and mature plant parts. Moreover, papyrus plants were harvested in different time periods following the flood pulse: flood expansion, high flood, and flood recession. The first method of this MSc project utilized high temperature combustion for the analysis of TOC and TN. The second method is a wet chemical digestion technique for biogenic silica (BSi), which dissolves all amorphous silica components in the samples using a weak base solution. Lastly, previous studies are used to compare the results obtained.

1.2 The vegetation in the Okavango Delta and *Cyperus papyrus*

The primary vegetation types in Africa mainly follow the rainfall distribution on the continent. These vegetation complexes have one feature in common: extremely shallow hydrologic gradients. Moreover, there are similitudes in their origins: tectonic activity, massive deposition of sediments, or both. For instance, the swamps of the Okavango Delta are thought to originate from an ancient rift valley system, now filled with

~150 metres of sediments brought into the basin by the Okavango River (Denny, 1985).

The permanent inland waterbodies, such as the Okavango Delta, have floodplains. They are classified as lacustrine or riverine floodplains. The former is the area of land above water level, that is inundated at least once a year. The latter is delimited by the levee. Levees are formed along the margins of river channels by sediment deposition. During flooding, coarser particles, like sand, deposit first, forming the levees, while the finer particles, like silt, make up the backwater swamps. A similar classification is also used when talking about the papyrus swamps. Papyrus swamps (Fig. 2) are typically found in stable hydrological regimes, but they can also prosper with water level changes. Papyrus swamps are found from sea level to over 2000 m altitude, and usually have ~pH 6.5, but the plant itself can tolerate a pH range of 4-8. In the Okavango Delta, papyrus swamps make up ~20% of the total reed swamp (Fig. 3; Denny, 1985).

The most important plant family in permanently herbaceous swamps is Cyperaceae. *Cyperus* is one of the major genera in this family and contains more than 600 tropical and sub-tropical species living on mostly poor, heavy soils or in deep water (Denny, 1985). *Cyperus papyrus* (Fig. 4) is the most ecologically important aquatic emergent in the genus and has an almost entire African distribution (Thompson, 1976). Furthermore, *C. papyrus* is the biggest sedge worldwide, reaching up to 9 metres in height in Ethiopia. It is usually a sudd (Arabic word meaning



Figure 2. An example of channel dominated by *Cyperus papyrus* in the Okavango Delta (<https://i2.wp.com/www.marieangeostre.com>).



Figure 3. An example of reed swamp in the Okavango Delta (<https://live.staticflickr.com/>).

“blockage” or “barrier”) dominant species. This word was first used referring to the massive papyrus blockages in the Nile swamps (Hope, 1902; Drar, 1951). *Cyperus* species are present in every type of sudd, and *C. papyrus* is the only species which dominates a major sudd type. Indeed, the fringes of almost all riverine and lacustrine papyrus swamps are floating, and thanks to papyrus’s exceptional growth rate, it quickly occludes channels. This type of sudd is bound together by papyrus’s rhizomes, the underground plant stem producing roots and new shoots (Denny, 1985).

Aquatic emergent plants living in wetlands had to develop some adaptations to thrive in such a particular environment. There are numerous adaptations, ranging from morphological to anatomical to physiological.

In *C. papyrus* the first morphological adaptation is seen in the leaves. Each umbel is made of hundreds of small bracteoles (leaves directly subtending the flowers) that create a perfectly spherical radiation interceptor, and at the same time retain a prime mechanism for cooling. A second morphological adaptation is in the roots. *C. papyrus* developed a dimorphic root structure: roots suspended in water are large, white, and fleshy, while roots in alluvium are small, dark, and springy. This difference is related to nutrient uptake, as non-aquatic plants do not need to develop “water roots” in soil (Denny, 1985).

The main anatomical adaptation is related to aeration tissues. Papyrus has developed aerenchyma tissues (spongy tissues that create air channels in the

stems) in the culm that perform aeration service for the submerged roots and rhizomes. Gaseous diffusion occurs across the restriction of the basal intercalary meristems (region of cells capable of division and growth) located at the junction of vertical culm with horizontal rhizome. Once the basal meristem ceases activity, approximately one month after the beginning of culm’s extension, the diffusion channels are completed. Until the juvenile culm is mature, oxygen diffuses down the adjacent mature culm and the submerged rhizome to supply young growing tissues (Denny, 1985).

Lastly, physiological adaptations took place as well. The first adaptation regards anaerobic respiration (Denny, 1985). In fact, Thompson (unpublished data) made an experiment where he put a sectioned rhizome of papyrus under water with a very low oxygen content and noticed that it was still forming new culms. This suggests that proper metabolic pathways are present in papyrus to make anaerobic respiration possible. The second physiological adaptation is about germination. Many species have long-lived seeds since most of the time the germinations’ requirements are not met in their living environment. Consequently, most reeds, and *C. papyrus* as well, had to adapt because their seeds require nutrient-rich, wet, and muddy substrates. The Okavango habitat is nutrient poor, so the wet muddy substrate is fundamental for seedling development. The third adaptation takes nutrients into consideration. The plant’s productivity is determined by temperature and nutrient availability (Denny, 1985). A study conducted by Thompson et al. (1979) showed that papyrus’s biomass was unaffected by the amount of nutrients present in its growing environment. Nev-



Figure 4. The aquatic sedge *Cyperus papyrus*. In this photo it is possible to see the umbel and the culm (<https://www.turn-it-tropical.co.uk/>).

ertheless, productivity was largely affected by the stable or seasonal presence of water: in the first case, individual plants were robust but with a low culm density, while in seasonal water regimes individual plants were scrubby but with a high culm density.

1.3 Carbon and nitrogen in *Cyperus papyrus*

The first aim of this MSc project is to investigate total organic carbon (TOC) and total nitrogen (TN) contents in *C. papyrus*. The Okavango Delta wetland system sequesters and accumulates significant amounts of carbon in both detritus and peat (Saunders et al., 2012). Papyrus wetlands have high rates of primary productivity and they have been classified as some of the most productive natural ecosystems on the planet (Saunders et al., 2013) with a net average production of 48-143 t ha⁻¹ y⁻¹ (Thompson et al., 1979). This is caused by papyrus's continual development and growth throughout the year, with growth units emerging from rhizomes in multiple age classes (Jones & Muthuri, 1997). Papyrus is characterized by massive rhizome development, with an estimate of 30-50% of the total biomass being underground (Thompson, 1976). This underground biomass is of crucial importance in maintaining a high productivity in papyrus. It has been suggested that 50% of carbon in the biomass of a mature culm is recycled within the plant as it gets old and eventually dies, by translocating it to the rhizome system. This reuse of carbon is then provided

to young culms (Denny, 1985). The constant growth builds a stable canopy structure ensuring more than 95% light interception (Jones, 1988). Another important character of papyrus is that it is a C₄ sedge, and it is one of only two or three permanent aquatic species in the world to have the C₄ photosynthetic pathway (Denny, 1985). This means that it has high efficiency in converting solar radiations into dry matter as well as in the management of light, water, and nutrients, resulting in elevated rates of carbon assimilation and net primary productivity (NPP, Piedade et al., 1991). Its outstanding growth rate is undoubtedly linked to this adaptation and nutrient conservation is the prime benefit obtained by the C₄ photosynthetic pathways (Denny, 1985). This type of photosynthesis is not usually associated with aquatic plants, but it is mostly found in plants living in hot, arid, and high light conditions (Björkman, 1973). In particular, one characteristic linked to this photosynthetic pathway are advantageous in a wet environment: C₄ species have been shown to have a higher nitrogen use efficiency than C₃ plants (Wilson, 1975; Bolton & Brown, 1980). Since wetlands are often limited in nitrogen content, papyrus has the capability of using nitrogen more efficiently, and thus achieves a higher NPP and is therefore more competitive than C₃ species (Jones, 1987).

The presence of nitrogen in the Okavango system is fundamental for papyrus's productivity. *C. papyrus* can permanently remove N from the system and store it in its biomass (Saunders et al., 2013). Most of

the N uptake probably goes on within the top 20-30 cm of the dense tangle of roots and detritus of the flowing mat. It has been suggested that papyrus has developed a system for N fixation where the rhizomes are the centre of intense N fixation together with the root system (Patriquin & Knowles, 1972; Bristow, 1974; Muthuri & Jones, 1997).

1.4 Biogenic silica in *Cyperus papyrus*

The second aim is to measure the amount of biogenic silica stored in the different parts of *C. papyrus*. The main biological sinks for Si are diatoms and vegetation. Diatoms take up dissolved silica (DSi) and deposit it as amorphous silica (ASi), also known as biogenic silica (BSi), in the protective layer of the frustule (hard and porous cell wall of diatoms; Struyf & Conley, 2009). The biological Si pump is a fundamental mechanism by which carbon moves from the atmosphere to the deep ocean, together with ASi, is buried at the ocean floor (Dugdale et al., 1995). As a consequence, ocean food webs would not work if buried ASi was not restored by inputs by rivers (Struyf & Conley, 2009). Plants also take up DSi, and deposit it as ASi in siliceous structures known as phytoliths (Fig. 5; Piperino, 1988). As mentioned for diatoms, the recycling of

ASi is essential for terrestrial Si cycle as well. In fact, Conley (2002) estimated that the global annual fixation of vegetation silica is on the same order of magnitude as the one in ocean diatom communities, and sometimes the terrestrial environment contains even more ASi.

Wetlands in general and also the Okavango Delta are dominated by grasses and sedges, that are both well-known silica accumulators (Struyf et al., 2005). Sedges like *C. papyrus* are among the best representatives in the Si-accumulating species (Struyf & Conley, 2009). Silicon is present in the soil as DSi, which is monosilicic acid, $\text{Si}(\text{OH})_4$ (McKeague & Cline, 1963), and it is absorbed by the plant and transported in the xylem (tissue transporting water and nutrients from the roots to the leaves; Handreck & Jones, 1967; Hartely & Jones, 1972). Once it is absorbed, it is then deposited as amorphous silica, $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ (Fessenden & Fessenden, 1967). Silica furnishes plants with numerous advantages, such as greater shoot rigidity, defence against physical stresses, enhancement of photosynthesis, and lastly resistance to disease, herbivores, metal toxicity, and salinity (Epstein, 2001).

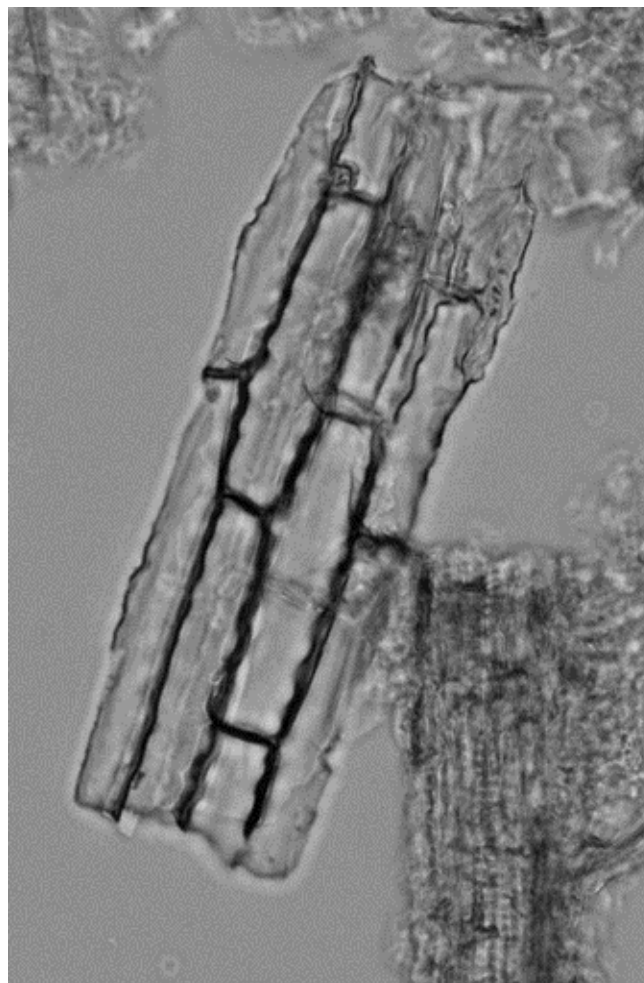


Figure 5. An example of papyrus phytolith found in the umbel (picture by Karolina Brylka).

Wetlands are some of the biggest storage and recycling hotspots for ASi. Some factors governing this feature are inundation volume, water residence time, flooding frequency, and ecosystem structure. Flooding frequency intensifies the deposition of suspended material, which contains both phytoliths and diatom ASi. A long water residence time enhances ASi retention potential as well as high evaporation (Struyf & Conley, 2009). Because of that, the recycling of DSi will slow down (Van Cappellen, 2003). Lastly, the ecosystem structure, particularly grass and sedge abundance, is extremely dependent upon hydrology (Struyf & Conley, 2009).

1.5 The hydrology of the Okavango Delta

The hydrology of the Okavango Delta is characterized by an annual flood pulse that inundates the wetland. The flooded area of the Delta is about 6000 km² during low flow seasons but it can be up to 15000 km² in high flow seasons, depending on the size of the flood event (Struyf et al., 2015). The climate of the Okavango Delta has to be taken into account when thinking about this flooding since it is located in a semi-arid region. In fact, during November-March, a seasonal rainfall of 300-500 mm a⁻¹ occurs during the time period when evaporation can be up to 2100 mm a⁻¹ (Wolski et al., 2006). The flood event starts in the Angola's highlands as precipitation and then it arrives to Botswana in the Moembo inlet in February, reaching its maximum in April (Struyf et al., 2015). The flood reaches the distal part of the Okavango Delta in August-November, after

flowing more than 600 km through the Okavango River and the alluvial fan. The long duration of this specific flood pulse is due to the long distance covered and the low topographic gradient of the fan (Wolski et al., 2006).

1.6 Nutrient status of the Okavango Delta

Nutrients in the Okavango Delta have two primary sources: the Okavango River and atmospheric aerosol deposition (Wolski et al., 2005). The surface water is known to have a generally low concentration of nutrients (Sawula & Martins, 1991; Cronberg et al., 1995; Garstang et al., 1998). The main causes for these low amounts are the numerous biological processes triggered by the flood's onset, i.e., the increase in primary productivity rates in floodplains and the increased production of both phytoplankton and zooplankton (Krah et al., 2006).

Aerosols are the second source of nutrients (Fig. 6), quantitatively important and characterized by a reasonably uniform spatial distribution (Garstang et al., 1998). Nitrogen found in aerosols arise from fires occurring in the region and are transported in both dust and ash. N is then primarily carried by an anticyclonic circulation that originates every year during late winter (August). N is redistributed along the Delta also at smaller scales by the wind-induced motion of dust (Krah et al., 2004). Cronberg et al. (1996) found that the concentrations of N in the Okavango River are



Figure 6. Kalahari Desert. Sand and dust from the Kalahari Desert are the main source of nutrients in the Okavango Delta (<https://www.bwindiugandagorillatrekking.com/>).

similar to global averages in river water. In particular, they found a total nitrogen (TN) concentration of 0.35-0.88 mg/dm³ in the Okavango River, while the global average is 0.2 mg/dm³ (Mitsch & Gosselink, 2000). Moving to the permanent swamp, nutrients brought by the Okavango River are immediately scavenged by the channel vegetation, mainly composed of *C. papyrus* (Garstang et al., 1998). Papyrus can internally cycle nutrients (Denny, 1985), but a small portion of nutrients might get trapped in peat and it cannot be exploited by papyrus. For it to be available for plants again, oxidization or fires are needed (Wolski et al., 2005).

2 Study area

The Okavango Delta is a remarkable area of northern Botswana for many reasons. First of all, it is historically important both as a source of water during drought and as a refuge in past centuries during troubled times. It is ecologically important because a relevant amount of Botswana's wildlife can be found in that area. It is then economically important as a source of tourism and of water for northern and central Botswana. Moreover, it is scientifically important because of its biodiversity, its association of abundant water and the arid environment in which the Okavango Delta resides, and because of the impressive palaeoclimates' record contained in its sediments (Shaw, 1988).

The Panhandle is a permanently flooded landscape characterized by the flowing of the Okavango River, one of the largest rivers in southern Africa (Fig. 7). It forms in the Angola highlands and then starts its

flow southwards entering Namibia and finally reaching Botswana. Here, the Okavango River creates the inland Okavango Delta in the core of the Kalahari Desert. When entering Botswana, the Okavango River movement is controlled by two parallel faults that shaped the 90-km-long and 15-km-wide (Nash et al., 2006) region of the Panhandle (West et al., 2015). By flowing in this restricted area, the Okavango River undergoes constant changes in its flow, confirmed by the presence of numerous oxbow lakes and lagoons (Smith et al., 1997), either isolated or connected to the main channel by smaller and narrower secondary channels (West et al., 2015). The channel margins are elevated above the surrounding floodplain and are confined by peat levees, stabilized by living plant communities dominated by *C. papyrus* and *Phragmites* spp. (Stanistreet & McCarthy, 1993).

At the end of this region, the river flows into the permanent swamps with a very low gradient of 1:5500 (McCarthy et al., 1997). The permanent swamps are characterized by numerous large lakes, most of which are ancient oxbow lakes (McCarthy & Ellery, 1998). Moreover, in this area, the Okavango River divides into three distributary channels: the Nqoga channel flowing to the east, the Jao channel flowing to the southeast, and the Thaoqe channel flowing to the south (Struyf et al., 2015). As in the Panhandle, the channels' levees are almost entirely topped by papyrus (McCarthy et al., 1988), but it can be found also as floating mats of rhizomes (modified subterranean plant stems that send out roots and shoots from their nodes; Ellery et al., 1995). The areas between the channels



Figure 7. Okavango River in the Panhandle (<https://franks-travelbox.com/>).

receive significant amounts of water that permeate through the levees during the entire flood pulse. Thanks to this percolation, the vegetation in this area of the Okavango Delta flourish and, as a result, the sedimentary material that accumulates is only composed of peat (Stanistreet & McCarthy, 1993). Consequently, since the peat is wet throughout the year, fires have less impact on vegetation and peat degradation in the sedimentary system (Ellery et al., 1989).

The further region of the fan is composed of the seasonal swamp, an area where the flow is not confined to channels but proceeds as a slow sheet flooding. The topography of this section of the fan is gently undulating with some reliefs reaching 1.5 m in height. The depth of flooding is usually less than 1 m, that means that the higher grounds form local islands. The southern end of the fan is marked by the Thamalakane River and the smaller Kunyene River. They are also influenced by the seasonality of the flood as they flow only when water gets as far as the most distal borders of the fan (McCarthy & Ellery, 1998). Furthermore, the seasonal swamps are a major site of water leakage into the groundwater system below the numerous islands of this area during flood times. These islands are bordered by arboreal vegetation and are known to be

excessive transpiration and evaporation sites (McCarthy & Metcalfe, 1990).

3 Geological history of the Okavango Delta

The Okavango Delta is thought to be a relict of a past internal drainage system that emptied into the Kalahari basin, in southern Africa. The Kalahari basin developed around 140 million years ago when Gondwana was breaking up (Fig. 8; Thomas & Shaw, 1988). The final division of Gondwana resulted in an uplifted marginal hinge line, today represented by the Great Escarpment (Fig. 8; De Swardt & Bennet, 1974; Ollier, 1985), and a shallow depressed interior basin (Dingle et al., 1983; Thomas, 1984).

Two different types of drainage evolved from this setting: the first was characterized by short streams with sharp gradients flowing from the hinge line to the coast, the second was composed of major rivers running in the opposite direction as the first one, and the Okavango River is the last perennial river belonging to this system today (Thomas & Shaw, 1988). The fact that the Okavango River is the last major river flowing to the interior of the continent can be ex-

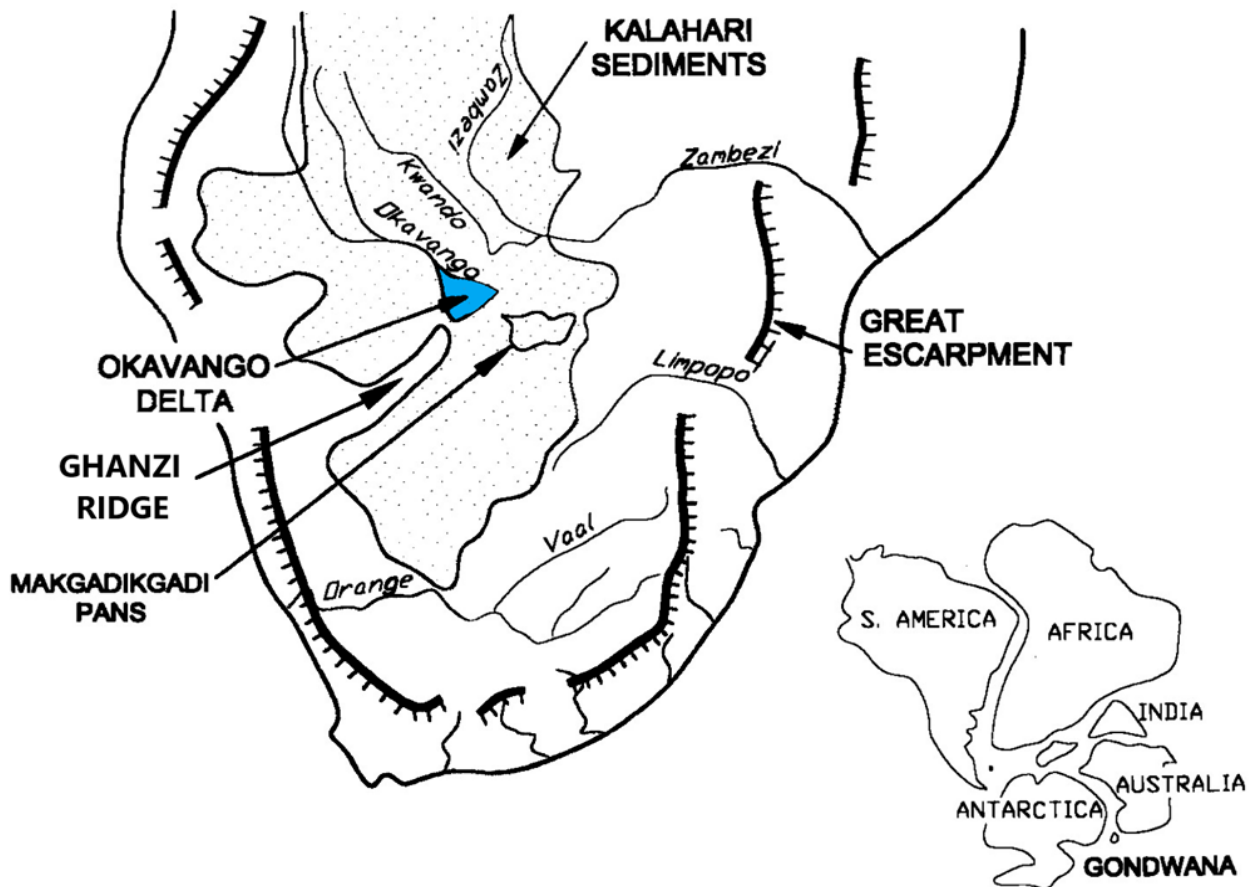


Figure 8. Map showing the relationship of the Kalahari basin and the marginal escarpment of southern Africa, and their association with the pre-rifting configuration of Gondwana (modified from McCarthy & Ellery, 1998, fig. 4).

plained by the endoreic system getting smaller during the late Jurassic evolution of the entire drainage system (De Heinzelin, 1963). However, a significant endoreic system had to be present after the Gondwana division as it is one of the few possible explanation for the initial deposition of the Kalahari sediments (Fig. 8; Thomas & Shaw, 1988), that resulted in over 300 m in thickness locally (Thomas & Shaw, 1991). These sediments are diverse, from water-born material to wind-blown sand, the latter being the upper portion of the Kalahari sediments called “Kalahari sand” (McCarthy & Ellery, 1998). Aeolian sand comes during arid periods while riverine sediments are dominant during wetter periods as today. This second type of sediments is made of very fine-grained aeolian and fluvial material. The Kalahari sands dominate the Okavango Delta sediments and are known to be nutrient-deficient (Thomas & Shaw, 1990). As a result, soils of the Okavango region are mostly structureless fine sands, in short supply of fundamental plant nutrients and with a low organic matter content (Perkins & Thomas, 1993).

The Kalahari basin and the Okavango system have been deeply modified by continuous rifting of the African continent (Hutchins et al., 1976). In the Red Sea, the East African rift system starts and extends towards the south into the continent. Once it reaches Malawi, the rift system divides, and the western ramification stretches towards the southwest crossing Zambia and northern Botswana. In Botswana, the rift system is recognizable as two depressions, one hosting the Makgadikgadi pans (Fig. 8) and the other the Oka-

vango Delta, separated by the uplifted Ghanzi ridge (Fig. 8; Scholz et al., 1976; Hutchins et al., 1976; McCarthy et al., 1993a). The section containing the Okavango Delta is characterized by east-west extension that developed a graben bounded by faults orientated NE-SW of which the Thamalakane fault (Fig. 9) is the major. Perpendicular to this set of faults, another set has formed with an overall subsidence effect. These faults contain the Panhandle region of the Okavango Delta (McCarthy et al., 1993a). There are two hypotheses on the ambiguous origin of the Panhandle (McCarthy, 1992). The first is that it might be an example of a confined graben perpendicular to the main rift (Mallick et al., 1981), the second is that it may correspond to an erosionally incised river segment on the upper part of the Gumare fault (Fig. 9; McCarthy, 1992). The general subsidence of the area is filled up with both aeolian sand and riverine sediments brought by the Okavango River, that is responsible for the development of the alluvial fan whose age is still unknown (McCarthy & Ellery, 1998). However, smaller independent blocks uplifted exposing themselves as islands, such as the Chief’s Island (Fig. 9; McCarthy et al., 1993a).

4 Material and methods

4.1 Papyrus samples

A number of samples from papyrus plants were collected at three study sites in the Panhandle region, namely Sepopa, Guma, and Etsatsa, and of those, 261 samples were analysed in this study. At every study site, three transects were established spanning from the

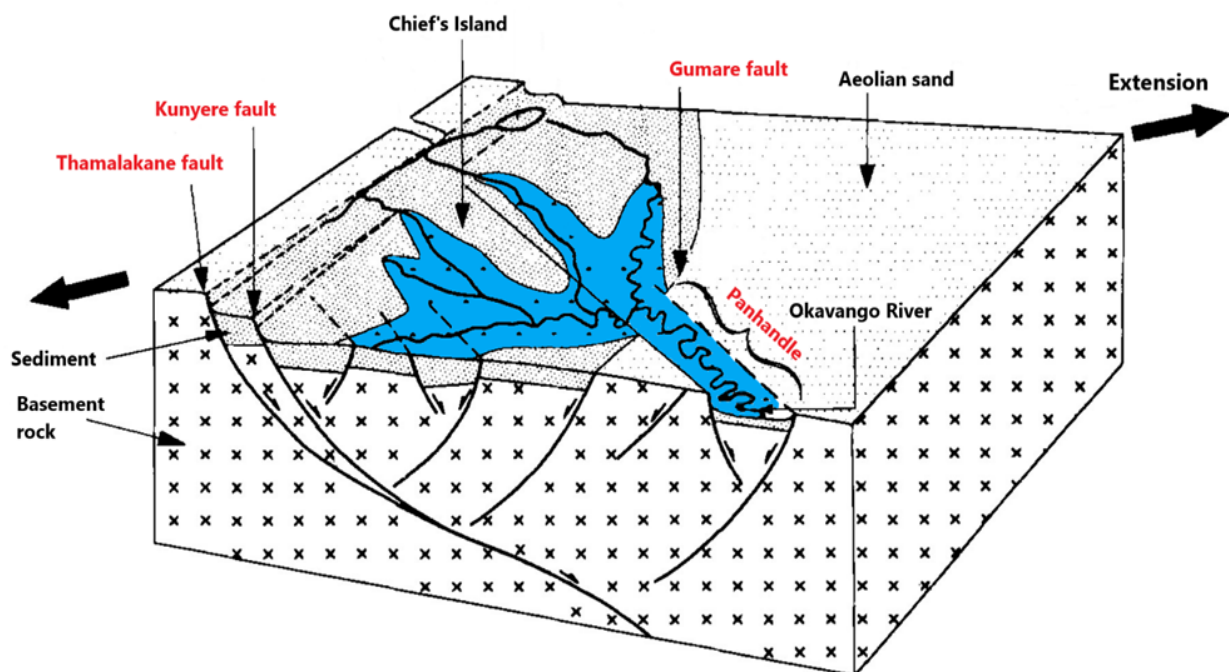


Figure 9. A schematic map showing the control of faulting on the Okavango Delta (modified from McCarthy & Ellery, 1998, fig. 8).

channel margin to the backswamp. Each transect measured a distance between 45 and 60 m. Sampling was done at every 15 m distance category (0 m, 15 m, 30 m, 45 m, and 60 m). For this study, samples from 0 m and 45-60 m were chosen. Starting from the channel margin to the backswamp, papyrus plants were harvested and separated into the different organs with respect to the age of the plants. The organs of papyrus are umbel, culm, scales, roots, and rhizome (Fig. 10), and all of them were collected both as juvenile and mature except for roots. Harvesting of plants was executed during different stages of the flood pulse: flood expansion (February 2017), high flood (May 2017), and flood recession or low flood (August-November 2017). Yet, for this study samples from high flood and flood recession were chosen.

4.2 Total organic carbon (TOC) and total nitrogen (TN)

Total organic carbon (TOC) and total nitrogen (TN) were measured with a Costech ECS 4010 elemental analyzer. Subsamples of dried homogenized sediment

(~2-3 mg) were packed in tin capsules. During system operation, helium carrier gas moves within the combustion reactor. At the beginning of the analytical cycle, helium is swapped to a volume of oxygen. The samples are dropped consecutively into the combustion reactor before oxygen arrives. Then, the sample and the tin capsule react with oxygen and combust at temperatures of 1700-1800°C, and the sample is broken down to its elemental components: N₂, CO₂, H₂O, and SO₂. The excess oxygen is absorbed by high-performance copper wires. After, the gases flow through the gas chromatographic separation column and they are then separated in C and N and detected sequentially by the thermal conductivity detector (TCD). The TCD creates a signal proportional to the amount of element in the sample. Lastly, the data handling system correlates the elemental peak to a known standard material, after it has been calibrated, and then generates a report for each element on a weight basis. The measurements were calibrated with a 5-point calibration curve with acetanilide as a standard (10.34% N, 71.10% C). Precision and accuracy were checked with reference soil samples with known carbon and

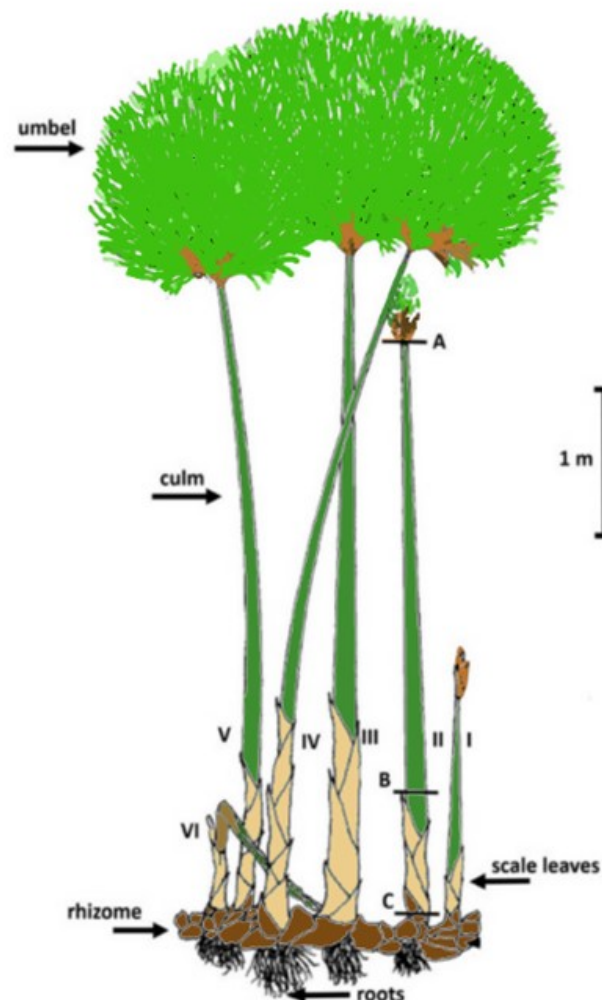


Figure 10. Sketch of papyrus. The different organs of papyrus are represented as well as the different growth stages (I and II represent the juvenile stages while III and IV represent the mature ones (modified from Muthuri & Kinyamario, 1989, fig. 1).

nitrogen contents (0.06% N, 0.73% C), barley flour standards (1.9% N, 43.51% C), and high organic sediment standards (0.52% N, 7.45% C).

4.3 Dissolved silicon (DSi)

Samples were freeze-dried to maintain a better sample integrity and homogenized. Subsamples were weighed containing between ~28-31 mg of sample because of potential weight effects (Conley & Schelske, 2006) and placed into polypropylene round bottles. To digest papyrus, 40 mL of 1% Na₂CO₃ solution were added to the papyrus subsamples. The bottles were put in a covered shaking water bath (Julabo) at 85°C for 3 hours, with caps slightly loosened to vent gases. Then, the bottles were removed from the shaking bath and placed into a room temperature water bath and cooled for 3-5 minutes to slow down further dissolution. Subsequently, 1 mL of the samples was pipetted into plastic bottles containing 9 mL of 0.017 M HCl to neutralize the Na₂CO₃ digestion solution. The subsamples were then analysed for dissolved silicate using the Smartchem 200 (AMS System) wet chemistry analyzer. For this study, an automated molybdate-blue method was used (Grasshoff et al., 1999). The principle behind this method is the reaction of monomeric silicic acid with ammonium molybdate, that results in a molybdosilicic acid complex. This complex is then reduced to heteropoly-molybdenum by ascorbic acid and measured at 660 nm by a spectrophotometer.

4.4 Statistics: *T*-Test and ANOVA

Two sample *T*-Tests were run in the software R and used to test whether the averages of the two groups of variables (juvenile vs mature, channel margin vs back-swamp, high flood vs recession) were equal or not. Before running the *T*-Tests, two assumptions were verified. The first was the Shapiro-Wilk Normality Test, a test for normality used to determine whether a sample has a normal distribution. The second was the Levene's Test for Homogeneity of Variance, a test used to determine whether samples have equal variances. Lastly, the Bonferroni correction, a method to counteract the multiple comparisons problem, was not used because the p-values obtained were either < 0.001 or non-significant.

A number of two-way ANOVAs were also run in R and used to analyse the differences among means. A two-way analysis of variance determines whether there is a statistically significant difference between the averages of three or more independent groups that have been divided into two variables or factors. The factors used in these analyses were basically the same as the ones used for the *T*-Tests: part of the plant, environment, flood period, age. For the results of an ANOVA to be valid, the following assumptions had to be met: normality of residuals, tested with the Shapiro-Wilk Normality test and the Two-Sample Kolmogorov

-Smirnov test, and homogeneity of variance, tested with the Levene's Test for Homogeneity of Variance.

In the Appendix, degrees of freedom, *t* statistics and p-values for both *T*-Tests and ANOVAs are presented in tables. In this study, the p-values considered significant are p-values <0.05. P-values between 0.05 and 0.01 are marked with one star (*), p-values between 0.01 and 0.001 are marked with two stars (**), while p-values <0.001 are marked with three stars (***)

5 Results

5.1 Mean TN, TOC, and BSi concentrations in *Cyperus papyrus*

The highest TN contents are found in umbels and rhizomes. The TN concentrations are 1.39±0.27% in juvenile umbels and 1.05±0.28% in mature umbels, while in rhizomes 1.36±0.33% and 0.91±0.31% for juvenile and mature, respectively. Culms and scales have shown to have the lowest TN concentrations: 0.77±0.18% in juvenile culms and 0.46±0.22% in mature culms, and 0.59±0.12% for juvenile scales and 0.34±0.08% in mature scales. Roots had a mean TN concentration of 0.94±0.23%.

All the parts of papyrus have similar TOC concentrations. Juvenile and mature umbels have 44.36±0.83% and 43.34±1.70%, juvenile and mature culms have 42.41±0.60% and 42.55±1.10%, juvenile and mature scales have 42.08±0.69% and 43.28±0.61%, and juvenile and mature rhizomes have 43.32±1.04% and 44.45±0.44%. Roots have an average of 39.34±3.75%.

Lastly, BSi had the highest concentration in mature umbels with 7.19±3.12%. The second and third highest amounts are found in mature culms (4.03±1.30%) and in roots (3.10±1.56%). All the other parts of papyrus have Si-concentrations around 1%.

5.2 Two sample *T*-Test

5.2.1 Nutrient contents by age

T-Tests were made to find out if there were statistical and significant differences between the juvenile and mature parts of papyrus (umbel, culm, scales, and rhizome) regarding nutrient concentrations. *T*-Tests were done on the single nutrient concentrations, so for TN, TOC, and DSi separately (Fig. 11). All the *T*-Tests had a significant difference with p-values < 0.001 except for TOC in umbels and culms and DSi in scales which had non-significant results and for TOC in umbels with a p-value of 0.004.

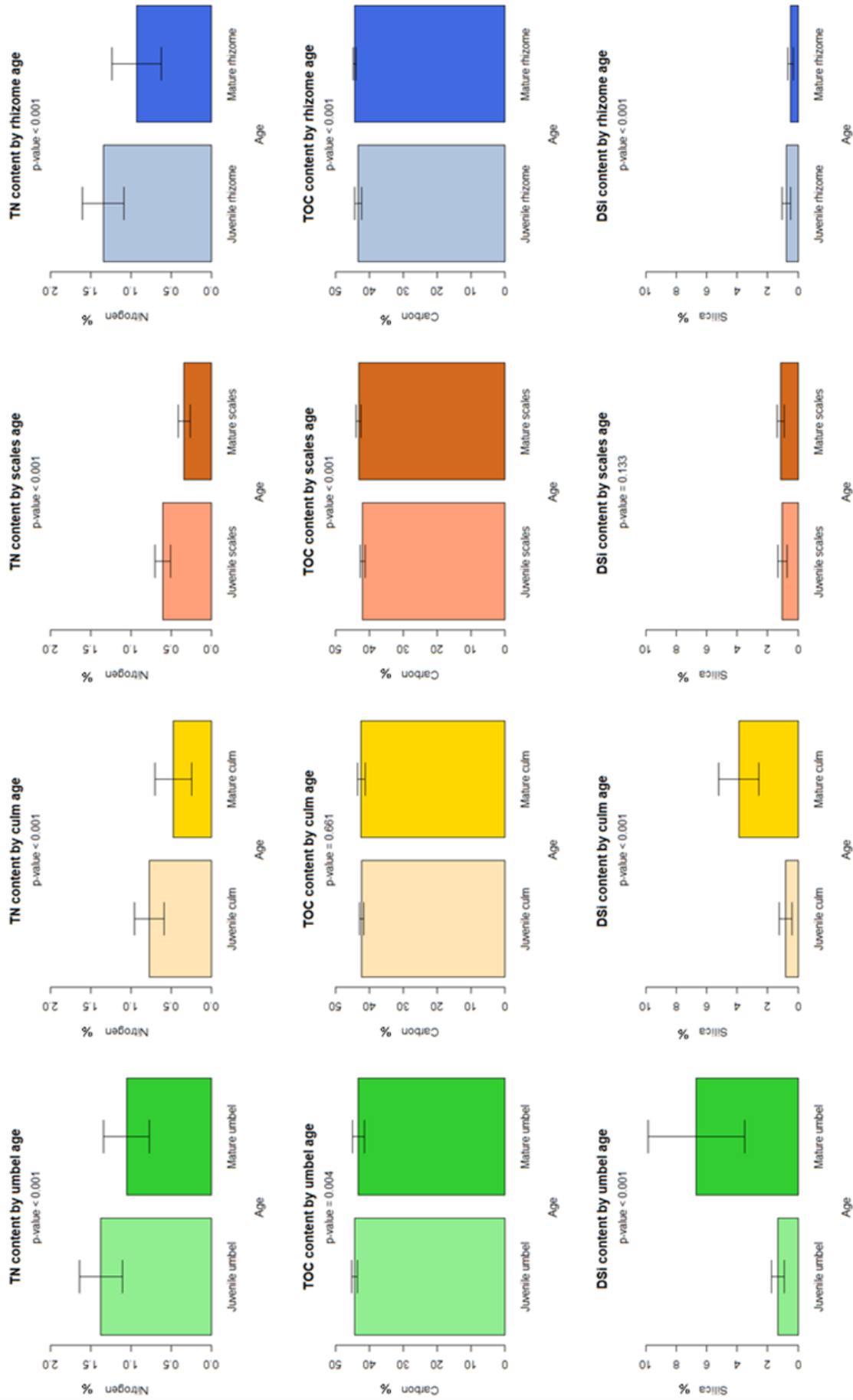


Figure 11. Bar plots representing 7-Tests results on nutrients content by the age of the different parts of the papyrus.

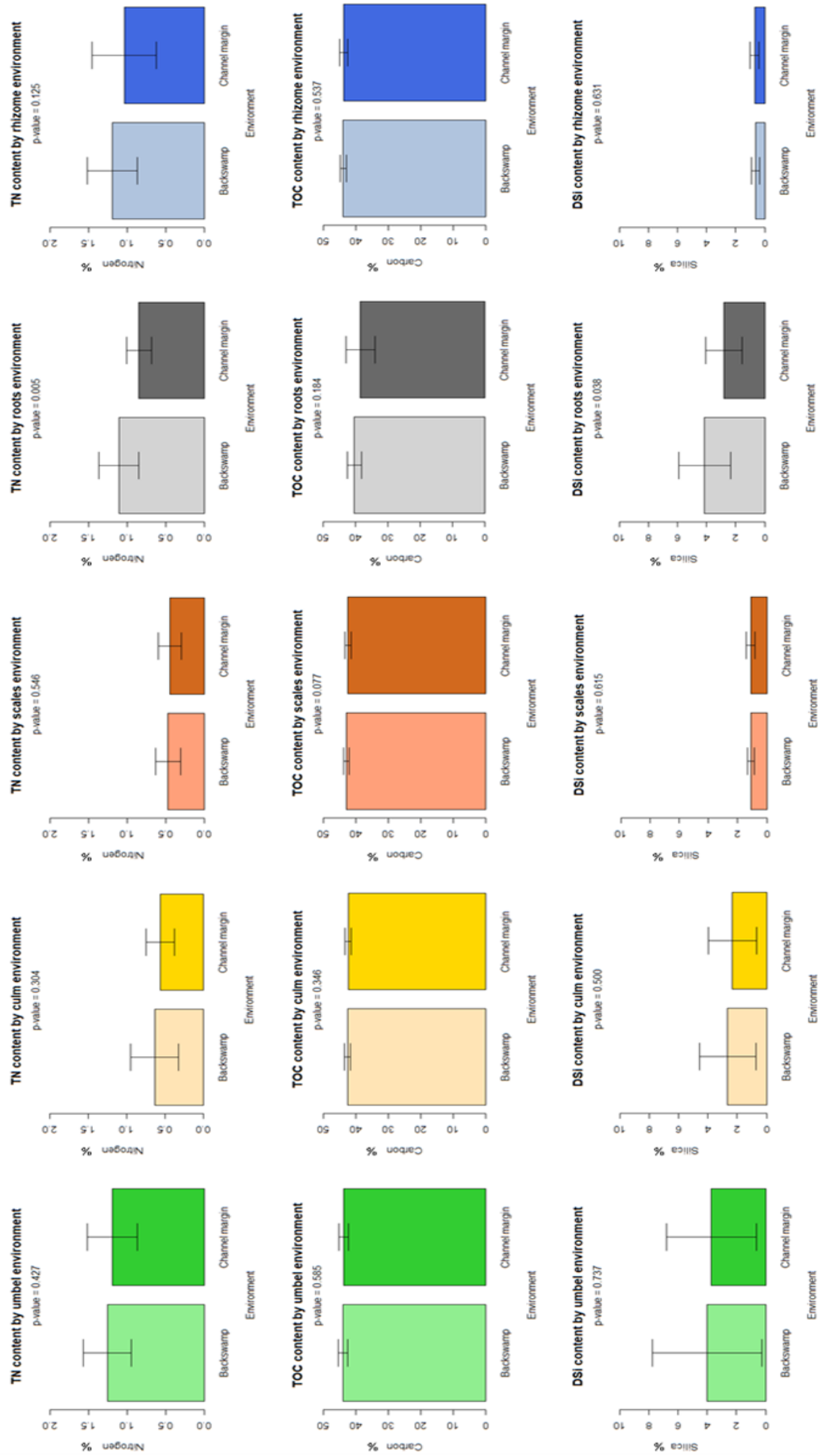


Figure 12. Bar plots representing T-Tests results on nutrients content by the environment of the different parts of the papyrus.

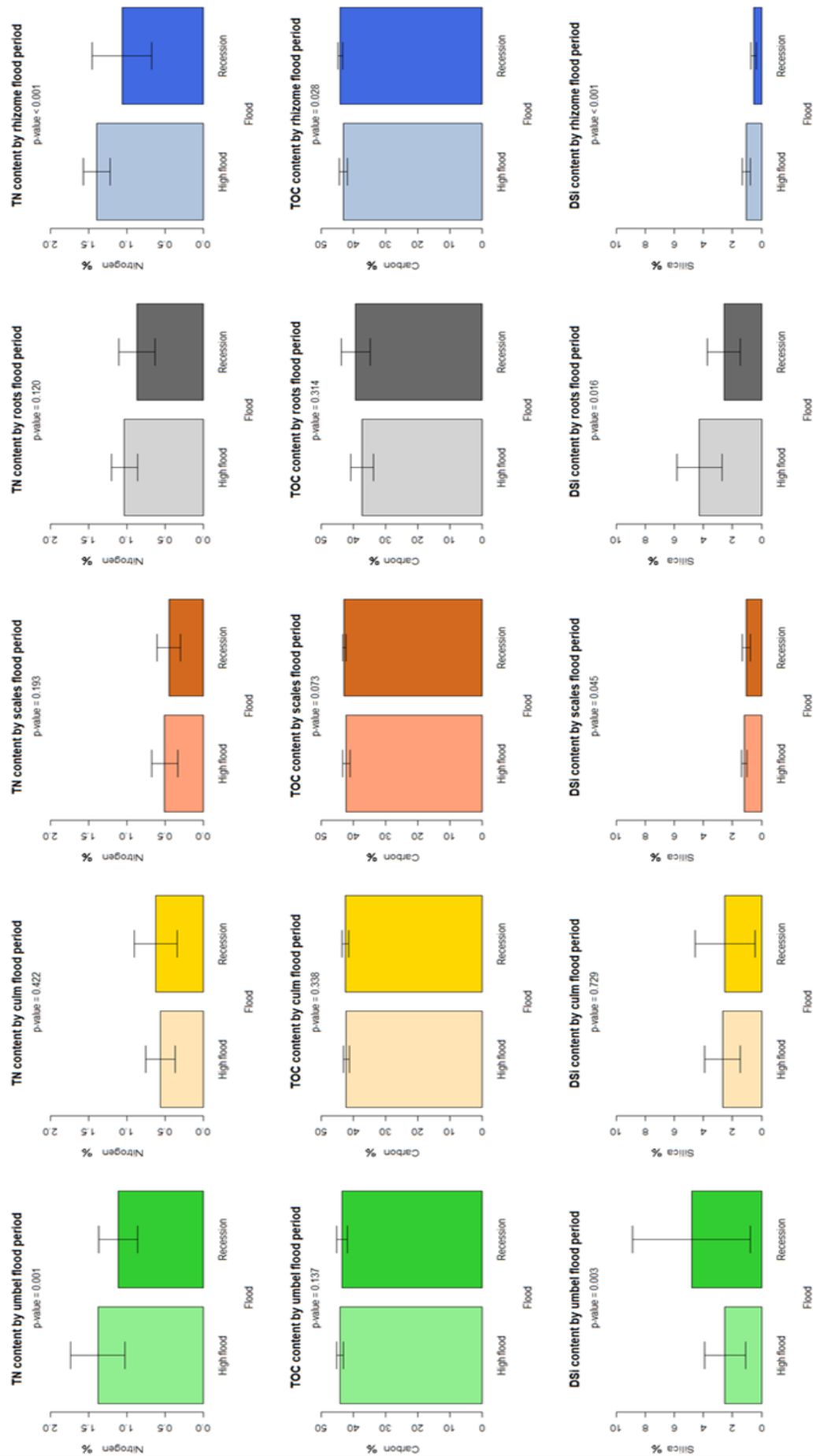


Figure 13. Bar plots representing T-Tests results on nutrients content by the flood period of the different parts of the papyrus.

See the Appendix for degrees of freedom, t statistics and p-values (Table A).

5.2.2 Nutrient contents by environment

A second round of *T*-Tests was made comparing the environment in which papyrus was growing: channel margin or backswamp. In this second round, the parts of the plant were not divided into juvenile and mature parts, and roots were also considered in the analysis (Fig. 12). Contrary than the first round, this time all the *T*-Tests have a non-significant result except for TN and DSi in roots.

See the Appendix for degrees of freedom, t statistics and p-values (Table B).

5.2.3 Nutrient contents by flood period

A third round of *T*-Tests was made comparing the flood period during which papyrus was harvested: high flood or flood recession. As in the second round, the parts of the plant were not divided into juvenile and mature parts and roots were included as well (Fig. 13). Differently from the previous rounds, there are almost half significant and half non-significant results.

See the Appendix for degrees of freedom, t statistics and p-values (Table C).

5.3 Two-way ANOVA

5.3.1 Two-way ANOVA on TN

The first ANOVA was made on the part of the plant and the environment (Fig. 14). Contrary to the results from the *T*-Test, the environment in which papyrus is growing had a significant result, with a p-value of 0.02, as well as the part of the plant with a p-value $< 0.02 \cdot 10^{-18}$. However, the interaction between the part of the plant and the environment was not statistically significant.

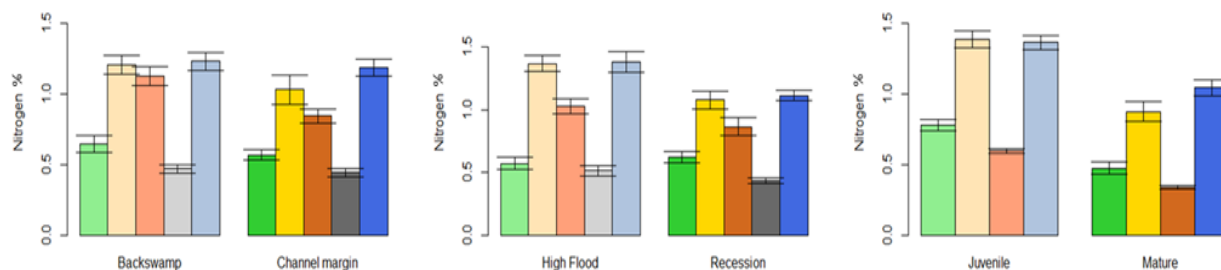


Figure 14. Bar plots representing the data analysed with the two-way ANOVA on nitrogen. The bar plot on the left shows the TN concentration in the different parts of papyrus and their environment. The bar plot in the centre shows the TN concentration in the different parts of the plant during the two periods of the flood pulse. The bar plot on the right shows the TN concentrations in the different parts of the plant (except roots) and their age. Green represents umbels, yellow represents culms, brown represents scales, grey represents roots, and blue represents rhizomes.

The second ANOVA was run on the part of the plant and the flood period (Fig. 14). In this analysis both the factors were significant with p-values of $< 0.22 \cdot 10^{-17}$ and $0.65 \cdot 10^{-5}$, as well as the interaction with a p-value of 0.03.

The third ANOVA was made on the part of the plant and the age (Fig. 14). As in the second ANOVA, the two factors and the interaction were significant: both the part of the plant and the age had a p-value $< 0.02 \cdot 10^{-18}$ while the interaction had a p-value of 0.04.

See the Appendix for degrees of freedom, t statistics and p-values (Table D).

5.3.2 Two-way ANOVA on TOC

A second set on ANOVA was done on TOC concentrations (Fig. 15). The first ANOVA was done on the parts of papyrus and the environment. TOC had a statistical difference only on the parts of the plant with a p-value $< 0.02 \cdot 10^{-18}$ while both the environment and the interaction were not statistically significant.

The second ANOVA (Fig. 15) had a statistical result for the factor “part of the plant” with a p-value $< 0.02 \cdot 10^{-18}$ and for the interaction with a p-value of 0.03. The factor “flood period” was not statistically significant.

The third ANOVA (Fig. 15) gave significant results for two categories. The factor “part of the plant” had a p-value of $1.09 \cdot 10^{-14}$, the factor “age” had a p-value of 0.06, and the interaction between the two had a p-value of $4.49 \cdot 10^{-8}$.

See the Appendix for degrees of freedom, t statistics and p-values (Table E).

5.3.3 Two-way ANOVA on BSi

The last set of ANOVA was done on BSi concentrations (Fig. 16). Once more, the factors were always the

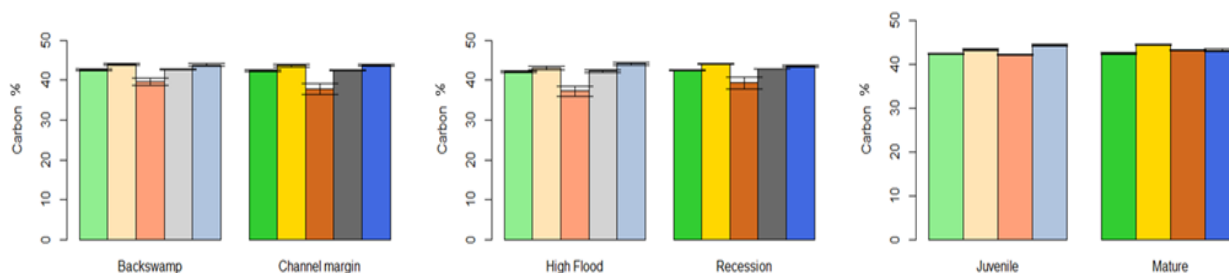


Figure 15. Bar plots representing the data analysed with the two-way ANOVA on carbon. The bar plot on the left shows the TOC concentration in the different parts of papyrus and their environment. The bar plot in the centre shows the TOC concentration in the different parts of the plant during the two periods of the flood pulse. The bar plot on the right shows the TOC concentrations in the different parts of the plant (except roots) and their age. Green represents umbels, yellow represents culms, brown represents scales, grey represents roots, and blue represents rhizomes.

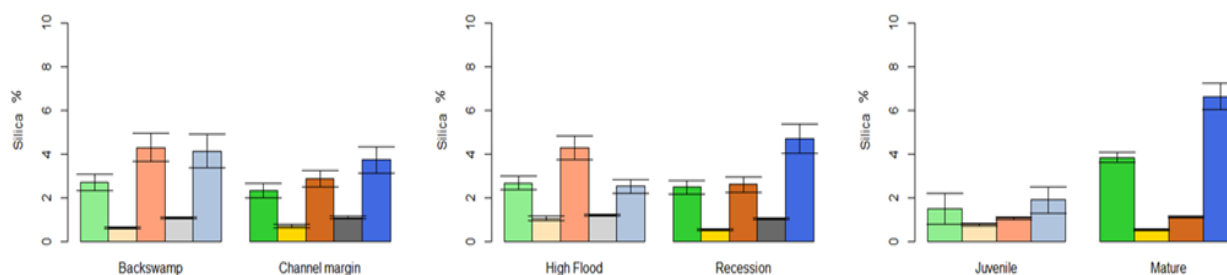


Figure 16. Bar plots representing the data analysed with the two-way ANOVA on BSi. The bar plot on the left shows the BSi concentration in the different parts of papyrus and their environment. The bar plot in the centre shows the BSi concentration in the different parts of the plant during the two periods of the flood pulse. The bar plot on the right shows the BSi concentrations in the different parts of the plant (except roots) and their age. Green represents umbels, yellow represents culms, brown represents scales, grey represents roots, and blue represents rhizomes.

same. This time, the first ANOVA on the part of the plant and the environment had a statistically significant result only for the first factor, the part of the plant, with a p-value of 4.86×10^{-16} .

The second ANOVA (Fig. 16) had a highly significant p-value for the part of the plant (p-value $< 0.22 \times 10^{-17}$) while the second factor was not significantly different. Nonetheless, the interaction between the part of the plant and the flood period was significant, with a p-value of 0.08×10^{-6} .

The third ANOVA (Fig. 16) gave highly significant results for all the three categories. In fact, the p-values obtained with this last analysis of variance were: $< 0.22 \times 10^{-17}$ for the first factor, 1.39×10^{-9} for the second factor, and 7.51×10^{-10} for the interaction.

See the Appendix for degrees of freedom, t statistics and p-values (Table F).

6 Discussion

6.1 TN in *Cyperus papyrus*

The highest concentrations of TN were found in the umbel. This organ functions as both a photosynthetic organ and an inflorescence, so a high TN concentra-

tion reflects its services. The second highest TN concentration was found in the rhizome, which acts as a storage for nutrients (Muthuri & Jones, 1997). Ultimately, high levels of TN in roots can be associated with nitrogen fixing bacteria (Muthuri & Jones, 1997). A study by Mwaura (1981) found that the root system was colonized by N_2 -fixing bacteria, and it was recorded a high rate of nitrogen fixation in roots.

In addition, the TN concentrations found in this study have been compared with measurements from papyrus samples collected either in the Okavango Delta (McCarthy et al., 1989) or in other wetlands in Africa (Table 1): Lake Naivasha, Kenya (Muthuri & Jones, 1997; Boar et al., 1999); Lake Victoria, Uganda (Lind & Visser, 1962).

TN concentrations have been observed to be higher in juvenile parts of papyrus than in mature parts, supporting the hypothesis. This can be connected to the productivity of the plant. In fact, juvenile plants are known to be more productive than mature ones, meaning that they grow faster. This consideration is in accordance with previous studies (Gaudet, 1977; Muthuri & Jones, 1997; Hes et al., 2021), where a higher concentration of TN was found in juvenile plants than in mature ones. Muthuri & Jones (1997)

Table 1. TN values and ranges in papyrus found in this study compared with TN values and ranges found in other studies.

Part of papyrus	TN	TN range	TN in Boar et al. (1999)	TN in Muthuri & Jones (1997)	TN in McCarthy et al. (1989)	TN in Gaudet (1977)	TN range in Gaudet (1977)	TN in Lind & Visser (1962)
Umbel	1,23	0,55-2,05	1,98	2	0,93	1,74	0,38-3,43	1,71
Culm	0,59	0,28-1,47	0,60	0,72	0,63	0,73	0,01-3,63	0,49
Scales	0,45	0,18-0,82		0,50				
Roots	0,94	0,48-1,63	0,94	1,4	0,75	1,12	0,48-1,69	0,75
Rhizome	1,14	0,41-2,15	0,99	1,4		1,29	0,28-2,50	1,11

Table 2. TN, TOC, and C/N ratios in papyrus found in this study compared to TN, TOC, and C/N ratios from McCarthy et al. (1989).

Age of papyrus	Part of papyrus	TN	TOC	C/N ratio	TN in McCarthy et al. (1989)	TOC in McCarthy et al. (1989)	C/N ratio in McCarthy et al. (1989)
Juvenile	Umbel	1,39	44,36	31,91			
	Culm	0,77	42,41	55,41	0,68	42,92	63,12
	Scales	0,59	42,08	71,57			
	Rhizome	1,36	43,32	31,94			
Mature	Umbel	1,05	43,34	41,32			
	Culm	0,46	42,55	92,32	0,35	41,83	119,50
	Scales	0,34	43,28	127,56			
	Rhizome	0,91	44,45	48,81			

reported that the biggest difference between juvenile and mature organs in TN concentration was found in umbels, with a concentration of 2.44% in juvenile umbels and 0.78% in mature umbels, while in this study it has been found 1.39% and 1.05% respectively. A similar decreasing trend with senescence of papyrus was observed also for the other organs of the plant but with lower gradients, the same trend observed by Muthuri & Jones (1997).

Another explanation for this is the active translocation and recycling in the juvenile stages of papyrus (Rejmánková, 2005; Asaeda et al., 2008). Emergent macrophytes like papyrus have a high efficiency in recycling elements because of both the high productivity and the nutrient translocation between the shoots and the rhizomes. The effects of this conservative strategy can be seen by comparing the concentrations of nitrogen in both juvenile and mature parts of papyrus and to the C/N ratios (McCarthy et al., 1989). In fact, the C/N ratios of mature organs is always higher or even double than in juvenile organs (Table 2).

The study by Boar et al. (1999) showed that there was no difference in nitrogen concentrations in the different organs of papyrus collected next to the river or far from the river. This can explain why the interaction between the part of the plant and the environment in the ANOVA was not statistically significant. Since papyrus has a high internal nitrogen's supply, the external supply from the river does not significantly affect TN accumulation in the different organs of papyrus (Boar et al., 1999). Nevertheless, higher concentrations of TN were found in papyrus growing

in the backswamp rather than on the channel margin, and the ANOVA on TN between the two environments was statistically significant. This result is opposite than what was hypothesized.

Regarding the flood periods, it has been observed that the highest productivity is achieved in sites where water regimes are stable (Thompson et al., 1979). In fact, a higher amount of TN has been found in papyrus during high flood periods rather than during flood recession, and this can reflect a higher productivity in the first case when water is stable and always present.

6.2 TOC in *Cyperus papyrus*

As found by Boar et al. (1999), carbon can make up to ~45% of papyrus's biomass. TOC concentrations found in this study have been compared to the ones from McCarthy et al. (1989) and Boar et al. (1999) and the percentages agree well (Table 3).

For the flood period, a higher concentration of TOC was found in rhizomes during recession than during high flood (43.05% during high flood, 44.22% during flood recession) while umbels had the opposite trend (44.22% during high flood, 43.63% during flood recession). This can be explained by a stressful condition in which papyrus is living during flood recession's times, as less water is present in the system. A study from Geremiew et al. (2018) found that under stressful conditions, of which flood recession can be an example, there was a morphological flexibility to

Table 3. TOC values in papyrus found in this study compared with values from Boar et al. (1999) and McCarthy et al. (1989).

Part of papyrus	TOC	TOC range	TOC in Boar et al. (1999)	TOC in McCarthy et al. (1989)
Umbel	43,86	39,40-46,57	45,6	41,73
Culm	42,49	40,38-45,64	43,6	41,66
Scales	42,74	40,33-44,70		
Roots	39,34	29,14-43,86	41,6	39,77
Rhizome	43,88	40,96-45,37	44,3	

Table 4. TOC values of the different organs of papyrus during the two flood periods (high flood or recession) and in the two different environments (channel margin or backswamp).

Flood period	Part of papyrus	TOC	Environment	Part of papyrus	TOC
High flood	Umbel	44,22	Channel margin	Umbel	43,77
	Culm	42,27		Culm	42,36
	Scales	42,29		Scales	42,56
	Roots	37,31		Roots	38,70
	Rhizome	43,05		Rhizome	43,71
Recession	Umbel	43,63	Backswamp	Umbel	44,02
	Culm	42,55		Culm	42,66
	Scales	42,90		Scales	42,91
	Roots	39,32		Roots	40,37
	Rhizome	44,22		Rhizome	43,91

smaller shoots and denser rhizomes, and this might be an explanation for the results presented above.

It was not possible to obtain a straightforward result for the hypotheses on TOC being higher both during high flood and on the channel margin than during flood recession and in the backswamp. In fact, considering the flood period, some parts show a higher concentration during high flood while some others have the opposite trend (Table 4). In addition, the ANOVA on TOC did not have a significant result when comparing values between the two different flood times but then the interaction between the parts of papyrus and the flood was significant. This could mean that carbon is redistributed within the plant according to the flood period. Whereas for the TOC in the environments, no statistical differences were found between the two environments.

6.3 BSi in *Cyperus papyrus*

The highest concentrations of BSi were found in mature organs, as was hypothesized, while in rhizomes the highest BSi is found in juveniles. This is the consequence of silica being accumulated by the plant throughout its life (Jones & Handreck, 1967). Moreover, BSi is a less labile plant element than nitrogen and carbon, and that is why there is more BSi increases with age as well (Eleuterius & Lanning, 1987).

The fact that BSi is not distributed uniformly among the different parts of plants and of papyrus can be explained by a passive transport of silica through the transpiration system and deposited in the regions mostly affected by water loss (Jones & Handreck, 1967). High BSi content in roots might improve plant resistance to both disease and drought stress (Hodson et al., 2005). Moreover, high BSi content in roots and culm may be important for the protection of the vascular tissues that are found in the internal regions of these two organs (Lux et al., 2003).

A comparison of the data obtained for BSi has been done, even if the studies on the amount of BSi in papyrus are very limited (Table 5).

The environmental factor was not significant for the BSi concentration in papyrus. ANOVA results were not statistically significant for the environment and *T*-Tests results were also not significant for all the organs except for roots. Moreover, Struyf et al. (2015) found that floodplain vegetation stores similar amounts of BSi in both permanently flooded and temporary flooded landscape.

BSi in the leaves is present in the form of opal bodies (Jones & Milne, 1963; Jones & Beavers, 1967) in epidermal cells (Parry & Smithson, 1964), in the walls of leaf cells (Dinsdale et al., 1979; Sakai & Thom, 1979), and in intercellular spaces (Parry &

Table 5. BSi values in papyrus from this study compared with values from Struyf et al. (2015) and Hodson et al. (2005).

Part of papyrus	BSi	BSi in Struyf et al. (2015)	BSi in Hodson et al. (2005)
Umbel	4,78		
Culm	2,73		1,07
Scales	1,08		
Roots	3,24		
Rhizome	0,61		
TOTAL	2,49	1,9	

Table 6. BSi values in different plants from other studies compared with BSi values of papyrus from this study.

Plant	Part of the plant	BSi	Struyf et al. (2015)	Struyf et al. (2005)	Hodson et al. (2005)	Lux et al. (2003)	Lux et al. (2002)	Motomura et al. (2000)	Meunier et al. (1999)	Jones & Handreck (1967)	Yoshida et al. (1962)
Papyrus	Umbel	4,78									
	Culm	2,73			1,07						
	Scales	1,08									
	Roots	3,24									
	Rhizome	0,61									
	TOTAL	2,49	1,9								
Oat	Umbel									7,72	
	Culm									1,03	
Bamboo spp.	Leaves							10,55			7,6
	Roots					2,4					
Nastus	Culm								58,73		
	Leaves								41,13		
	Rhizome								3,01		
Sorghum	Leaves				1,54						3,7
	Roots						2,8				
Rice	Culm				4,17						
	Leaves										18,3
	Roots										5,1
Reed	Culm			40,68	0,98						
	Leaves			18,28							
	TOTAL			39,77							
Nettle	Culm			4,32	1,34						
	Leaves			8							
	TOTAL			6,84							
Winter heater	Culm										
	Leaves								0,75		
	Roots								0,2		
Himalayan balsam	Culm			3,3							
	Leaves			0,63							
	TOTAL			3,52							

Smithson, 1964). The same silica deposition is found in the inflorescence (Parry & Smithson, 1964; Hayward & Parry, 1980). The deposition in the roots occurs in different ways and has various function depending on the plant species. In rice, silica is deposited within the inner wall of the cells of the roots (Parry & Soni, 1972), while in sorghum as an aggregate on the surface of the inner wall (Sangster & Parry, 1976). Anyhow, the function of silica in roots has been associated with the maturation of the cells, excretion of excess of monosilicic acid, and a system of strengthening the cell walls (Bennett & Sangster, 1981).

Furthermore, differential strategies exist in the uptake of dissolved silica from the environment. These are reflected in diverse trends in BSi concentrations in the different parts of the plant. For example, the nettle has almost double amount of silica in its leaves than in its culm (Table 6). While both papyrus and reed show the opposite trend. A larger concentration of BSi in the culm helps the plant to stand straight and to resist environmental stresses such as tides and wind (Struyf et al., 2005).

A variability of BSi in rhizomes has been observed both in this study and in Struyf et al. (2005).

Table 3. BSi values in papyrus and reed rhizomes during two different seasons. BSi values found in this study are compared with the values found from Struyf et al. (2005).

	Season	BSi	BSi in Struyf et al. (2005)
Papyrus rhizome	Winter	1,04	
	Summer	0,53	
Reed rhizome	Winter		15
	Summer		8

During winter, the time when the Okavango Delta is characterized by high flood, the amount of BSi in rhizomes is double than during the summer (flood recession; Table 7). The same trend has been detected in the amount of BSi in the reed's rhizome (Struyf et al., 2005). However, a seasonal variability caused by retranslocation of DSi is questionable, because, once BSi is deposited in the plant's tissues, it is immobilised (Struyf et al., 2005). A higher concentration of BSi during winter might be due to a higher amount of dissolved silica being transported during the flood.

7 Conclusion

To summarise, the main results found in this study are the following:

- Nitrogen is a fundamental nutrient for papyrus's growth and productivity. TN has been found in a higher concentration in juvenile plants, that are more productive than mature ones. An active translocation of N exists from mature to juvenile plants that explains the higher concentration in young papyrus. Moreover, a higher productivity was observed on the channel margin, where the water regime is stable. Umbels were the organs containing more TN as they are both photosynthetic organs and inflorescences; then rhizomes had the second highest, being a storage for nutrients; lastly, the third highest concentration was in roots where the nitrogen fixation takes place.
- TOC concentration of 39-43% were found in the study, the lowest being in roots and the highest in umbels and rhizomes. A higher concentration of TOC was found during high flood than during flood recession. The concentrations of TOC in the two environments did not have a statistically significant difference.
- Silicon is a very important element for papyrus and plants in general, favouring the shoots' rigidity and defence against diseases. Mature plants had more BSi than juvenile, reflecting the fact that silicon is accumulated into plants throughout their lives. Additionally, BSi was not distributed equally between the different

parts of papyrus. This might be caused by a passive transport of silica through the transpiration system and deposited in the regions mostly affected by water loss, as umbels might be. Moreover, a high concentration of BSi in roots can be explained as a mechanism increasing the plant's resistance to disease and drought. To conclude, the environment in which papyrus is growing does not seem to affect BSi concentration.

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9 References

- Asaeda, T., Rajapakse, L., & Fujino, T. (2008). Applications of organ-specific growth models; modelling of resource translocation and the role of emergent aquatic plants in element cycles. *Ecological Modelling*, 215, 170-179. <https://doi.org/10.1016/J.ECOLMODEL.2008.02.033>
- Bennett, D.M., & Sangster, A.G. (1981). The distribution of silicon in the adventitious roots of the bamboo *Sasa palmata*. *Botany*, 59, 1680-1684. <https://doi.org/10.1139/B81-226>
- Björkman, O. (1973). Comparative studies on photosynthesis in higher plants. In A. Giede (Eds.), *Current topics in photobiology, photochemistry and photophysiology Vol III* (pp. 1-63). Academic Press. <https://doi.org/10.1016/B978-0-12-282608-5.50007-2>
- Boar, R.R., Harper, D.M., & Adams, C.S. (1999). Biomass allocation in *Cyperus papyrus* in a tropical wetland, Lake Naivasha, Kenya. *Biotropica*, 31(3), 411-421. <https://doi.org/10.1111/j.1744->

[7429.1999.tb00383.x](#)

Bolton, J.K., & Brown, R.H. (1980). Photosynthesis of grass species differing in carbon dioxide fixation pathways V. Response of *Panicum maximum*, *Panicum milioides* and tall fescue (*Festuca arundinacea*) to nitrogen nutrition. *Plant Physiology*, 66, 97-100. <https://doi.org/10.1104/pp.66.1.97>

Bristow, J.H. (1974). Nitrogen fixation in the rhizosphere of freshwater angiosperms. *Canadian Journal of Botany*, 52, 217-221. <https://doi.org/10.1139/B74-025>

Christison, K.W., Shinn, A.P., & Van As, J.G. (2005). Gyrodactylus thlapi n. sp (Monogenea) from Pseudocrenilabrus philander philander (Weber) (Cichlidae) in the Okavango Delta, Botswana. *Systematic Parasitology*, 60(3), 165-173. <https://doi.org/10.1007/s11230-004-6342-x>

Conley, D.J. (2002). Terrestrial ecosystems and the global biogeochemical silica cycle. *Global Biogeochemical Cycles*, 16, 1121. <https://doi.org/10.1029/2002GB001894>

Conley, D.J., & Schelske, C.L. (2006). Biogenic Silica. In J.P. Smol, H.J.B. Birks, & W.M. Last (Eds.), *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators* (pp. 281–293). Kluwer Academic Publishers. https://doi.org/10.1007/0-306-47668-1_14

Cronberg G., Gieske A., Martins E., Prince Nengu J., & Stenström I. (1995). Hydrological studies of the Okavango Delta and the Kwando/Linyanti/Chobe River, Botswana. I: Surface Water Quality Analysis. *Botswana Notes and Records*, 27, 181-226.

Cronberg, G., Gieske, A., Martins, E., Prince-Nengu, J., & Stenström, I. (1996). Major ion chemistry, plankton, and bacterial assemblages of the Jao-Boro River, Okavango Delta, Botswana: the swamps and flood plains. *Archiv für Hydrobiologie - Supplementbände*, 3(107), 335-407.

De Heinzelin, J. (1963). A tentative paleogeographic map of Neogene Africa. In F.C. Howell, & F. Bouliere (Eds.), *African ecology and human evolution* (pp. 648-654). Viking Fund Publications in Anthropology.

De Swardt, A.M.J., & Bennet, G. (1974). The structural and physiographic evolution of Natal since the Late Jurassic. *Transactions of the Geological Society of South Africa*, 77(3), 309-322. https://doi.org/10.10520/AJA10120750_1292

Denny, P. (1985). *The ecology and management of African wetland vegetation: a botanical account of African swamps and shallow waterbodies*. Reidel Publishing Company.

Dingle, R.V. (1982). Continental margin subsidence: a comparison between the east and west coasts of Africa. In R.A. Scrutton (Eds.), *Dynamics of passive margins* (pp. 59-71). American Geophysical Union. <https://doi.org/10.1029/GD006p0059>

Dingle, R.V., Siesser, W.G., & Newton, A.R. (1983). *Mesozoic and Tertiary geology of southern Africa*. Balkema. <https://doi.org/10.1017/S0016756800029502>

Dinsdale, D., Gordon, A.H., & George, S. (1979). Silica in the Mesophyll Cell Walls of Italian Rye Grass (*Lolium multiflorum* Lam. cv. RvP). *Annals of Botany*, 44, 73-77. <https://doi.org/10.1093/oxfordjournals.aob.a085708>

Drar, M. (1951). The problem of the Sudd in relation to stabilizing and smothering plants. *Botaniska Notiser*, 1951(1), 32-46.

Dugdale, R.C., Wilkerson, F.P., & Minas, H.J. (1995). The role of a silicate pump in driving new production. *Deep-Sea Research Part I*, 42, 697-719. [https://doi.org/10.1016/0967-0637\(95\)00015-X](https://doi.org/10.1016/0967-0637(95)00015-X)

Eleuterius, L.N., & Lanning, F.C. (1987). Silica in relation to leaf decomposition of *Juncus roemerianus*. *Journal of Coastal Research*, 3(4), 531-534.

Ellery, W.N., Ellery, K., Rogers, K.H., & McCarthy, T.S. (1995). The role of *Cyperus papyrus* L. in channel blockage and abandonment in the northeastern Okavango Delta. *African Journal of Ecology*, 33(1), 25-49. <https://doi.org/10.1111/j.1365-2028.1995.tb00779.x>

Ellery, W.N., Ellery, K., McCarthy, T.S., Cairncross, B., & Oelofse, R. (1989). A peat fire in the Okavango Delta and its importance as an ecosystem process. *African Journal of Ecology*, 27, 7-21. <https://doi.org/10.1111/j.1365-2028.1989.tb00924.x>

Epstein, E. (2001). Silicon in plants: facts vs concepts. In L.E. Datnoff, G.H. Snyder, & G.H. Korndörfer (Eds), *Silicon in agriculture* (pp. 1-15). Elsevier Science. [https://doi.org/10.1016/S0928-3420\(01\)80005-7](https://doi.org/10.1016/S0928-3420(01)80005-7)

Fessenden, R.J., & Fessenden, J.S. (1967). The biological properties of silicon compounds. *Advances in drug research*, 4, 95-132.

Garstang, M., Ellery, W.N., McCarthy, T.S., Scholes, M.e., Scholes, R.J., Swap, R.J., & Tyson, P.D. (1998). The contribution of aerosol- and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana. *South African Journal of Science*, 94(5), 223-229. https://doi.org/10.10520/AJA00382353_210

Gaudet, J. J. (1977). Uptake, accumulation, and loss of nutrients by papyrus in tropical swamps. *Ecology*, 58(2), 415-422. <https://doi.org/10.2307/1935616>

Geremew, A., Stiers, I., Sierens, T., Kefalew, A., & Triest, L. (2018). Clonal growth strategy, diversity and structure: A spatiotemporal response to sedimentation in tropical *Cyperus papyrus* swamps. *PLoS ONE*, 13(1), 1-19. <https://doi.org/10.1371/journal.pone.0190810>

Grasshoff, K., Kremling, K., & Ehrhardt, M. (1999). *Methods of Seawater Analysis, Third Edition*. WILEY-VCH Verlag GmbH.

Handreck, K.A., & Jones, L.H. (1967). Uptake of Monosilicic Acid by *Trifolium incarnatum* (L.). *Australian Journal of Biological Sciences*, 20, 483-486. <https://doi.org/10.1071/B19670483>

Hartley, R.D., & Jones, L.H.P. (1972). Silicon Compounds in Xylem Exudates of Plants. *Journal of Experimental Botany*, 23(3), 637-640. <https://doi-org.eres.qnl.qa/10.1093/jxb/23.3.637>

Hayward, D.M., & Parry, D.W. (1980). Scanning electron microscopy of silica deposits in the culms, floral bracts and awns of barley (*Hordeum sativum* Jess.) *Annals of Botany*, 46, 541-548.

Hes, E.M.A., Yatoi, R., Laisser, S.L., Feyissa, A.K., Irvine, K., Kipkemboi, J., & Van Dam, A.A. (2021). The effect of seasonal flooding and livelihood activities on retention of nitrogen and phosphorous in *Cyperus papyrus* wetlands, the role of aboveground biomass. *Hydrobiologia*, 848, 4135-4152. <https://doi.org/10.1007/s10750-021-04629-3>

Hodson, M.J., White, P.J., Mead, A., & Broadley, M.R. (2005). Phylogenetic variation in the silicon composition of plants. *Annals of Botany*, 96, 1027-1046. <https://doi.org/10.1093/aob/mci255>

Hope, C.W. (1902). The "Sadd" of the Upper Nile: its botany compared with that of similar obstructions in Bengal and American waters. *Annals of Botany*, 16, 495-516. <https://doi.org/10.1093/oxfordjournals.aob.a088886>

Hutchins, D.G., Hutton, L.G., Hutton, S.M., Jones, C.R., & Loenhardt, E.P. (1976). A summary of the geology, seismicity, geomorphology and hydrogeology of the Okavango Delta. *Botswana Geo-*

logical Survey, *Bulletin* 7, 1-27.

Jones, L.H.P., & Handreck, K.A. (1967). Silica in soils, plants, and animals. *Advances in Agronomy*, 19, 107-149. [https://doi.org/10.1016/S0065-2113\(08\)60734-8](https://doi.org/10.1016/S0065-2113(08)60734-8)

Jones, L.H.P., & Milne, A.A. (1963). Studies of silica in the oat plant. 1. Chemical and physical properties of the silica. *Plant and Soil*, 18, 207-220. <https://doi.org/10.1007/BF01347875>

Jones, M. (1988). Photosynthetic responses of C3 and C4 wetland species in a tropical swamp. *Journal of Ecology*, 76, 253-262. <https://doi.org/10.2307/2260467>

Jones, M., & Muthuri, F. (1997). Standing biomass and carbon distribution in a papyrus (*Cyperus papyrus* L.) swamp on Lake Naivasha, Kenya. *Journal of Tropical Ecology*, 13, 347-356. <https://doi.org/10.1017/S0266467400010555>

Jones, M.B. (1987). The photosynthetic characteristics of papyrus in a tropical swamp. *Oecologia*, 71, 355-359. <https://doi.org/10.1007/BF00378707>

Jones, R.L., & Beavers, A. (1963). Some mineralogical and chemical properties of plant opal. *Soil Science*, 96, 375-379.

Krah, M., McCarthy, T.S., Annegarn, H., & Ramberg, L. (2004). Airborne dust deposition in the Okavango Delta, Botswana, and its impact on landforms. *Earth Surface Processes and Landforms*, 29 (5), 565-577. <https://doi.org/10.1002/ESP.1051>

Krah, M., McCarthy, T.S., Huntsman-Mapila, P., Wolski, P., Annegarn, H., & Sethebe, K. (2006). Nutrient budget in the seasonal wetland of the Okavango Delta, Botswana. *Wetlands Ecology and Management*, 14, 253-267. <https://doi.org/10.1007/s11273-005-1115-0>

Lind, E., & Visser, S. (1962). A study of a swamp at the north end of Lake Victoria. *Journal of Ecology*, 50, 599-613. <https://doi.org/10.2307/2257472>

Lux, A., Luxová, M., Abe, J., Morita, S., & Inanaga, S. (2003). Silicification of bamboo (*Phyllostachys heterocycle* Mitf.) root and leaf. *Plant and Soil*, 255, 85-91. https://doi.org/10.1007/978-94-017-2923-9_9

Lux, A., Luxová, M., Hattori, T., Inanaga, S., & Sugimoto, Y. (2002). Silicification in sorghum (*Sorghum bicolor*) cultivars with different drought tolerance. *Physiologia plantarum*, 115(1), 87-92. <https://doi.org/10.1034/J.1399-3054.2002.1150110.X>

Mallick, D.I.J., Hapgood, F., & Skinner, C.A. (1981). *A geological interpretation of Landsat imagery and air photography of Botswana*. Institute of Geological Sciences.

McCarthy, T.S. (1992). Physical and biological processes controlling the Okavango Delta – A review of recent research. *Botswana Notes and Records*, 24(1), 57-86.

McCarthy, T.S., & Ellery, W.N. (1998). The Okavango Delta. *Transactions of the Royal Society of South Africa*, 53(2), 157-182. <https://doi.org/10.1080/00359199809520384>

McCarthy, T.S., & Metcalfe, J. (1990). Chemical sedimentation in the semi-arid environment of the Okavango Delta, Botswana. *Chemical Geology*, 80, 157-178. [https://doi.org/10.1016/0009-2541\(90\)90065-F](https://doi.org/10.1016/0009-2541(90)90065-F)

McCarthy, T.S., Green, R.W., & Franey, N.J. (1993). The influence of neo-tectonics on water dispersal in the northeastern regions of the Okavango swamps, Botswana. *Journal of African Earth Sciences*, 17, 23-32. [https://doi.org/10.1016/0899-5362\(93\)90019-M](https://doi.org/10.1016/0899-5362(93)90019-M)

McCarthy, T.S., McIver, J.R., Cairncross, B., Ellery, W.N., & Ellery, K. (1989). The inorganic-chemistry of peat from the Mau-nachira channel-swamp system, Okavango Delta, Botswana. *Geochimica et Cosmochimica Acta*, 53(5), 1077-1089. [https://doi.org/10.1016/0016-7037\(89\)90212-3](https://doi.org/10.1016/0016-7037(89)90212-3)

McCarthy, T.S., Rogers, K.H., Stanistreet, I.G., Ellery, W.N., Cairncross, B., Ellery, K., & Grobicki, T.S.A. (1988). Features of channel margins in the Okavango Delta. *Palaeoecology of Africa*, 19, 3-14.

McKeague, J. A., & Cline, M. G. (1963). Silica in soil solutions: II. The adsorption of monosilicic acid by soil and by other substances. *Canadian Journal of Soil Science*, 43(1), 83-96. <https://doi.org/10.4141/cjss63-01>

Mendelsohn, J.M., vanderPost, C., Ramberg, L., Murray-Hudson, M., Wolski, P., & Mosepele, K. (2010). *Okavango Delta: Floods of Life*. RAISON.

Meunier, J.D., Colin, F., & Alarcon, C. (1999). Biogenic silica storage in soils. *Geology*, 27(9), 835-838. [https://doi.org/10.1130/0091-7613\(1999\)027<0835:BSSIS>2.3.CO;2](https://doi.org/10.1130/0091-7613(1999)027<0835:BSSIS>2.3.CO;2)

Mitsch, W.J., & Gosselink, J.G. (2000). *Wetlands*. John Wiley and Sons. <https://doi.org/10.1002/rrr.637>

Motomura, H., Fujii, T., & Suzuki, M. (2000). Distribution of Silicified Cells in the Leaf Blades of *Pleioblastus chino* (Franchet et Savatier) Makino (Bambusoideae). *Annals of Botany*, 85, 751-757. <https://doi.org/10.1006/ANBO.2000.1124>

Muthuri, F.M., & Kinyamario, J.I. (1989). Nutritive value of papyrus (*Cyperus papyrus*, Cyperaceae), a tropical emergent macrophyte. *Economic Botany*, 43(1), 23-30. <https://doi.org/10.1007/BF02859321>

Muthuri, F.M., & Jones, M.B. (1997). Nutrient distribution in a papyrus swamp: Lake Naivasha, Kenya. *Aquatic Botany*, 56, 35-50. [https://doi.org/10.1016/S0304-3770\(96\)01093-5](https://doi.org/10.1016/S0304-3770(96)01093-5)

Mwaura, F.R. (1981). Nitrogen fixation in the papyrus swamps of Lake Naivasha. MSc Thesis, University of Nairobi, Kenya.

Nash, D.J., Meadows, M.E., & Gulliver, V.L. (2006). Holocene environmental change in the Okavango Panhandle, northwest Botswana. *Quaternary Science Reviews*, 25, 1302-1322. <https://doi.org/10.1016/j.quascirev.2005.11.004>

Ollier, C.D. (1985). Morphotectonics of continental margins with great escarpments. In M. Morisawa, & J.T. Hack (Eds.) *Tectonic geomorphology* (pp. 3-25). Allen and Unwin. <https://doi.org/10.1002/esp.3290120410>

Parry, D.W., & Smithson, F. (1964). Types of Opaline Silica Depositions in the Leaves of British Grasses. *Annals of Botany*, 28, 169-185. <https://doi.org/10.1093/oxfordjournals.aob.a083891>

Parry, D.W., & Soni, S.L. (1972). Electron-probe microanalysis of silicon in the roots of *Oryza sativa* (L.). *Annals of Botany*, 36, 781-783. <https://doi.org/10.1093/oxfordjournals.aob.a084633>

Patriquin, D., & Knowles, R. (1972). Nitrogen fixation in the rhizosphere of marine angiosperms. *Marine Biology*, 16, 49-58. <https://doi.org/10.1007/BF00347847>

Perkins, J.S., & Thomas, D.S.G. (1993). Spreading deserts or spatially confined environmental impacts? Land degradation and cattle ranching in the Kalahari Desert of Botswana. *Land Degradation and Rehabilitation*, 4, 179-194. <https://doi.org/10.1002/ldr.3400040307>

Piedade, M., Junk, W., & Long, S. (1991). The productivity of the C4 grass *Echinochloa polystachya* on the Amazon floodplain. *Ecology*, 72, 1456-1463. <https://doi.org/10.2307/1941118>

- Piperno, D.R. (1988). *Phytolith analysis – an archeological and ecological perspective*. Academic Press. <https://doi.org/10.1002/gea.3340050207>
- Rejmánková, E. (2005). Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytologist*, 167, 471–482. <https://doi.org/10.1111/J.1469-8137.2005.01449.X>
- Sakai, W.S., & Thom, M. (1979). Localization of Silicon in Specific Cell Wall Layers of the Stomatal Apparatus of Sugar Cane by Use of Energy Dispersive X-ray Analysis. *Annals of Botany*, 44(2), 245–248. <http://www.jstor.org/stable/42770195>
- Sangster, A.G., & Parry, D.W. (1976). The ultrastructure and electron-probe microassay of silicon deposits in the endodermis of the seminal roots of *Sorghum bicolor* (L.) Moench. *Annals of Botany*, 40, 447–459. <https://doi.org/10.1093/OXFORDJOURNALS.AOB.A085153>
- Saunders, M.J., Kansime, F., & Jones, M.B. (2012). Agricultural encroachment: implications for carbon sequestration in tropical African wetlands. *Global Change Biology*, 18, 1312–1321. <https://doi.org/10.1111/j.1365-2486.2011.02633.x>
- Saunders, M.J., Kansime, F., Jones, M.B. (2013). Reviewing the carbon cycle dynamics and carbon sequestration potential of *Cyperus papyrus* L. wetlands in tropical Africa. *Wetlands Ecology and Management*, 22, 143–155. <https://doi.org/10.1007/s11273-013-9314-6>
- Sawula, G.M., & Martins, E. (1991). Major ion chemistry of the lower Boro River, Okavango Delta, Botswana. *Freshwater Biology*, 26, 481–493. <https://doi.org/10.1111/J.1365-2427.1991.TB01413.X>
- Scholz, C.H., Koezyski, T.A., & Hutchins, D.G. (1976). Evidence for incipient rifting in southern Africa. *The Geophysical Journal of the Royal Astronomical Society*, 44, 135–144. <https://doi.org/10.1111/j.1365-246X.1976.tb00278.x>
- Shaw, P.A. (1988). After the flood: the fluvio-lacustrine landforms of northern Botswana. In J. Firman (Eds.) *Landscapes of the Southern Hemisphere* (pp. 449–456). Elsevier Science Publishers B.V. [https://doi.org/10.1016/0012-8252\(88\)90011-6](https://doi.org/10.1016/0012-8252(88)90011-6)
- Smith, N.D., McCarthy, T.S., Ellery, W.N., Merry, C.L., & Rutter, H. (1997). Avulsion and anastomosis in the Panhandle regions of the Okavango fan, Botswana. *Geomorphology*, 20, 49–65. [https://doi.org/10.1016/S0169-555X\(96\)00051-7](https://doi.org/10.1016/S0169-555X(96)00051-7)
- Stanistreet, I.G., & McCarthy, T.S. (1993). The Okavango fan and the classification of subaerial fan systems. *Sedimentary Geology*, 85 (1–4), 115–133. [https://doi.org/10.1016/0037-0738\(93\)90078-J](https://doi.org/10.1016/0037-0738(93)90078-J)
- Struyf, E. & Conley, D.J. (2009). Silica: an essential nutrient in wetland biogeochemistry. *Frontiers in Ecology and the Environment*, 7, 88–94. <https://doi.org/10.1890/070126>
- Struyf, E., Van Damme, S., Gribsholt, B., Middelburg, J., & Meire, P. (2005). Biogenic silica in freshwater marsh sediments and vegetation. *Marine Ecology Progress Series*, 303, 51–60. <https://doi.org/10.3354/MEPS303051>
- Struyf, E., Mosimane, K., Van Pelt, D., Murray-Hudson, M., Meire, P., Frings, P., Wolski, P., Schaller, J., Gondwe, M.J., Schoelynck, J., & Conley, D.J. (2015). The role of vegetation in the Okavango Delta silica sink. *Wetlands*, 35, 1–11. <https://doi.org/10.1007/s13157-014-0607-1>
- Summerfield, M.A. (1985). Plate tectonics and landscape development in Africa. In M. Morisawa, & J.T. Hack (Eds.) *Tectonic geomorphology* (pp. 27–51). Allen and Unwin. <https://doi.org/10.1002/esp.3290120410>
- Thomas, D.S.G. (1984). Ancient ergs of the former arid zones of Zimbabwe, Zambia and Angola. *Transactions of the Institute of British Geographers*, 9(1), 75–88. <https://doi.org/10.2307/621868>
- Thomas, D.S.G., & Shaw, P.A. (1988). Late Cainozoic drainage evolution in the Zambezi basin: geomorphological evidence from the Kalahari rim. *Journal of African Earth Sciences*, 7, 611–618. [https://doi.org/10.1016/0899-5362\(88\)90111-X](https://doi.org/10.1016/0899-5362(88)90111-X)
- Thomas, D.S.G., & Shaw, P.A. (1990). The deposition and development of the Kalahari Group sediments, Central Southern Africa. *Journal of African Earth Sciences*, 10, 187–197. [https://doi.org/10.1016/0899-5362\(90\)90054-1](https://doi.org/10.1016/0899-5362(90)90054-1)
- Thomas, D.S.G., & Shaw, P.A. (1991). *The Kalahari Environment*. Cambridge University Press. <https://doi.org/10.2307/1159756>
- Thompson, K. (1976). Swamp development in the headwaters of the White Nile. In J. Rzoska (Eds.) *The Nile, Biology of an Ancient River* (pp. 177–196). Springer. <https://doi.org/10.1007/978-94-010-1563-9>
- Thompson, K., Shewry, P.R., & Woolhouse, H.W. (1979). Papyrus swamp development in the Upemba Basin, Zaire: studies of population structure in *Cyperus papyrus* stands. *Botanical Journal of the Linnaean Society*, 78, 299–316. <https://doi.org/10.1111/J.1095-8339.1979.TB02573.X>
- Van Cappellen, P. (2003). Biomineralization and global biogeochemical cycles. *Reviews in Mineralogy and Geochemistry*, 54, 357–381. <https://doi.org/10.1515/9781501509346-017>
- West, D.T., van As, J.G., & van As, L.L. (2015). Surface water quality in the Okavango Delta panhandle, Botswana. *African Journal of Aquatic Science*, 40(4), 359–372. <https://doi.org/10.2989/16085914.2015.1104288>
- Wilson, J.R. (1975). Comparative response to nitrogen deficiency of a tropical and temperate grass in the interrelation between photosynthesis, growth and accumulation of non-structural carbohydrate. *Netherlands Journal of Agricultural Science*, 23, 104–112. <https://doi.org/10.18174/njas.v23i2.17189>
- Wolski, P., Savenije, H.H.G., Murray-Hudson, M., & Gumbrecht, T. (2006). Modelling of the flooding in the Okavango Delta, Botswana, using a hybrid reservoir-GIS model. *Journal of Hydrology*, 331, 58–72. <https://doi.org/10.1016/J.JHYDROL.2006.04.040>
- Wolski, P., Murry-Hudson, M., Fernkvist, P., Lidén, A., Huntsman-Mapila, P., & Ramberg, L. (2005). Islands in the Okavango Delta as sinks of water-borne nutrients. *Botswana Notes & Records*, 37, 253–263. <https://doi.org/10.2307/40980418>
- Yoshida, S., Ohnishi, Y., & Kitagishi, K. (1962). Chemical Forms, Mobility and Deposition of Silicon in Rice Plant. *Soil Science and Plant Nutrition*, 8, 15–21. <https://doi.org/10.1080/00380768.1962.10430992>

10 Appendix

Table A. T-Tests results comparing the age of papyrus and nutrient concentrations.

NITROGEN	Degrees of freedom	t statistics	P value	
Juv/Mat umbels	57	4	4,05E-02	***
Juv/Mat culms	57	5	9,58E-04	***
Juv/Mat scales	62	12	< 2,2E-16	***
Juv/Mat rhizomes	58	6	6,48E-04	***
CARBON	Degrees of freedom	t statistics	P value	
Juv/Mat umbels	41	3	4,955E-03	***
Juv/Mat culms	57	-0,441	0,661	
Juv/Mat scales	62	-7	3,11E-06	***
Juv/Mat rhizomes	38	-6	2,27E-06	***
SILICA	Degrees of freedom	t statistics	P value	
Juv/Mat umbels	55	-9	2,00E-09	***
Juv/Mat culms	55	-11	7,52E-13	***
Juv/Mat scales	62	-2	0,134	
Juv/Mat rhizomes	53	4	1,83E-04	***

Table B. T-Tests results comparing the environment of papyrus and nutrient concentrations.

NITROGEN	Degrees of freedom	t statistics	P value	
Chan/Back umbels	55	0,799	0,428	
Chan/Back culms	55	1,036	0,305	
Chan/Back scales	61	0,607	0,546	
Chan/Back roots	23	3,070	0,005	**
Chan/Back rhizomes	55	1,556	0,125	
CARBON	Degrees of freedom	t statistics	P value	
Chan/Back umbels	55	0,549	0,585	
Chan/Back culms	53	0,951	0,346	
Chan/Back scales	61	1,795	0,078	
Chan/Back roots	22	1,372	0,184	
Chan/Back rhizomes	55	0,621	0,537	
SILICA	Degrees of freedom	t statistics	P value	
Chan/Back umbels	53	0,338	0,737	
Chan/Back culms	53	0,678	0,501	
Chan/Back scales	60	-0,505	0,615	
Chan/Back roots	23	2,192	0,039	*
Chan/Back rhizomes	51	-0,483	0,632	

Table C. T-Tests results comparing the flood period of papyrus and nutrient concentrations.

NITROGEN	Degrees of freedom	t statistics	P value	
Flood/Recumbels	55	3,289	0,002	**
Flood/Rec culms	54	-0,809	0,422	
Flood/Rec scales	56	1,317	0,193	
Flood/Rec roots	16	1,642	0,120	
Flood/Rec rhizomes	38	3,926	0,0004	***
CARBON	Degrees of freedom	t statistics	P value	
Flood/Recumbels	55	1,509	0,137	
Flood/Rec culms	53	-0,965	0,339	
Flood/Rec scales	19	-1,895	0,073	
Flood/Rec roots	16	-1,039	0,315	
Flood/Rec rhizomes	12	-2,497	0,028	*
SILICA	Degrees of freedom	t statistics	P value	
Flood/Recumbels	48	-3,072	0,004	**
Flood/Rec culms	42	0,348	0,729	
Flood/Rec scales	55	2,050	0,045	*
Flood/Rec roots	16	2,679	0,017	*
Flood/Rec rhizomes	43	6,598	4,929E-08	***

Table D. ANOVA results on TN concentration comparing the part of the plant with the environment (orange), flood period (blue), and age (yellow).

NITROGEN	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	22.2535	5.5634	70.8524	<2e-16	***
Environment	1	0.4574	0.4574	5.8252	0.01664	*
Part of the plant:Environment	4	0.3072	0.0768	0.9780	0.42047	
Residuals	213	16.7249	0.0785			
NITROGEN	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	22.2535	5.5634	75.0060	<2.2e-16	***
Flood period	1	0.8887	0.8887	11.9813	0.0006492	***
Part of the plant:Flood period	4	0.8021	0.2005	2.7034	0.0314821	*
Residuals	213	15.7987	0.0742			
NITROGEN	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	3	22.0710	7.3570	140.2536	<2e-16	***
Age	1	5.9046	5.9046	112.5651	<2e-16	***
Part of the plant:Age	3	0.4314	0.1438	2.7413	0.04444	*
Residuals	197	10.3336	0.0525			

Table E. ANOVA results on TOC concentration comparing the part of the plant with the environment (orange), flood period (blue), and age (yellow).

CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	457.08	114.270	47.7651	<2e-16	***
Environment	1	6.82	6.825	2.8527	0.09269	
Part of the plant:Environment	4	10.74	2.685	1.1225	0.34681	
Residuals	213	509.57	2.392			
CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	457.08	114.270	49.3679	<2e-16	***
Flood period	1	8.25	8.248	3.5634	0.06043	
Part of the plant:Flood period	4	25.86	6.465	2.7932	0.02724	*
Residuals	213	493.02	2.315			
CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	3	81.612	27.2041	27.0361	1.092e-14	***
Age	1	3.672	3.6723	3.6497	0.05753	
Part of the plant:Age	3	40.906	13.6352	13.5511	4.488e-08	***
Residuals	197	198.224	1.0062			

Table F. ANOVA results on BSi concentration comparing the part of the plant with the environment (orange), flood period (blue), and age (yellow).

CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	457.08	114.270	47.7651	<2e-16	***
Environment	1	6.82	6.825	2.8527	0.09269	
Part of the plant:Environment	4	10.74	2.685	1.1225	0.34681	
Residuals	213	509.57	2.392			
CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	4	457.08	114.270	49.3679	<2e-16	***
Flood period	1	8.25	8.248	3.5634	0.06043	
Part of the plant:Flood period	4	25.86	6.465	2.7932	0.02724	
Residuals	213	493.02	2.315			
CARBON	Df	Sum Sq	Mean Sq	F value	P value	
Part of the plant	3	81.612	27.2041	27.0361	1.092e-14	***
Age	1	3.672	3.6723	3.6497	0.05753	
Part of the plant:Age	3	40.906	13.6352	13.5511	4.488e-08	***
Residuals	197	198.224	1.0062			

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