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The role of vegetation in the Okavango Delta silica sink

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Abstract

We assessed the role of vegetation and hydrology in the Si cycle in the Okavango Delta. Our results show a large storage of biogenic Si (BSi) in vegetation and the sediments. The biological storage is among the highest observed so far for any ecosystem worldwide. Floodplain vegetation accumulates similar amounts of BSi in both the temporary floodplains and the permanent floodplains, with most values observed between 20-100 g Si m^{-2}. This vegetation Si, after litterfall, contributes to a large biogenic Si storage in the sediments. In temporary floodplains, sediments contain less BSi (375 -1950 g Si m^{-2} in the top 5 cm) than in the permanent floodplains (1950 - 3600 g Si m^{-2} in the top 5 cm). BSi concentrations in the floodplain sediments decline exponentially indicating rapid dissolution. In the occasional and seasonal floodplains, unidirectional solute transfer from floodplains to the islands will remove Si from the riverine systems. Our work clearly emphasizes the crucial role of floodplains and wetlands in Si transport through tropical rivers, and the potential interference of hydrology with this role.

Introduction

Research on Si cycling in continental ecosystems has received increasing attention in the past decade. While it is clear that large amounts of weathered Si are cycling through ecosystems (Conley 2002; Carey and Fulweiler 2012), the quantification of biogenic Si in ecosystem soils and sediments (Barao et al. 2014), how this is related to biogenic Si (BSi) accumulation in vegetation and how this influences Si transport in rivers is still largely enigmatic (Struyf & Conley 2012). Current studies clearly point to the role of wetlands as Si-accumulators in the global biogeochemical Si cycle. Wetlands, situated at the interface between terrestrial and aquatic ecosystems, can act as strong filters on the transport of Si from the continents to the coastal environment (Struyf & Conley 2009), especially because large amounts of Si accumulating grasses often dominate the vegetation. More and more evidence points to the accumulation of Si in wetlands grasses being a functional trait, where uptake of Si is dependent on the environmental stressors experienced by the vegetation, e.g. herbivory or flooding dynamics (Schoelynck et al. 2014; Carey & Fulweiler 2014). As such, wetlands are essential ecosystems to study in the emerging research field of biological control on the continental Si mobilization (Derry et al. 2005). In temperate and subarctic climates, both riparian (e.g. Struyf et al. 2009; 2010) and tidal wetlands (e.g. Struyf et al. 2006; Müller et al. 2013) have been studied, but tropical wetlands have not yet received attention.

The Okavango Delta (Botswana) is one of the world's largest tropical wetland systems, and hence an interesting study area in this regard. It consists of a mosaic of permanent and temporary floodplains, intersected with tree-covered islands (McCarthy et al. 2012). The Okavango Delta's water balance is dominated by evapotranspiration: 98% of all water is lost to the atmosphere before reaching the outlets. The islands play an unusual and essential ecological role in the Okavango Delta as they act as permanent sinks for a major part of the solutes (ca. 360 000 tons a^{-1}) that enter the system (Ramberg & Wolski 2008). Various biological mechanisms result in unidirectional solute transfer from the floodplains to the islands that allow the Delta to remain a productive freshwater wetland ecosystem (Ramberg & Wolski 2008). Evapotranspiration by island trees induces a local lowering of the water table below the islands, creating large hydraulic gradients and inducing lateral groundwater flow. As a result, water infiltrates into the floodplains and flows belowground from the floodplains to the islands bringing dissolved salts with water flow.

The concentration of dissolved Si (DSi) increases below the islands due to evaporative enrichment, causing precipitation of base-cation rich clays, carbonates and amorphous Si (McCarthy et al. 1998). This causes volumetric expansion, which is a key mechanism of island growth. More soluble

components reach the center of the islands (e.g. sodium bicarbonate), where they are lost to deeper groundwater via a density fingering process (Bauer et al. 2006, Zimmerman et al. 2006).

The role of biota in the formation of islands has been recognized. Islands in the Delta initiate around a termite mound, gradually building from this basis (McCarthy et al. 1998). Large trees – which are especially dense on the island fringes (McCarthy et al 2012) - play an essential role in maintaining the hydraulic pressure gradient through transpiration. However, while the role of islands in sequestering Si is known, we have little understanding of the role of vegetation in depositing and sequestering Si in the floodplains, though they actually cover a much greater surface area. We here hypothesize that floodplain vegetation plays an essential role in the assimilation of dissolved Si from the water and, after dissolution of plant material, its delivery to the island sub surfaces. The selective removal of dissolved Si from the Okavango Delta surface waters has been identified, based on its relative enrichment in concentration below that expected from evaporation and rain water input (Sawula & Martins 1991). However, Si precipitation has not been linked earlier to floodplain vegetation associated processes.

Vegetation in the Okavango Delta floodplains mainly consists of sedges and grasses, with key species including *Miscanthus junceus*, *Cyperus papyrus* and *Phragmites australis.* These species are well known Si accumulators, with elemental Si concentrations in *P. australis* reaching 5% of dry biomass (e.g. Struyf et al. 2007). Si in vegetation occurs as BSi mainly in structures called phytoliths, deposited at sites of transpiration. Plant BSi plays a role in stress resistance and intra/interspecific competition, e.g. increasing resistance against flow shear stress and salt stress (e.g. Cooke & Leishman 2011). In aquatic macrophytes, BSi has a role similar to lignin and cellulose, increasing the capability of vegetation to withstand high flows and to maintain an upright stature, important for sustained photosynthesis in flooded environments (Schoelynck et al. 2010). Apart from vegetation, diatoms are also prominent in the Delta floodplains (e.g. Mackay et al. 2012; Davidson et al. 2012) and have an obligate requirement for dissolved Si for building their frustules. Thus, there is a large potential for biologically mediated Si accumulation in the floodplains of the Okavango Delta, corroborated by previous research which suggests the substantial occurrence of plant phytoliths in the peat of the permanent floodplains (McCarthy et al. 1989).

We hypothesize that biogenic Si accumulation in the vegetation functions as a trapping mechanism for most of the DSi entering and flowing through the Delta. After vegetation senescence, the BSi contributes to the accumulation of biogenic Si in floodplain sediments, where it is available for dissolution. After dissolution, DSi may be taken up again by the vegetation or transported further

down the Delta. Crucially, a significant part may also be transported along with lateral water flow to the island sub-surfaces.

We sampled the uppermost sediments on both islands and floodplains and the associated vegetation, along gradients from island centers to the channels bordering the floodplains at both a temporary and a permanent floodplain and their adjacent islands. We make conservative estimates of the storage of BSi in the vegetation and compare it to annual inputs of Si into the Delta, then relate this to Si storage patterns across hydrological gradients within floodplain sediments. We hypothesize that the highest storage of biogenic Si in the sediments will occur in areas with permanent inundation, while the highest dissolution potential of accumulated BSi exists in the temporal floodplains, where strong hydraulic pressure from floodplains to islands causes more frequent water refreshing, enhancing porewater leaching of DSi (recycled from BSi).

112 Study site and transect sampling

113 The Okavango Delta (Fig. 1) is in fact not a delta but a low gradient (1:3400) alluvial fan (McCarthy et
114 al. 1998). The inundated area of the Delta fluctuates from 6,000 km^2 during low flow seasons to over
115 15,000 km^2 during high flow seasons (Gumbritch et al 2004). The annual flood pulse that inundates
116 the Okavango Delta originates as precipitation in the highlands of Angola and reaches the Mohembo
117 inlet (Botswana) by February through June, peaking in April. The mean annual discharge into the
118 Delta is approximately 9.0 x 10^9 m^3 (McCarthy et al., 2003). It takes about four months for the flood
119 water to reach the most downstream distal reaches of the Delta near Maun, Botswana about 260 km
120 from the inlet at Mohembo (Wolski et al. 2006). Direct rainfall into the Delta contributes about 42 %
121 (about 6 × 109 m^3 per annum) to the mean flow, mostly by summer rains out of phase with the
122 riverine flood-pulse (Ramberg and Wolski, 2008). The Okavango Delta annually receives between
123 0.0024 and 0.0036 TMol (x10^{12} mol) of DSi from the Okavango River which flows into the Delta
124 through a narrow conduit called the Panhandle (Ramberg & Wolski 2008, calculated using water
125 input and measured Si concentrations in the Panhandle).
126
127 The Okavango Delta has been divided into physiographic regions: (i) the Panhandle, the confined
128 entry channel; (ii) the permanent swamp; (iii) the seasonal and occasional swamps. The Okavango
129 River (~100 m width) flows into the Panhandle (~25km wide) where it meanders through a
130 permanently-flooded *Cyperus papyrus* dominated landscape. From the Panhandle the Okavango
131 River enters the permanent swamps where it divides into three main distributary channels. The
132 permanent swamp is intersected by channels, lagoons and lakes, dominated by emergent *C. papyrus*.
133 Water movement in the permanent swamps is slow due to the low gradient and the submerged and
134 emergent vegetation, and dry land surfaces are relatively small. The seasonal swamp and occasional
135 swamps (hereafter referred to as temporary swamps) have more prominent dry land areas. In the
136 temporary swamp, flood waters flow mainly through channels, bordered by grasses and reeds, and
137 overflow onto shallow, grassy floodplains. Most islands are thus found in the temporary floodplains
138 in the distal ends of the delta, where they cover over 50% of the total surface area. The exact
139 proportion is variable and depends on the actual extent of the flooding (Gumbricht et al. 2004).
140
141 Subsurface geology of the 165,000 km^2 catchment is dominated by Precambrian/Palaeozoic
142 continental cratons and is nearly entirely overlain by highly weathered Kalahari sands of Cenozoic
143 age, in places >300 m deep, whose influence dominates the Okavango River dissolved and suspended
144 loads. Clay mineral neoformation occurs throughout the Delta – when the geochemistry permits

(Frings et al. 2014): however, the majority of element sequestration occurs beneath the islands (Frings et al. 2014).

We selected two island-floodplain gradients in the Okavango Delta: one in the permanently flooded wetlands ("Guma") and one in the temporary wetlands ("Nxaraga") (Fig. 1). At both locations, we sampled sediment and vegetation along full hydrological gradients, from the center of the islands to the edges of the channel bordering floodplain. These gradients were subdivided into 9 (Guma) and 12 (Nxaraga) sampling locations respectively, representing the visual variability in vegetation cover (or absence thereof). Vegetation and surface sediment samples (25 cm) were taken at each of these sampling sites, as described below. Additionally, at Nxaraga, deeper (max 8m) boreholes were drilled in 5 island sampling sites and one floodplain sampling site.

Materials and methods

Sampling

Aboveground vegetation and litter samples were taken from two random quadrats (0.25 m^2) at each selected sampling site (no trees were sampled, only herbaceous/grass vegetation and litter). Standing biomass is at its peak at the time of sampling. Vegetation species composition was determined during cutting (Table 1). At each selected sampling point along the transects, three sediment cores (25 cm length and 28 mm ø) were sampled using a hammer auger with a removable plastic lining (Eijkelkamp 04.15.SA Foil sampler). The sediment cores were each subsampled at 6 different depths and pooled per depth per sampling spot. The litter layer was included in the vegetation samples and not the sediment core. Depths at which samples were taken were not exactly the same at all sampling spots, as we took into account clearly visible horizons of organic and inorganic sediment. In general, the first 10 cm was sliced into three parts and the next 15 cm also. The samples were wet-weighed, immediately frozen and stored until analysis. Along an overlapping transect at Nxaraga (Fig. 1), six boreholes were drilled by large-diameter hand-auger (Eijkelkamp) along the island-floodplain gradient to a maximum depth of 8m using hole casing and a bailer where necessary. Samples of ~40g were taken every 25cm from the visually undisturbed/uncontaminated centre of the auger, and stored cool in zip-lock bags until freeze-drying.

Si Analysis

Vegetation samples (litter + aboveground vegetation) were thoroughly rinsed and cleaned to remove sediments, epiphytic algae and macro-invertebrates. Subsequently, they were oven dried at 75˚C for three days (72 hours). The dried samples were weighed immediately after removing from the oven and then ground and homogenized (< 0.5 mm) in bulk. The total BSi content of the bulk vegetation from every quadrat was analysed: 25 mg biomass was digested with 25 ml 0.094 M Na_2CO_3 for 6 hours at 80 °C (e.g. Struyf et al. 2005). For the most abundant species, individuals were selected in the area directly next to the sampling spots, for analysis of BSi in these individual species. Individual species analyses refer to the whole aboveground biomass: no organ-specific extraction was performed.

Sediment samples were dried using an IMA-Telstar Cryodos-50 freeze dryer, sieved at 500 µm to remove macroscopic plant and shell material before analysis, and weighed for bulk density. Subsequently, they were digested in 30 ml of 0.094 M Na_2CO_3 in a shaking water bath at 80 °C (e.g. Struyf et al. 2009; 2010). After 4, 5 and 6 hours, subsamples were taken and analyzed with an ICP-OES (iCAP 6300 Duo, © Thermo Scientific) or by the molybdate blue spectrophotometric method (for the borehole samples only) for extracted DSi (all Si concentrations expressed as elemental Si further

192 on, and not SiO_2). To correct for the amount of Si resulting from mineral dissolution, the Si content of
193 the subsamples was plotted against dissolution time. All biogenic Si dissolves within the first few
194 hours: the y-axis intercept of the linear least-squares regression line through the measured values
195 represents the estimated BSi content (DeMaster 1981). Recent research has clearly shown that non-
196 biogenic Si fractions can interfere with the extraction of BSi (Struyf & Conley 2012), e.g. other
197 amorphous Si fractions like adsorbed Si. The term ASi (amorphous Si) has therefore been adopted by
198 other studies. The analysis is currently undergoing rapid methodological development (Barao et al.
199 2014). Recent insights show that extraction using 0.094 M Na_2CO_3 could also lead to an
200 underestimation of the total BSi content, as some fractions of phytoliths only dissolve in stronger
201 alkaline solutions (e.g. 0.5 M NaOH) (e.g. Saccone et al. 2007; Meunier et al. 2014). However, these
202 stronger solutions also more readily extract mineral silicates. Due to the abundance of quartz and
203 kaolinite in Okavango sediments (e.g. McCarthy et al. 1989), we used 0.094 M Na_2CO_3. This also
204 facilitates comparison to most other studies on soil BSi storage, which have typically applied Na_2CO_3
205 to digest BSi (e.g. Clymans et al. 2011; Carey & Fulweiler 2013). In this manuscript, we decide to
206 adopt the term BSi for alkaline extracted Si in both surface sediments and vegetation. In sediment,
207 the mainly biogenic origin of the extracted Si was confirmed by microscopical analyses (Frings et al.
208 2014). However, for the deep cores we adopted the term ASi, as earlier research has confirmed that
209 large non-biogenic amorphous Si precipitates here constitute most of the amorphous Si. Si
210 concentrations in vegetation and litter are expressed as elemental Si per total dry biomass (%).
211 Sediment BSi or ASi (for the deep cores) is expressed as elemental Si relative to the total weight of
212 dry sediment (%). Si stock calculations were calculated from the multiplication of biomass per
213 quadrat and relative BSi content of the biomass. Sediment Si stocks are calculated from the total
214 sediment weight on a square meter basis, for either 5 or 25 cm depth, based on the bulk density, and
215 the relative elemental BSi (or ASi) content of the sediment.
216
217

218 Results

219

220 Vegetation BSi

221 Vegetation samples included only herbaceous vegetation, grass and leaf litter, and only leaf litter at
222 the forest site (GumDr5). The dominant species cover at each sample site is shown in Table 1.
223 Vegetation generally contained a higher stock of BSi in the Guma floodplain compared to the Guma
224 island (except for the riparian forest site). At Guma, floodplain vegetation contained between 20 and
225 80 g BSi m^{-2}, while island vegetation contained between 1 and 30 g m^{-2}. The tendency for lower
226 vegetation BSi stock on the island was also clear in Nxaraga (2 – 40 g m^{-2}), whereas floodplains
227 contained about 20-160 g BSi m^{-2} in the vegetation (Fig. 2). Vegetation BSi concentrations at islands
228 and floodplains showed no clear island/floodplain distinction. At Guma, island vegetation contained
229 (for complete sampled plots) on average 1.7% of BSi (range 1.2% - 2.8%) and floodplain vegetation
230 contained 2.5% BSi on average (range 1.0% - 3.4%). At Nxaraga, island vegetation contained (for
231 complete sampled plots) on average 2.3% of BSi (range 1.6% - 2.6%) and floodplain vegetation
232 contained 1.9% BSi on average (range 0.9% - 2.9%). Differences in stocks were fully attributable to
233 the high biomasses occurring in the floodplains.

234

235 Sediment BSi

236 *Permanent floodplains (Guma)*

237 At the Guma site, BSi in the island sediment was both low in concentration (Fig. 3) and in total stock
238 (Fig. 2). In the driest parts of the island, sediment BSi concentrations were between 0 and 0.5%. In
239 the riparian forest (GumDr5), sediment BSi concentrations were slightly higher than at the other
240 island sites (Fig. 3). In the permanent floodplains, BSi exhibited different behaviour. Surface BSi
241 concentrations ranged between 1 and 5% BSi, then gradually decreased with depth to <0.5% in all
242 cores (Fig. 3). Stocks of BSi in the permanent floodplains (top 5 cm) were between 100 and 550 g BSi
243 m^{-2} at sites on the islands, and between 1950 and 3600 g m^{-2} in the floodplains themselves (Fig. 2).
244 Storage over the full 25 cm depth ranged between 1300 and 4600 g BSi m^{-2} on Guma island and
245 between 5200 and 10500 g BSi m^{-2} in the Guma floodplains.

246

247 *Temporary floodplains (Nxaraga)*

248 At the driest island sites in the temporary floodplain region, BSi concentrations were low throughout
249 the cores and generally below 0.5% BSi (Fig. 3). At the two riparian forest sites (NXADr4 and NXADr5),
250 concentrations were higher averaging 1% with slightly higher values in the deeper section (20-25
251 cm). Overall, variability in BSi from the island cores was low. In the Nxaraga floodplain cores, BSi

concentration decreased with depth in the 5 cores closest to the channel. Maximum concentrations at the surface between 0.6 and 1.7% BSi was always lower than in the permanent floodplains at Guma (Fig. 3). In the two floodplain cores closest to the island, surface BSi concentrations were always 0.4% BSi or lower. In all floodplain cores, BSi concentrations at depth (20-25 cm) were lower than 0.4%. BSi stocks in the top 5 cm of sediment were similar across the entire transect in cores from Nxaraga island and its floodplains, ranging between 175 – 1300 g m^{-2} (island cores) and 375-1950 g m^{-2} (floodplain cores). This is in stark contrast to the clear separation between floodplains and islands in the permanently flooded transect at Guma (Fig. 2). BSi stocks (25 cm profile) ranged between 800 and 7200 g m^{-2} in Nxaraga island and between 1300 and 3900 g m^{-2} in the floodplain with the highest BSi accumulation in the riparian forest sites on the island.

ASi concentrations at Nxaraga were also explored further in deep cores up to 8m depth (Fig. 4). The floodplain coring here clearly shows that negligible concentrations of ASi (<0.3 %) occur through the deeper layers up to 8 m depth. In the island cores, a clear accumulation peak of ASi can be observed at about 3-3.5 meters in the centre of the island and the riparian forest, with concentrations up to 4.5%. Concentrations in the other island cores generally ranged between 0.5 and 2% throughout the depth profile.

Discussion

Our results indicate that in the Okavango Delta, the trapping of DSi by vegetation is an important step in the retention of Si. Floodplain vegetation stores similar amounts of BSi in both the temporary floodplains and the permanent floodplains, with most values observed between 20-100 g Si m^{-2}. For sediment BSi storage, most of the BSi occurs in the upper layers. The temporary floodplains (375 - 1950 g BSi m^{-2} in the top 5 cm) contain less BSi than the permanent floodplains (1950 - 3600 g ASi m^{-2} in the top 5 cm). BSi concentrations in the floodplain sediment decline exponentially indicating rapid dissolution of BSi with most dissolution occurring within the first 5 cm. The top sediment layers represent a reservoir of biologically accumulated Si that rapidly recycles.

Sediment accumulation rates in the Okavango Delta can reach up to 5 cm per year in certain settings (McCarthy et al. 1989). If we assume a recent estimate of ~0.25 cm a^{-1} is more representative of average accumulation (Bernal and Mitsch 2013), this implies between 100 and 175 g of BSi is recycled annually to DSi per m^2 in the top 5 cm in the permanent floodplain, based on the decrease in BSi concentrations in the sediment. Rapid rates of recycling from marsh grass litter have been shown in tidal wetlands and under experimental conditions (Struyf et al. 2007; Schaller & Struyf 2013), but are unavailable currently for tropical wetlands. Future studies on dissolution rates of Si from tropical wetland litter are necessary to quantify recycling rates in more detail. Most of the “recycled” DSi will end up in the vegetation again, as annual biomass production is approximately double the standing vegetation stock in the permanent floodplains (McCarthy et al. 1989), requiring annual uptake of 40-200 g DSi m^{-2} a^{-1}. Spatially distributed riverine annual input from the Okavango river is ca. 20 g m^{-2} in the permanent floodplains (assuming 6000 km^2 of permanent floodplain and an annual input of 0.0030 Tmole of Si). Our calculations require efficient recycling to support the majority of BSi production. Some fraction of the dissolved BSi will not be taken up again by vegetation, and will be exported as DSi from the floodplain sediment, either infiltrating deeper into the sediment or transported further downstream into the Delta. This can be replenished by the spatially distributed annual riverine input into the permanent floodplain.

In the temporary floodplains, abundant islands create a larger hydraulic head between surface water and island groundwater. This probably is an important cause for both lower BSi concentrations and stocks in the temporary floodplain relative to the permanent floodplain. Despite approximately equal amounts of BSi in vegetation in the two regions, the lowest values for sediment BSi storage in the permanent floodplains were greater than the highest values in the seasonal floodplains. In contrast to the permanent floodplains, a strong unidirectional transport of water from floodplains to

island interiors is present in the temporary inundated areas. Given the large surface area of islands in the temporary floodplains, the vast majority of Si accumulated is in the interior of the islands, in contrast to the permanent floodplain where island surface area is limited (Gumbricht et al. 2004). This is confirmed in the ASi data in deep cores. It is not surprising that the islands only accumulate small amounts of ASi in the top layers: most Si accumulates underneath the islands in the deeper sediment horizons, especially below the riparian forest. Earlier and our data show the greatest accumulation of Si and other elements in the islands at the sites of strongest evapotranspiration, i.e. the forested island fringes (Bauer et al 2004). The importance of amorphous Si precipitates in the build-up of islands has been pointed to in earlier research (e.g. Ramberg & Wolski 2008; McCarthy et al. 2012).

Tropical wetlands and Si cycling

Our results clearly show a large surficial storage of biogenic Si in the Okavango Delta. We used estimates of the areas of islands, permanent and temporary floodplains from Gumbricht et al. (2004) to assess total storage of BSi in the top 25cm only of the Okavango Delta sediment, not taking into account deeper storage. Taking the lowest BSi storage amounts observed for the different delta sections, we can conservatively estimate total surficial BSi storage of 0.4 Tmole of Si in the permanent floodplains, 0.2 Tmole in the temporary floodplains and 0.01 Tmole in the islands, leading to a minimum estimate of 0.6 Tmole of BSi storage in the Delta. Alternatively, taking the upper-end estimates of our data results in storage values of 0.8 Tmole, 0.4 Tmole and 0.07 Tmole respectively, implying total Delta storage of 1.3 Tmole of Si in the top 25 cm. This surface storage represents about 200-400 years of DSi input into the Delta, as annual (modern day) input equals ~0.003 Tmole. Based on a vegetation BSi turnover (see earlier) of 100 g Si m^{-2} a^{-1}, vegetation uptake in the floodplains represent about 0.020 Tmole a^{-1}, compared to an annual input of 0.003 TMole of Si into the Delta.

The BSi storage in both the permanent and temporary floodplains is among the highest observed so far for any ecosystem worldwide (Struyf & Conley 2012), at 110-220 x 10^3 kg SiO_2 ha^{-1} and 42-80 10^3 kg SiO_2 ha^{-1} respectively. This exceeds the highest values published to date, where BSi pools over a full soil profile of between 30 and 104 x 10^3 kg SiO_2 ha^{-1} were observed in soils from the Great Plains grasslands and equatorial rain forests (Blecker et al. 2006; Alexandre et al. 1997). The floodplains of the Okavango Delta also greatly exceed values observed in temperate tidal marshes and subarctic peat bogs (between 12-32 x 10^3 kg SiO_2 ha^{-1}) (Struyf et al. 2005; 2010). It should be emphasised that our estimates are conservative, particularly since we used a weak base extraction (0.094 M Na_2CO_3) and we are only integrating the top 25 cm of the sediment horizon whereas the other estimates are typically based on 1-2 m horizons. Some aged phytolith material as well as sponges may not have

completely dissolved after only a few hours in 0.094 M Na_2CO_3 (Meunier et al. 2014). However, given the rapid recycling of BSi in sediments, we assume that aged diagenetically altered phytoliths are unlikely to represent a major fraction of BSi in our sediments. Part of the BSi we analysed likely derives from sponges (unpub. data), base-cation rich clays, reactive secondary silicate minerals and from non-biogenic amorphous reactive Si phases, including Si adsorbed to aluminum- or iron oxy-hydroxides (McKeague and Cline 1963). Fractionation between these non-biogenic and biogenic Si phases should be a research priority in the future.

Recently, Carey & Fulweiler (2013) estimated annual, BSi uptake in global vegetation of about 85 Tmole. Of this, they calculated that the total surface of wetlands worldwide contributes approximately 4.16 Tmole a^{-1}. Our conservative vegetation BSi production estimate of 0.02 Tmole of Si a^{-1} would represent about 0.4% of total annual uptake in wetland vegetation worldwide within the Okavango Delta alone, despite it covering only about 0.1% of global wetland area (Mitsch et al. 2013). Although data for other tropical wetlands are limited, Cary et al. (2005) observed 2-4 % of BSi in swamp soils in the Nyong river basin in Cameroon, in the same range as concentrations in the Okavango. Tropical rivers deliver about 70-80% of the global DSi load into the ocean (Jennerjahn et al. 2006), implying it is crucial to assess environmental factors that can influence its transport. Our data and the limited available literature data available clearly show that wetlands and floodplains are an important yet understudied component. Other studies have indicated the potential influence of Si uptake by giant grasses and sedges (e.g. Ding et al. 2008) through Si-isotope biogeochemistry in tropical rivers.

The hydrology of many tropical wetlands is undergoing major changes due to human alteration of river morphology and watersheds. Model predictions also project substantial future changes in hydrology and climate (Hamilton 2010; Wolski et al. 2014). This will have implications for flooding extent and seasonality, factors that may induce changes in Si storage in the Okavango Delta. While vegetation is an important trap for Si in the permanently inundated wetlands, permanent long-term burial in sediments is likely low, as indicated by near-negligible BSi concentrations in the deeper layers. These conditions imply that reactive Si stores in the permanent floodplains are still intimately connected to flooding water, and thus a significant part of recycled Si is leaching back into “river” water after BSi dissolution. However, in the occasional and seasonal floodplains, unidirectional solute transfer from floodplains to the islands will remove reactive Si from the riverine systems (Figure 5).

Outlook

Our results show that wetland vegetation in the Okavango Delta plays a key role in the annual Si budget of the Okavango Delta. Most of the DSi entering the permanent floodplains cycles through vegetation before transport further downstream. There is a clear distinction in the amount of BSi sequestered between permanent and temporary floodplains. While BSi stores are actively recycled in the sediments of the permanent floodplains (implying strong potential for leaching to surface waters), unidirectional transport of Si leads to the loss of recycled BSi into the tree covered islands in the temporary floodplains. Our work clearly emphasizes the crucial role of floodplains and wetlands in Si transport through tropical rivers.

Although our results are conservative estimates, our analysis indicates that the sediments of the Okavango Delta represent the largest store of sediment or soil BSi per m^{-2} yet identified worldwide. This emphasizes the necessity to construct an estimate of worldwide BSi storage and accretion or depletion rates in soils and sediments, which has still only been quantified in a limited number of ecosystems and with a restricted global distribution of sites studied (Struyf & Conley 2012), and to initiate studies on how the storage is affected by environmental conditions, e.g. flooding frequency, sediment and porewater pH and salinity in wetlands. Future studies in wetlands should also investigate the exact nature of stored Si through microscopical studies, and better constrain dissolution/retention fluxes through e.g. the detailed study of porewater profiles and potentially isotope fractionation. A recent study by Frings et al. (2014) shows this potentially provides added insight on processing of the large stocks of Si present in the Okavango delta, and wetlands in general. This will further allow a more nuanced understanding of whether the global Si cycle operates in steady state, or is instead characterised by time-lagged responses to anthropogenic or natural changes (Frings et al. 2014).

Based on high rates of vegetation accumulation we observed in the Okavango, the most recent estimate of annual uptake of vegetation BSi production (Carey & Fulweiler 2013) of ~84 Tmole Si $year^{-1}$ could be underestimated. In our dataset, storage in floodplain sediments is 45 times greater than annual vegetation uptake. In *Phragmites australis* dominated tidal temperate wetlands, where daily tidal immersion/emersion cycles induce strong recycling potential, the uptake/storage ratio was about 40 (Struyf et al. 2005), while for bamboo, deciduous and coniferous forests with perennial vegetation, ratios of over 1000 are proposed (Conley 2002). This represents massive soil storage relative to annual continental Si fluxes (7.2 Tmole Si a^{-1}; Tréguer & De La Rocha 2013) and annual weathering fluxes (10-40 Tmole Si a^{-1}, Hilley & Porder 2008), showing the clear need for a better quantification of sediment BSi accumulation rates.

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413 Table 1

414 Dominant vegetation (all species with higher than 5% cover in the plot) summarized for all
415 the sampling spots. In the site column, the first three letters refer to the sampling location
416 (Nxa : Nxaraga, Gum : Guma). “Dr” and “Wet” refer to respectively islands and floodplain
417 sites.

site	**total cover**	**Dominant species**
NxaDr1	20	*Sporoblus spicatus* (20%)
NxaDr2	25	*Cynadon dactylon* (15%), *Schoenoplectus corymbosus* (5%), *Cyperus longus* (5%)
NxaDr2	80	*Eragrostis lappula* (75%), *Cynadon dactylon* (5%)
NxaDr2	85	*Panicum repens* (40%), *Cynadon dactylon* (20%)
NxaDr2	100	*Imperata cylindrica* (99%)
NxaWet1	90	*Imperata cylindrica* (60%), *Panicum repens*(25%)
NxaWet2	70	*Imperata cylindrica* (20%), *Panicum repens* (40%), *Fuirena pubescens* (10%)
NxaWet3	90	*Imperata cylindrica* (80%), *Panicum repens* (5%), *Cyperus longus* (5%)
NxaWet4	95	*Miscanthus junceus* (90%), *Schoenoplectus corymbosus* (5%)
NxaWet5	90	*Oxycaryum cubense* (85%), *Vossia cuspidate* (5%), *Oryza longistaminata* (5%)
NxaWet6	70	*Schoenoplectus corymbosus (55%), Drascenia sp (10%), Eleocharis dulcis (5%)*
NxaWet6b	100	*Cyperus papyrus* (100%)
GumDr1	40	*Sporoblus spicatus* (40%)
GumDr2	30	*Sporoblus spicatus* (15%), *Panicum repens* (10%), Gis sp (5%)
GumDr3	15	*Sporoblus spicatus* (15%)
GumDr4	20	*Cynadon dactylon* (15%), *Sporoblus spicatus* (5%)
GumWet1	40	*Cyperus dives* (20%), *Leersia hexandra* (10%), *Eleocharis dulcis* (5%), *Oryza longistaminata* (5%)
GumWet2	55	*Cyperus dives* (15%), *Schoenoplectus corymbosus* (15%), *Nymphaea nouchali* (10%), *Phragmites australis* (5%), *Leersia hexandra* (5%), *Eleocharis dulcis* (5%)
GumWet3	45	*Eleocharis dulcis* (35%), *Nymphaea nouchali* (10%)
GumWet4	35	*Cyperus papyrus* (25%), *Eleocharis dulcis* (10%)

418

420 Figure legends

421 Figure 1: Map of the Okavango Delta with location of sample stations and gradients, and the flooding
422 regime.
423
424 Figure 2. Vegetation BSi content (top panels) and sediment BSi content (lower panels, for top 5 cm of
425 the sediment profile) in Guma (left) and Nxaraga (right), expressed as Si per m^2. Sediment samples
426 are pooled samples of 3 cores per location per depth. Right of the line are the floodplain sites, to the
427 left island sites. The line itself indicates the last island site. Note the different scale of the vegetation
428 BSi axis for both sampling sites (top panels).
429
430 Figure 3: Sediment BSi in the Guma and Nxaraga sampling gradient, expressed as weight percent in
431 percent BSi per sediment dry mass. The islands sites are in the top panels (GumDr and NxaDry), the
432 wetland floodplain sites are in the lower panels (GumWet and NxaWet).

433 Figure 4. ASi in the deep cores from Nxaraga (weigth percent in percent ASi per sediment dry mass),
434 in sample sites from the center of the island, through intermediate samplings and the riparian forest
435 to the floodplain. The exact location of the deep cores can be found in Fig. 1 (Deep 1-6). We have
436 specifically indicated the island center core, the riparian forest core and the floodplain core, as they
437 are specifically referred to in the results section.

438 Figure 5. Conceptual figure of Si cycling in permanent and seasonal swamps. While temporary BSi
439 storage is higher in the permanent swamps, recycling to the water column here is near complete. In
440 contrast, floodplain storage is low in the seasonal swamps, and a strong unidirectional Si transfer to
441 the islands dominates recycling to the water column.

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443

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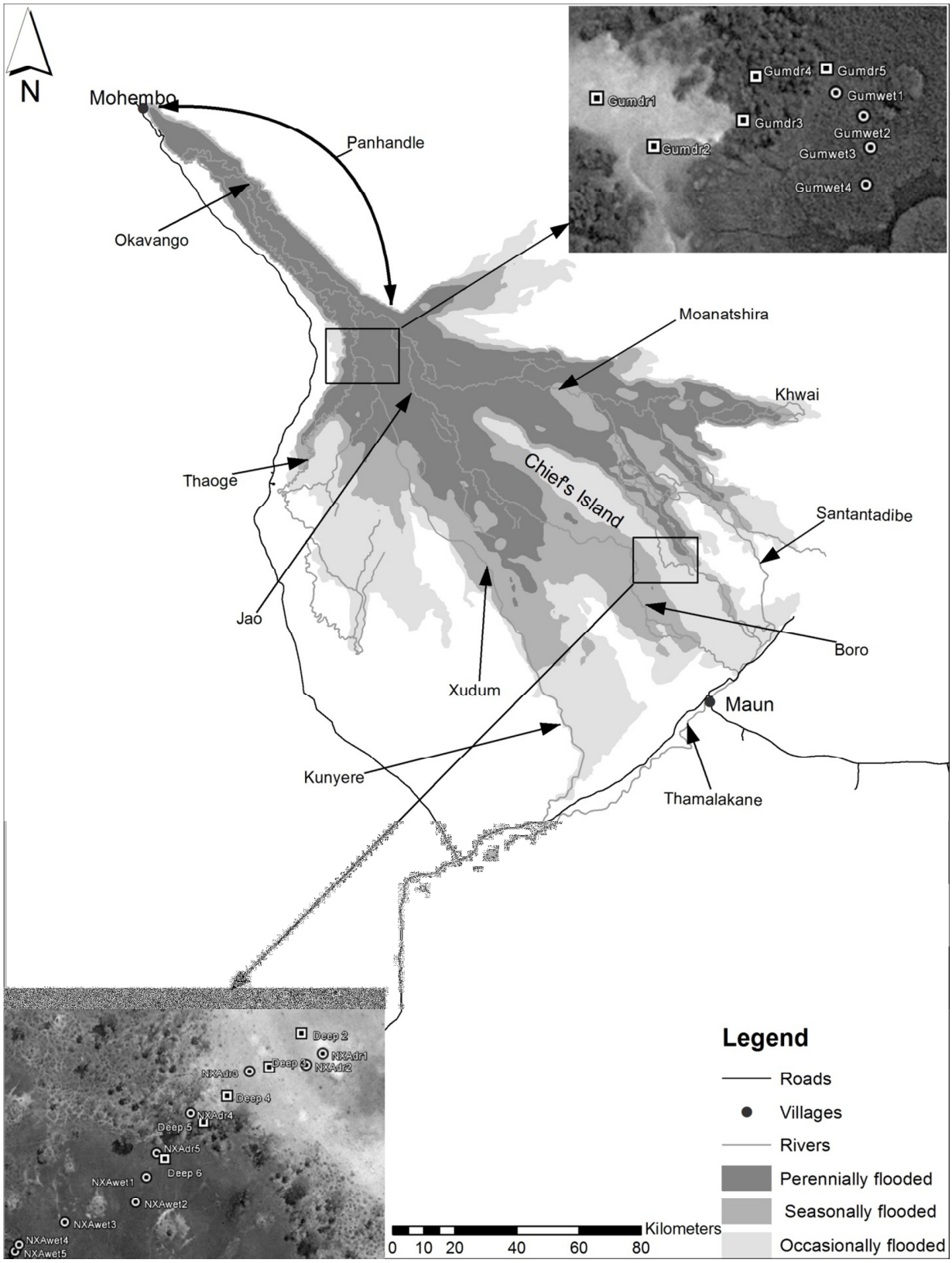
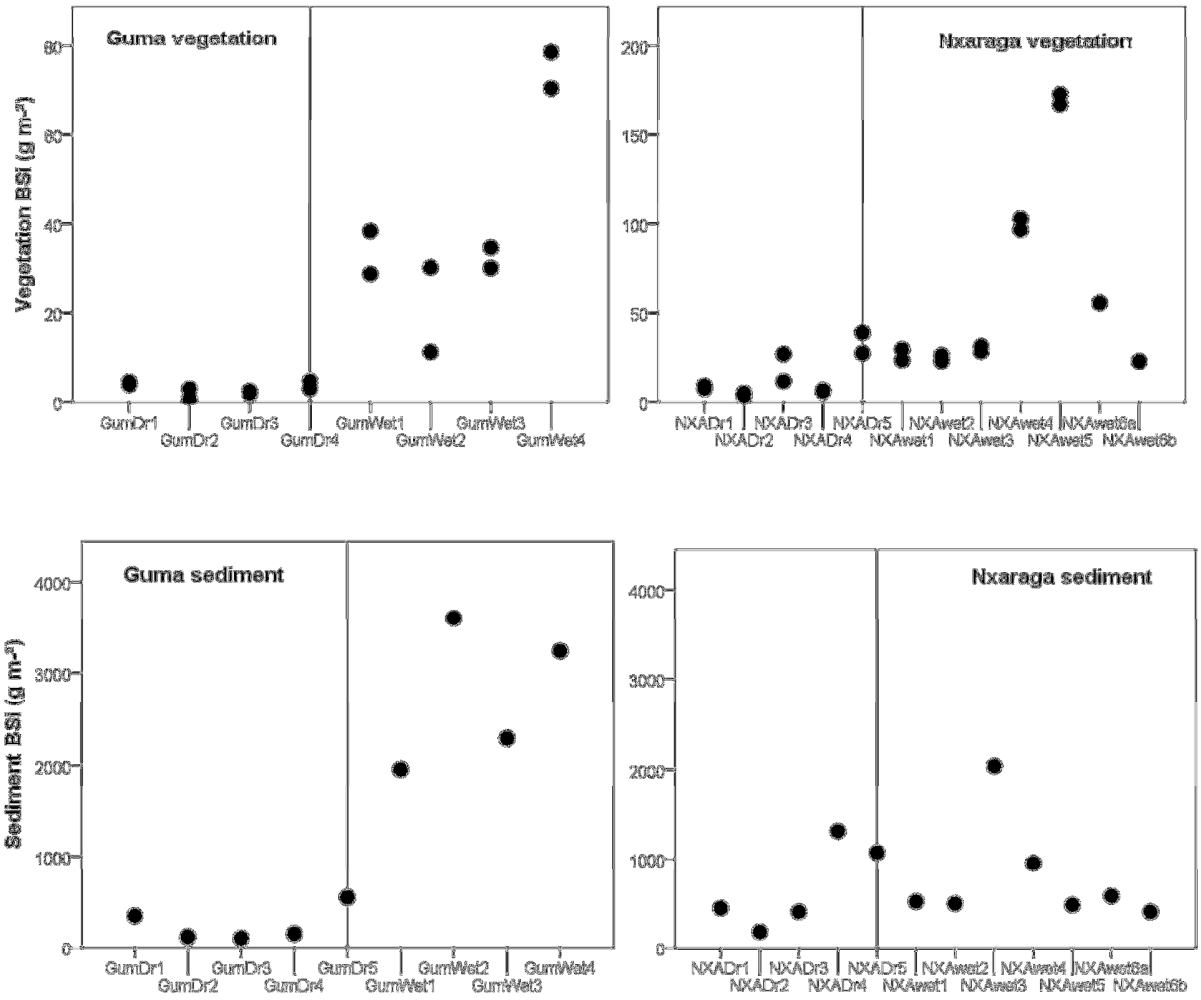

N
Mohembo
Panhandle
Okavango
Moanatshira
Khwai
Thaoge
Chief's Island
Santantadibe
Jao
Boro
Xudum
Maun
Kunyere
Thamalakane
Gumdr1
Gumdr2
Gumdr3
Gumdr4
Gumdr5
Gumwet1
Gumwet2
Gumwet3
Gumwet4
Deep 2
NXAdr1
Deep 3
NXAdr2
NXAdr3
Deep 4
NXAdr4
Deep 5
NXAdr5
Deep 6
NXAwet1
NXAwet2
NXAwet3
NXAwet4
NXAwet5
Legend
Roads
Villages
Rivers
Perennially flooded
Seasonally flooded
Occasionally flooded
Kilometers
0 10 20 40 60 80


Guma vegetation
Vegetation BSI (g m-2)
0
20
40
60
80
GumDr1
GumDr2
GumDr3
GumDr4
GumWet1
GumWet2
GumWet3
GumWet4
Nxaraga vegetation
0
50
100
150
200
NXADr1
NXADr2
NXADr3
NXADr4
NXADr5
NXAwet1
NXAwet2
NXAwet3
NXAwet4
NXAwet5
NXAwet6a
NXAwet6b
Guma sediment
Sediment BSI (g m-2)
0
1000
2000
3000
4000
GumDr1
GumDr2
GumDr3
GumDr4
GumDr5
GumWet1
GumWet2
GumWet3
GumWet4
Nxaraga sediment
0
1000
2000
3000
4000
NXADr1
NXADr2
NXADr3
NXADr4
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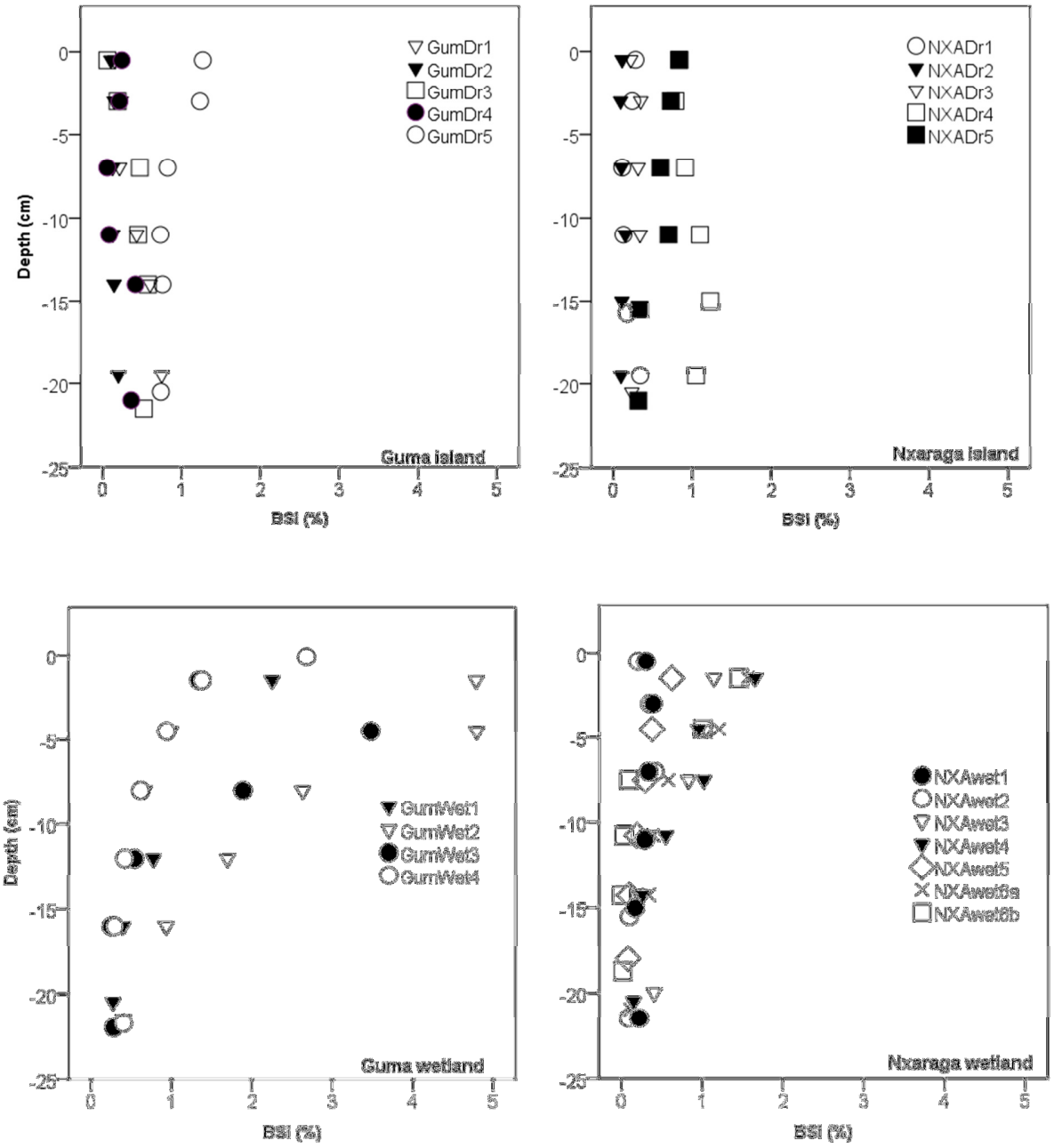
NXAwet6b


Depth (cm)
BSI (%)
GumDr1
GumDr2
GumDr3
GumDr4
GumDr5
Guma island
NXADr1
NXADr2
NXADr3
NXADr4
NXADr5
Nxaraga island
GumWet1
GumWet2
GumWet3
GumWet4
Guma wetland
NXAwet1
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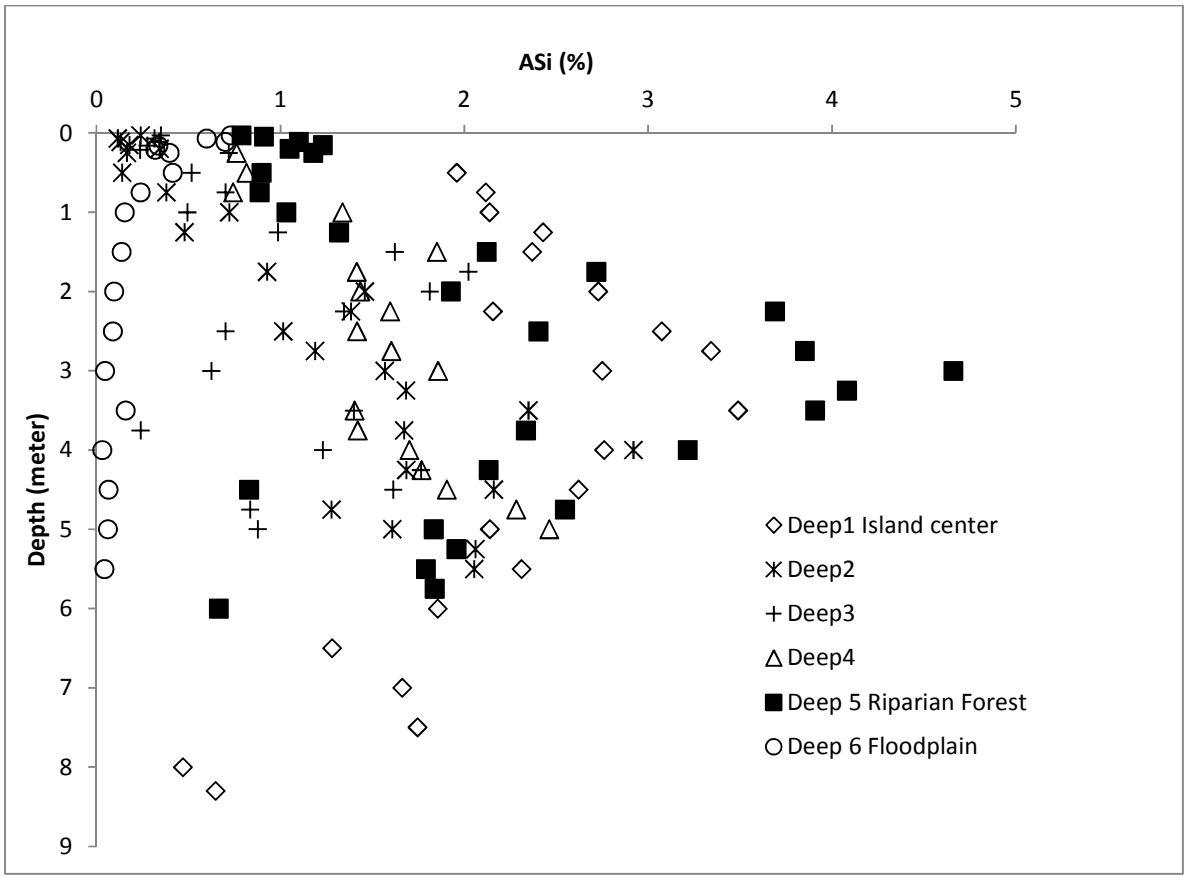
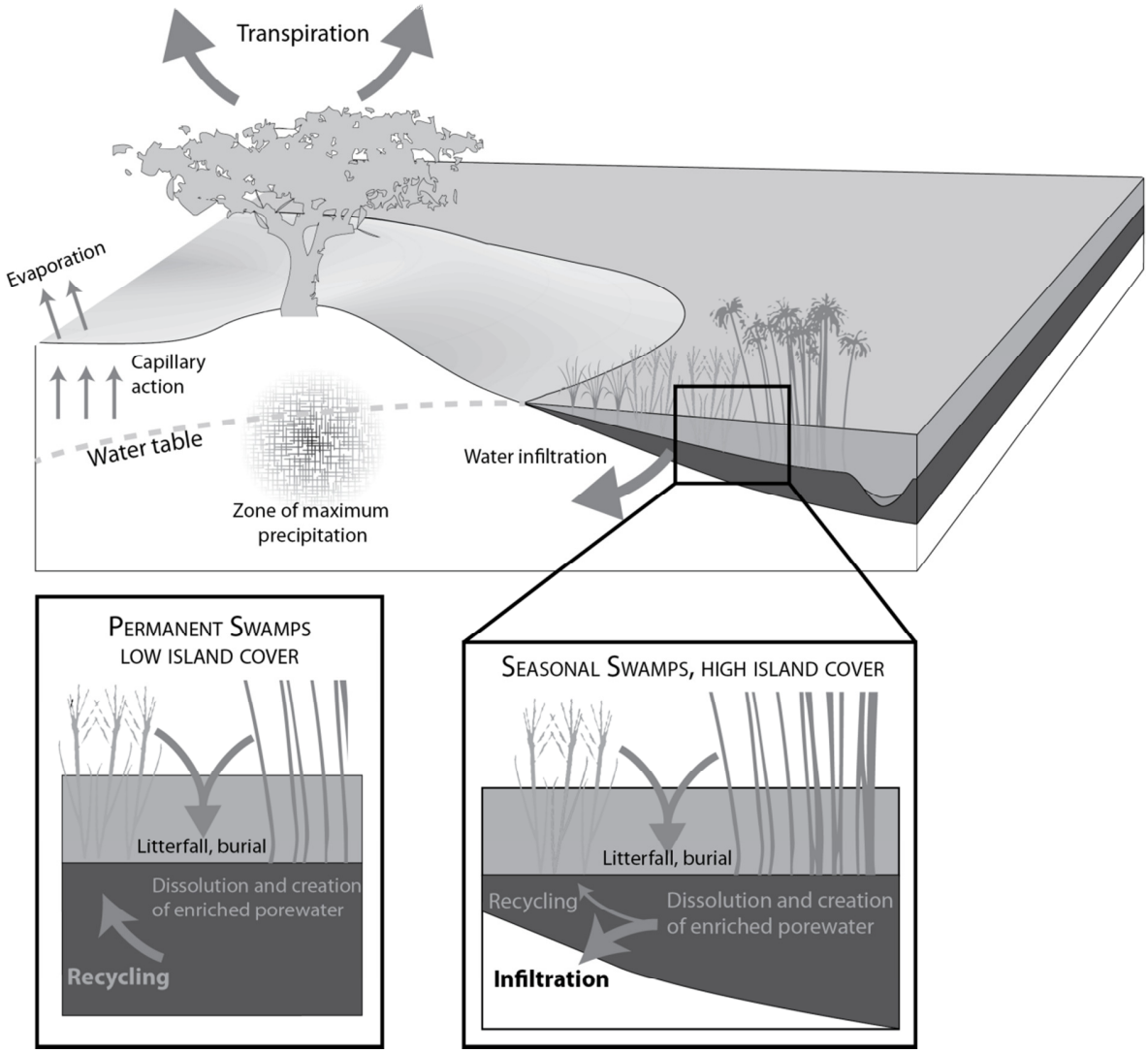
NXAwet3
NXAwet4
NXAwet5
NXAwet6a
NXAwet6b
Nxaraga wetland


ASi (%)
0
1
2
3
4
5
Depth (meter)
0
1
2
3
4
5
6
7
8
9
Deep1 Island center
Deep2
Deep3
Deep4
Deep 5 Riparian Forest
Deep 6 Floodplain


Transpiration
Evaporation
Capillary action
Water table
Zone of maximum precipitation
Water infiltration
PERMANENT SWAMPS
LOW ISLAND COVER
Litterfall, burial
Dissolution and creation of enriched porewater
Recycling
SEASONAL SWAMPS, HIGH ISLAND COVER
Litterfall, burial
Recycling
Dissolution and creation of enriched porewater
Infiltration