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The trapping of organic matter within plant patches in the channels of the Okavango Delta : a matter of quality

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36 Abstract

37 The role of in-stream aquatic vegetation as ecosystem engineers in the distribution of organic
38 matter was investigated in the Okavango Delta, one of the world's largest oligotrophic wetlands.
39 The Okavango channel beds are covered up to 50 % with submerged macrophyte patches. By
40 accumulating and concentrating organic matter in the sediments below the patches, macrophytes
41 are likely able to locally forestall a deficiency of nutrients. Up to 21 times more N, 18 times
42 more C, 13 times more P and 6 times more Si can be found in vegetated sediments compared to
43 non-vegetated sediments. Nutrient specific accumulation relates to its relative scarcity in the
44 overlaying water. There is a depletion of dissolved N relative to P, whereas Si is relatively
45 abundant. The Okavango Delta water can generally be characterised as oligotrophic based on
46 plant species composition (e.g. presence of carnivorous plants and absence of floating plants),
47 low plant N:P ratios, and low nutrient- and element concentrations. Local mineralization and
48 intensified nutrient cycling in the sediments is hypothesized to be crucial for the macrophytes'
49 survival because it provides a key source of the essential nutrients which plants otherwise cannot
50 obtain in sufficient quantities from the nutrient poor water. By engineering the ecosystem as
51 such, channel vegetation also retards the loss of elements and nutrients to island groundwater
52 flow, contributing to one of the key processes driving the high productivity of the Okavango
53 Delta, making it unique among its kind.

54

55 **Keywords:** aquatic ecosystem, carbon pools, nutrient accumulation, nutrient fixation, organic
56 rich sediments, wetland, ecosystem engineering

57 **Introduction**

58 The role of plants as channel system engineers is widely acknowledged (Gurnell, 2014 and
59 references therein), especially for their role in channel form and adjustment through the
60 processes of sedimentation and erosion (Tal and Paola 2007; Hicks et al. 2008; Larsen and
61 Harvey 2010; Schoelynck et al. 2012). Strongly linked to these geomorphological processes is
62 the role of aquatic vegetation in biogeochemical cycling in rivers and streams. Channel networks
63 are known to be major processors of organic matter, imported from the terrestrial environments
64 as well as produced *in-situ*, before entering the coastal environment (Vannote et al. 1980; Battin
65 et al., 2008). Carbon cycling and, intimately linked to that, nutrient (N, P, Si) cycling, is
66 primarily determined by the retention time of organic matter within the system and local
67 recycling of nutrients can be a major determinant of in-stream primary production. Submerged
68 macrophytes generally increase the hydraulic resistance in rivers (Green 2005): flow velocity is
69 reduced within, and downstream of the vegetation patches, as friction is generated by the
70 aboveground canopy (Schoelynck et al. 2012; 2013). This leads to longer residence time of water
71 and dissolved nutrients (Bal et al. 2013) as well as more retention of particulate organic matter
72 (Horvath 2004). Studies report accumulation of organic matter in macrophyte patches 3-12 times
73 greater than in non-vegetated areas (Sand-Jensen 1998; Cotton et al. 2006; Kleeberg et al. 2010;
74 Schoelynck et al. 2014). At non-vegetated locations, adjacent to plant patches, flow velocity is
75 increased because of flow deviation around the patches, and less material is retained (Schoelynck
76 et al. 2012; 2013). Higher sediment organic matter content may lead to higher nutrient and
77 carbon availability, improving plant productivity within the patches and supporting the foodweb,
78 especially where dissolved nutrients in the water are scarce (Schoelynck et al. 2012). This

79 control on the availability of resources makes macrophyte patches true ecosystem engineers
80 *sensu* Jones et al. (1994).

81

82 The Okavango Delta in Botswana, one of the world's largest tropical wetland systems, is an
83 interesting system in which to study submerged macrophytes as ecosystem engineers (Fig. 1). It
84 comprises a mosaic of permanent and seasonal floodplains and tree-covered islands (McCarthy
85 et al. 2012). With about 98 % of total annual inflow being lost to the atmosphere before reaching
86 the outlets, the Delta could be expected to become a saline system. However, the islands play an
87 essential ecological role in the Delta as they act as permanent sinks for a major part of the solutes
88 (ca. 360 000 tons yr⁻¹) that enter the system (Ramberg and Wolski 2008). In brief:

89 evapotranspiration by the island vegetation cover lowers the local water table, inducing a
90 permanent hydraulic gradient, and therefore a subsurface flow from the adjacent channels and
91 floodplains toward the island center. Here, solute concentrations increase, and if saturation is
92 reached, authigenic minerals – mostly various clays and carbonates – precipitate. The center of
93 the island eventually becomes too saline for most vegetation except for a select group of
94 halophilic grasses and a species of palm, *Hyphaene petersiana*, allowing the rest of the Delta to
95 remain a nutrient poor freshwater ecosystem.

96

97 Floodplain vegetation – lying between the islands and the open water channels – was recently
98 shown to play an important role in this mechanism (Mosimane et al. 2017). Struyf et al. (2015)
99 for instance, showed that most of the dissolved Si (DSi) is first taken up by the floodplain
100 vegetation from the water, thereby lowering ambient concentrations. Dead plant parts end up in
101 the vegetated floodplain sediments increasing the local biogenic Si (BSi) concentration. This BSi

102 partly dissolves which then can be partly recycled by the vegetation by uptake, but a significant
103 proportion is transported down the hydraulic head into the islands for (quasi-)permanent storage
104 (via the precipitation mechanism outlined above). The significance of this temporary BSi stock
105 cannot be overstated: it was calculated at around $10\text{-}220 \text{ } 10^3 \text{ kg SiO}_2 \text{ ha}^{-1}$, which ranks among
106 the highest observed to date for any ecosystem worldwide (Struyf and Conley 2012; Alfredsson
107 et al. 2015). It also suggests that local organic matter accumulation can have a major impact on
108 nutrient or element cycling in the Okavango Delta.

109

110 A vast amount of detritus (i.e. dead plant- or animal material) is produced in the Okavango Delta
111 (Fig. 2). The open channels discharge a considerable portion of this detritus downstream
112 ($0.0006\text{-}0.009 \text{ kg m}^{-3}$; McCarthy et al. 1991), despite their total area being rather small compared
113 to the whole Delta (5-7 % of the inundated area is open water). Most transported material must
114 be somehow stored or decomposed along the way, since distal outflow is negligible, and the
115 mechanism for island-storage is primarily for solutes rather than particulate organic matter. In-
116 stream macrophytes could play a crucial role in the process of local entrapment and storage of
117 organic matter. In this study we investigated the role of aquatic vegetation in the distribution of
118 organic matter in the Okavango Delta channels. We first characterized the abiotic conditions of
119 the water across a longitudinal gradient from the inlet towards the outlets. Next, we analyzed the
120 channel sediments for dry organic matter (OM), C, N, P and BSi and compared vegetated with
121 non-vegetated spots. Finally we estimated the amount of nutrients that are trapped in vegetation
122 patches.

123

124 **Materials and methods**

125 *Study site and transect sampling*

126 The Okavango Delta (Fig. 1) is in fact not a delta but a low gradient (1:3400) terminal alluvial
127 fan (McCarthy et al. 1998). The inundated area of the Delta fluctuates from 6,000 km² during
128 low flow seasons to over 15,000 km² during high flow seasons, dividing the wetland into an
129 upstream permanently flooded area and a downstream seasonally flooded area (Gumbrecht et al.
130 2004). The annual flood pulse that inundates the Okavango Delta originates as precipitation in
131 the highlands of Angola and reaches the Mohembo inlet (at the Botswana border) by February
132 through June, peaking in April. The mean annual discharge into the Delta is approximately 9.0 x
133 10⁹ m³ (McCarthy et al. 2003). The Okavango River (~100 m wide) flows into the Panhandle, a
134 confined entry channel (~12 km wide) where it meanders through a permanently-flooded
135 *Cyperus papyrus/Phragmites australis/Phragmites mauritianus* dominated landscape. From the
136 Panhandle, the Okavango River enters the permanent floodplain (starting at ~100 km distance
137 from Mohembo) that is intersected by channels, lagoons and lakes. Further downstream, in the
138 seasonal floodplain, flood waters flow through shallow grassy floodplains and channels of
139 varying width. Flow velocity in the channels is faster than that in the floodplains, but is still
140 relatively slow (up to 0.3 m s⁻¹, pers. obs.), allowing a rich and biodiverse submerged
141 macrophyte vegetation community to develop in places. It takes about four months for the flood
142 water to reach the most distal reaches (the outlets) of the Delta near Maun (Botswana) about 260
143 km from the inlet at Mohembo (Wolski et al. 2006).

144

145 *Sampling, sample preparation and analysis*

146 Samples were collected during two consecutive campaigns in September 2011 and 2012,
147 approximately one month after peak flood extent. In 2011, 15 water samples were taken at
148 relatively easily accessible locations throughout the Delta and analyzed for NO_3^- , NH_4^+ , and DSi.
149 In 2012, a 7-day boat expedition was undertaken on a longitudinal transect from the border
150 between Namibia and Botswana near the town of Mohembo to the outflow streams discharging
151 into the Kalahari, more than 260 km downstream (Fig. 1). During this 2012 campaign, a total of
152 33 sites were visited, roughly equally spread along the transect. The first 7 sites were situated in
153 the Panhandle, where surface water was collected at two depths: approx. 20 cm below surface
154 (Surface Water, SW), and approx. 20 cm above the sediment using a Niskin bottle (Deep Water,
155 DW). Because of the high current velocity in the Panhandle (Ellery and Tacheba, 2003), an
156 average depth of 3-6 m (McCarthy 1991) and scarce submerged vegetation cover, no distinction
157 was made between vegetated and non-vegetated plots and no sediment samples were taken. The
158 data obtained were used to characterize the water that flows into the Delta. The main research
159 was focused on the 21 sites situated in the open channels intersecting the floodplains of the Delta
160 itself (i.e. the permanent and seasonal floodplains), which starts at ~100 km distance from
161 Mohembo (the end of the Panhandle). Here, we distinguished between vegetated and non-
162 vegetated channel plots. The selected plant patches all contained mature shoots of various
163 species (Table 1), were 5-15 m long and occupied around 50 % of the channel width, so that a
164 free flowing, non-vegetated path was still present next to the patch. In every plot, SW, DW and
165 sediment samples were taken in the center of the vegetation patch and in the center of the non-
166 vegetated zone adjacent to the patch. Finally, we also sampled the five outlets to characterize the
167 outflowing water. Here, again no sediment samples were taken and water samples were restricted
168 to the SW on non-vegetated plots because of the relatively shallow water depths (<1 m).

169
170 Electric conductivity (EC in $\mu\text{S cm}^{-1}$), pH, oxygen (DO in mg L^{-1} and in % saturation) and
171 turbidity (in Nephelometric Turbidity Units - NTU) were directly measured in the field using a
172 Type 3110 SET 1 for EC and pH, a Type 3202 SET 3 for DO (both WTW, Wilhelm Germany),
173 and a Nephelometer for turbidity (TN-100, Eutech Instruments, Singapore). No turbidity
174 measurements were made on samples from within the macrophyte patches because leaves (and
175 loosely attached organic matter) disturbed the signal too much. Water samples were filtered
176 through $0.45 \mu\text{m}$ nitrocellulose Chromafil syringe filters (A-45/25) into clean sample bottles,
177 acidified in the field, and stored cool ($4 \text{ }^\circ\text{C}$) until analysis. Analysis for NH_4^+ , PO_4^{3-} and DSi was
178 done on a colorimetric segmented flow analyzer (SAN++, Skalar, Breda, The Netherlands).
179 Unfortunately, the 2012 samples for NO_3^- analysis were lost during transport from the field to the
180 lab. However, an additional sample taken at Wookie Channel (see “Measurements for stock
181 calculation”) was saved and analyzed colorimetrically (Skalar).

182
183 Sediment cores (25 cm long and 28 mm in diameter) were sampled using a hammer auger with a
184 removable plastic lining (Eijkelkamp 04.15.SA Foil sampler, Giesbeek, The Netherlands). At
185 each location, one core was taken at the center of a macrophyte patch, and one was taken at the
186 center of a non-vegetated channel plot in the flow path next to the respective vegetation patch.
187 Immediately after sampling, each core was sub-sectioned from 0 to -22 cm into 5 slices with
188 intervals at -2 cm, -4 cm, -9 cm and -14 cm, packed in vacuum plastic bags and stored cool (4
189 $^\circ\text{C}$) on return to the laboratory. Sediment samples were dried for 72 h at $70 \text{ }^\circ\text{C}$ and homogenized
190 by manual grinding. Subsamples were analyzed for organic matter, carbon, nitrogen, phosphorus
191 and BSi.

192 The organic matter content was determined by loss on ignition (Heiri et al. 2001). Samples were
193 heated to 105 °C for 2 h to drive off free water and weighed. Thereafter, samples were ignited at
194 550 °C for 4 h and weighed again. The difference between the two measurements gives an index
195 of the organic matter present in the sample.

196 Carbon and nitrogen concentrations were analyzed by using the FLASH 2000 Organic Elemental
197 Analyzer, based on Flash Dynamic Combustion (Thermo Fisher Scientific, 2014). An amount of
198 <20 mg of soil from each sample was weighed into a pressed tin cup and placed into the auto
199 sampler. The sample was entirely combusted within a high temperature reactor. C and N were
200 then determined by a chromatography column connected to a highly sensitive thermal
201 conductivity detector.

202 Phosphorus content was determined according to Walinga et al. (1989): samples were digested
203 with H₂SO₄, salicylic acid and H₂O₂ and analyzed on a colorimetric segmented flow analyzer
204 (Skalar).

205 The extraction of BSi was achieved following the sequential alkaline method of DeMaster
206 (1981). About 25-30 mg sediment was mixed with 25 mL of Na₂CO₃ solution (0.1 M) and
207 incubated in a water bath maintained at 85 °C for 4 hours. Subsamples (1 mL) were extracted at
208 2, 3 and 4 hours, diluted with 5 mL of the original Na₂CO₃-solution, and analyzed for DSi using
209 the spectrophotometric molybdate - blue method (Grasshoff et al. 1983) on a segmented flow
210 analyser (Skalar). Under these specific conditions the amount of silica extracted should increase
211 linearly with time. To determine the BSi content of a single sample the weight percent silica (per
212 incubated sediment mass) extracted was plotted against the three time intervals. The extrapolated
213 intercept of a least-squares regression line, where time is equal to zero is equal to the BSi content
214 of the sample (DeMaster 1981).

215

216 *Measurements for ratio and stock calculation*

217 More spatially detailed measurements were made at Wookie Channel (S19 33.563 E23 12.265;
218 around 200 km downstream of Mohembo; Fig.1). This channel lies in the seasonal floodplains
219 and is assumed to be representative of the channels in this area. Here, a 100 m stretch spanning
220 the entire width of the channel (ca. 14 m) was selected. In this transect, 10 vegetation patches
221 were selected containing each macrophyte species present in the transect (Table 1). In the same
222 transect, 10 non-vegetated locations were also selected for comparison. First, surface water
223 samples were taken at all locations and processed as previously described for total inorganic N,
224 total inorganic P and DSi analyses. Second, 10 cm deep sediment cores (rooting depth of
225 macrophytes) were taken at all 20 locations, as described previously, and analyzed later for total
226 N, total P, and BSi. Third, the size, position and species composition of each vegetation patch
227 was mapped manually. This enabled us to calculate the total coverage (in m² and %) of
228 vegetation in the channel for each species. Finally the biomass of each species in plots of 50
229 cm×50 cm (in g m⁻²) were measured by harvesting above ground parts. Each species sampled
230 was dried at 70 °C, ground and analyzed for C, N, P and BSi (using the methods described
231 earlier for sediment analysis).

232 Nutrient ratios in all three compartments (water, plant, sediment) were calculated by dividing the
233 average value of each nutrient per compartment, by the lowest concentration measured (*in casu*
234 P). For N in water, which was always below detection limit, we used the detection limit of NH₄
235 (0.08 mg N L⁻¹) as a conservative upper limit.

236 Plant nutrient concentrations (in mg g⁻¹) were multiplied by plant biomass (in g m⁻²) to obtain
237 nutrient stocks in the different species (g m⁻²). We averaged these data for the biomass, taking

238 the relative coverage of the species into account as a weighting factor. Sediment nutrient
239 concentrations (in mg g^{-1}) were multiplied with the bulk dry matter of the sampled core (in g)
240 and divided by the cross sectional area of the core ($6.16 \cdot 10^{-4} \text{ m}^2$) to estimate nutrient stocks (g m^{-2})
241 ²) in the top 10 cm sediment. Nutrient stocks in the water were not calculated because this would
242 require the amount of nutrients passing over an area of vegetation within a certain, relevant
243 period of time. These data are not available.

244

245 *Statistical analysis*

246 Averages are given with standard deviations. All datasets were normally distributed (Kruskal-
247 Wallis test). Significant differences between SW and DW and between open channel spots and
248 vegetated patches were tested with a paired t-test using R version 3.2 (R Core team, 2013).
249 Sediment data were linearly interpolated and plotted with Surfer plots.

250

251

252 **Results**

253 *Water samples*

254 The EC doubled from Mohembo to the outlets, where values were twice as high (Fig. 3a) and we
255 can recognize 2 distinct spatial signals. EC values were rather constant around $40 \mu\text{S cm}^{-1}$ until
256 20 km upstream of the boundary between the permanent and seasonal floodplains (which is ca.
257 160 km downstream of Mohembo). Thereafter, values rose up to $80 \mu\text{S cm}^{-1}$ in the seasonal
258 floodplain. Outlet values were all higher than $100 \mu\text{S cm}^{-1}$. No differences between SW and DW
259 ($t_{28} = -0.28$, $p = 0.78$) and between water in open channel spots and vegetated patches were
260 detected ($t_{18} = 1.13$, $p = 0.27$), indicating mixing of the water over the whole channel width and
261 depth, at all sites.

262 pH only changed marginally and is circumneutral, except in the outlets where it became slightly
263 more alkaline (Fig. 3b). Again no significant differences between SW and DW ($t_{28} = 0.91$, $p =$
264 0.37) and channel areas with and without vegetation cover were found ($t_{18} = -0.36$, $p = 0.73$).

265 The spatial DO concentrations (mg L^{-1}) could be divided into 4 phases: first DO steadily
266 decreased in the Panhandle to around ca. 90 km, which was near the boundary with the
267 permanent floodplains (Fig 3c). The second phase was characterized by a rather constant DO
268 concentration fluctuating around 5 mg L^{-1} from 100 to 190 km, the boundary between permanent
269 and seasonal floodplains. After that, in a third phase, DO concentration decreased again until ca.
270 230 km where it reached minimum concentrations of 2.4 mg L^{-1} . From there it increased again
271 towards its original Panhandle concentration in some of the outlets. Generally, no significant
272 differences between depth ($t_{28} = -2.15$, $p = 0.06$) and vegetation ($t_{18} = -0.32$, $p = 0.75$) cover were
273 measured. Water temperature was more or less constant at $22.5 \pm 1.7 \text{ }^\circ\text{C}$ throughout the Delta.

274 Therefore, oxygen saturation (%) followed the same trends as DO (not shown) with around
275 100% saturation at Mohembo and in the outlets, and 33 % at the lowest point.

276 Turbidity data were more scattered, with no significant differences between SW and DW (Fig.
277 3d; $t_{18} = 1.92$, $p = 0.07$). The overall trend showed that turbidity declines until it is nearly zero
278 NTU at the distal end of the Delta, but increased again in the outlets.

279
280 Nitrogen concentrations NH_4^+ and NO_3^- in the water column were always below the detection
281 limit of 0.08 mg N L^{-1} and 0.05 mg N L^{-1} respectively in both years (not shown). PO_4^{3-} was
282 detected in 2012 (no data for 2011), but no spatial trends could be observed, probably because
283 values were close to detection limits of 0.02 mg P L^{-1} (Fig. 3e; average $0.03 \pm 0.01 \text{ mg L}^{-1}$). No
284 differences between SW and DW ($t_{28} = -0.10$, $p = 0.92$) and between open channel plots and
285 vegetated patches were found ($t_{18} = 0.09$, $p = 0.93$). Finally, DSi shows two spatial trends that
286 are similar to those of EC in that DSi is rather constant around 5 mg L^{-1} until ca. 160 km
287 downstream Mohembo (Fig. 3f). It then increased further downstream, and quadruples by the
288 time it reached the outlets (except for 1 outlet). Trends for 2012 were similar to 2011 trends. No
289 differences between SW and DW ($t_{28} = -1.53$, $p = 0.14$) and between open channel spots and
290 vegetated patches were found ($t_{18} = -1.43$, $p = 0.17$).

291

292 *Sediment samples*

293 The background matrix of the sediment was uniform Kalahari fine-medium grained quartz sand.
294 Organic matter content (Fig.4a) in non-vegetated sediments was low throughout the entire Delta,
295 ranging between $0 - 27.1 \text{ g OM kg}^{-1}$ (average $2.4 \pm 0.7 \text{ g OM kg}^{-1}$, $n = 50$). The two highest
296 concentrations were found at the transition of the Panhandle and the permanent floodplain (ca.

297 100-120 km downstream of Mohembo; up to 27 g OM kg⁻¹) and around 160-180 km (up to 15 g
298 OM kg⁻¹), which corresponded to the boundary between the permanent and seasonal floodplains.
299 These values were low compared to the concentrations found in vegetated sediments throughout
300 the Delta which were up to one order of magnitude higher, ranging between 0.7 – 276.2 g OM
301 kg⁻¹ (on average 58.7 ± 9.1 g OM kg⁻¹, n = 50). Here, the highest value was again found at the
302 transition zone between the Panhandle and the permanent floodplain. The organic matter content
303 decreased with depth in the cores and also with distance from the Panhandle. Lowest values were
304 found at the distal end of the Delta. The data for the spatial pattern of C (Fig. 4b) were very
305 similar to those of organic matter. On average, there was 18 times less C stored in non-vegetated
306 sediments, ranging between 0.2 – 16.0 g C kg⁻¹ (on average 1.1 ± 0.4 g C kg⁻¹, n = 50), compared
307 to vegetated sediments where values ranged from 0.3 – 91.2 g C kg⁻¹ (on average 20.5 ± 3.0 g C
308 kg⁻¹, n = 50).

309
310 Spatial trends in sediment nutrient data were similar, pointing towards a strong link with the
311 organic matter. Nitrogen values (Fig. 4c) were up to 21 times higher in vegetated sediments (0 –
312 7.4 g N kg⁻¹, on average 1.3 ± 0.2 g N kg⁻¹, n = 50) compared to non-vegetated sediment (0 – 0.8
313 g N kg⁻¹, on average 0.1 ± 0.1 g N kg⁻¹, n = 50). Phosphorus values (Fig. 4d) were up to 13 times
314 higher in vegetated sediments (0 – 0.44 g P kg⁻¹, on average 0.05 ± 0.01 g P kg⁻¹, n = 50)
315 compared to non-vegetated sediments (0 – 0.02 g P kg⁻¹, on average 0.004 ± 0.001 g P kg⁻¹, n =
316 50), and P was nearly absent downstream ~190 km. A P-rich layer was found at a depth of -15
317 to -20 cm, throughout the whole Delta and regardless of vegetation cover. This was different
318 from the previous trends in organic matter, C and N. Finally, BSi values (Fig. 4e) were up to 6
319 times higher in vegetated sediments (0 – 6.7 g Si kg⁻¹, on average 1.5 ± 0.2 g Si kg⁻¹, n = 50)

320 compared to non-vegetated sediments ($0 - 1.5 \text{ g Si kg}^{-1}$, on average $0.3 \pm 0.1 \text{ g Si kg}^{-1}$, $n = 50$).
321 Its spatial trend was again different from the previous trends, as the BSi concentration was higher
322 towards the distal end of the Delta. In non-vegetated areas, a BSi rich layer was also found at the
323 depth of -15 to -20 cm, throughout the whole Delta. This corresponds to the P values previously
324 described. In vegetated areas, this high Si layer was only present at the distal end of the Delta.

325

326 *Plant samples and vegetation mapping*

327 Aquatic vegetation was abundant in the majority of the channels. Most of the species had a
328 submerged growth form, with or without floating leaves. Emergent species were less abundant,
329 because they are actually floodplain species, though the border between channel and floodplain
330 is not always obvious. Exclusively floating species were not found. *Ottelia ulvifolia* and
331 *Nymphaea nouchali* were most frequently found throughout the entire Delta. *Ottelia muricata*
332 and *Trapa natans* were only found in the upstream parts of the Delta and did not occur further
333 downstream. The rest of the species identified are listed in Table 1 along with their C, N, P and
334 BSi concentrations and N/P mass ratio and C/N mass ratios. In addition, samples of 7 further
335 species were taken on an *ad hoc* basis, unrelated to the sampling locations.

336 We calculated that the total coverage of the submerged vegetation in the detailed channel
337 transect (Wookie Channel) was about 50 %; the other half was bare sediment. This value is
338 representative for the seasonal floodplain channel vegetation, but is likely to be an
339 overestimation for the channels in the permanent floodplain where channels are much deeper and
340 flow velocities are higher. Individual species coverage and biomass are presented in Table 1.

341

342 *Ratio and stock calculation*

343 Nutrient concentrations in the water and sediment of Wookie Channel agreed well with values in
344 the rest of the Delta, corroborating the representativeness of this transect. The nutrient ratios in
345 the water clearly indicated a depletion of N relative to P, and a significant excess of Si compared
346 to N and P (Fig. 5). The total stock of N in the sediment was up to 10 times higher in the
347 vegetated sediment than in the non-vegetated sediments, and up to 6 times higher for P and Si
348 (Fig. 5). This led to similar P:Si ratios in both sediment types, but a higher N:P:Si mass ratio in
349 the vegetated sediments. The magnitude of the N and P stock in the vegetation was lower than in
350 the sediment, and ratios were intermediate between those of the water and those of the vegetated
351 sediment.

352

353

354 **Discussion**

355 The Okavango Delta is a unique ecosystem that is driven by evapotranspiration which keeps the
356 water fresh and the islands salty (Ramberg and Wolski 2008). This is reflected in the abiotic
357 parameters. The further downstream the water travels, the more the EC rises. Yet this rise is not
358 as extreme as would be expected from simple evaporative concentration: downstream values of
359 $80 - 100 \mu\text{S cm}^{-1}$ are still towards the lower end of observations from other freshwater systems
360 (Mackay et al. 2011). This is believed to be the direct result of evapotranspiration by island
361 vegetation with consequent sequestration of solutes in deeper groundwater (Ramberg and Wolski
362 2008). DSi concentrations are similarly less concentrated than expected but increase once the
363 water has entered the Delta. With ca. 98 % of total annual inflow evapotranspired, the DSi
364 concentration should increase dramatically until saturation ($\sim 50 \text{ mg L}^{-1}$), but the outlet
365 concentrations were not more than 4 times the concentration at Mohembo (see also Frings et al.
366 2014). This highlights the important role of the floodplain vegetation in taking up an important
367 part of inflowing DSi, and its transfer into the islands (Struyf et al. 2015).

368
369 In contrast, dissolved N (NH_4^+ and NO_3^-) was always below detection. Previous research has
370 demonstrated the oligotrophic character of the Delta channels, reflected by very low dissolved
371 nutrient concentrations and low phytoplankton production (e.g. Cronberg et al. 1996; Krah et al.
372 2006). Our analytical detection limits were too coarse to measure the actual concentrations of N
373 in the water, yet they confirm its nutrient poor status. This is also reflected in (i) the high
374 diversity of plant species (e.g., the presence of the carnivorous species *Aldrovanda vesiculosa*,
375 and several species of *Utricularia*, which supplement their intake of nutrients by trapping
376 plankton and small aquatic insects; Adamec 1997), (ii) the absence of free floating species which

377 rely mainly on nutrient uptake from the water whereas the other growth forms rely on root
378 uptake too (Janauer et al. 2013), and (iii) the low N:P mass ratio of most plant species in the
379 Delta. Generally a N:P mass ratio below 14 is thought to indicate a deficit of N relative to P
380 (Koerselman et al. 1996). It is exactly under these nutrient-poor conditions (at least for N) that
381 entrapment of organic matter and organic nutrients in vegetation patches can be most crucial for
382 successful macrophyte development.

383
384 By forming patches, macrophytes act as ecological engineers (*sensu* Jones et al. 1994), as they
385 alter the hydraulics, (bio)geomorphology, and biogeochemistry of the channels in which they
386 occur. This has been demonstrated for both freshwater macrophytes (Schoelynck et al. 2012;
387 2014) and their marine counterparts (Bouma et al. 2007; Temmerman et al. 2007; van
388 Wesenbeeck et al. 2008). Turbidity is relatively high in the Panhandle, and decreases through the
389 Delta, as part of the suspended material is accumulated in the patches. Sediments under
390 vegetated patches have much higher organic matter concentrations (on average 10 times higher),
391 and also higher C, N, P and BSi concentrations, than non-vegetated sediments (where organic
392 matter is virtually absent). The lettuce-shaped leaves of *Ottelia ulvifolia* dominant in the
393 channels in the Delta are exemplary of the trapping efficiency of vegetation (Fig. 1b; see also
394 movie in online supplementary material). Having many large submerged leaves helps species to
395 accumulate organic matter in running water, as was shown for the temperate species *Nuphar*
396 *lutea* (Schoelynck et al. 2014).

397
398 As a result of this accumulation, there is a large discrepancy between the nutrient stock in
399 vegetated sediment and that in non-vegetated sediment. Organic matter breakdown generally

400 proceeds in three distinct phases: (a) rapid loss due to leaching, (b) mechanical and invertebrate
401 fragmentation and (c) microbial decomposition and conditioning (Webster and Benfield, 1986;
402 Gessner et al. 1999). This recycling process is deemed to be an important nutrient source for
403 aquatic vegetation (Fig. 5; Madsen and Cedergreen 2002; Schaller and Struyf 2013). It is
404 nevertheless surprising that dissolved N in surface water is below detection limits even for the
405 samples collected near the bottom, while the diffusion potential to the water phase is inevitably
406 large (Fick's law of diffusion) since the concentration potential is large coupled with a relatively
407 small diffusive distance of a few centimetres between the sediment and the water. A possible
408 explanation is that the breakdown of organic matter is inefficient due to a number of factors and
409 as a result the organic matter is largely only accumulating instead of mineralizing. Another
410 explanation, which does not conflict with the first one, is a rapid uptake and retention of nutrients
411 by the plants (see below).

412
413 We see 3 arguments to support the inefficient decomposition hypothesis. Firstly, DO
414 concentration correlates well with the turbidity pattern. It decreases downstream until 230 km
415 where turbidity is virtually zero NTU and then DO increases again. It seems likely that part of
416 the DO is consumed by in-stream suspended and benthic organic matter breakdown, leaving little
417 DO to penetrate the sediment. This may result in the utilisation of less efficient mineralization
418 pathways under hypoxic conditions (e.g. denitrification, manganese, iron and sulfate reduction,
419 and methanogenesis), a phenomenon which has been observed in other tropical wetlands such as
420 the Everglades (Hagerthey et al. 2010). Radial oxygen loss from the roots of macrophytes is a
421 common process creating oxidized microzones in the anoxic sediment. Despite the fact that these
422 oxidized microzones are often only a few millimetres thick, they can be critical in regulating

423 redox processes including coupled nitrification–denitrification, which reduces the nitrogen
424 content of ecosystems (Caraco et al. 2006).

425
426 Secondly, invertebrate fragmentation is likely not a large-scale process: only a limited number of
427 families of invertebrates are found in the in-stream macrophyte patches and sediments, compared
428 to other habitats in the Delta (Dallas and Mosepele, 2006). These low abundances may be caused
429 by inhospitable conditions (low oxygen levels and/or shade-depressed primary productivity) in
430 much of the papyrus and other swamps, and predation pressure by a multitude of
431 opportunistically predatory fishes (Appleton et al. 2003). Notwithstanding studies like Masese et
432 al. (2014) showing that there can actually be high numbers of shredders in some cases, the
433 detritivorous shredder guild in tropical rivers is generally represented by very few taxa, mostly
434 crab and shrimp species (Dobson et al. 2002) and enhanced microbial activity is proposed
435 instead (Irons et al. 1994).

436
437 Litter stoichiometry is one of the factors controlling microbial decomposition, which is our third
438 argument. Low N/P ratios and high C/N ratios are good predictors of poor organic matter quality
439 and of low decomposition rates (Berg and McClaugherty 2003; Taylor et al. 1989). The N/P
440 ratios are generally low in the Delta, as discussed above, whereas the C/N mass ratio of the
441 macrophytes is high. A peak value of 70 C/N for instance, was found in *Cyperus papyrus* and
442 this species is the most dominant emergent species in the upstream reaches, with a standing
443 biomass in the order of 70-150 10³ kg dry weight ha⁻¹ (Thompson 1976). The *Cyperus* species
444 and others like *Eleocharis dulcis*, have also a fairly high BSi concentration (see Schoelynck and
445 Struyf (2016) for comparison with other macrophyte species throughout the world), and Si may

446 change macrophyte nutrient ratios in general (Schaller et al. 2016). Emsens et al. (2016)
447 demonstrated that anthropogenic nutrient enrichment of wetlands leads to consistently lower (up
448 to 50 % reduction) litter Si concentrations in all tested *Carex* species, suggesting a plant-
449 physiological response following the relief of nutrient stress. A negative correlation between
450 litter Si concentrations and litter decomposition rates under nutrient poor conditions suggested an
451 inhibiting effect of Si on decomposition. However, positive correlations between litter Si
452 concentrations and C:N and lignin:N ratios indicated a strong interdependence of Si with other
453 litter quality parameters that determine decomposition. An elaborate decomposition study was
454 done by Schaller and Struyf (2013) on *Phragmites australis*, whereby litter from plants exposed
455 to high Si availability degraded up to 90 % faster than controls. In the presence of macro-
456 invertebrate shredders however, degradation rates actually decreased when litter was more Si
457 rich. This points to a negative effect of Si in litter on shredder functionality, and thus on total
458 decomposition rates. It is clear that more and specific research is needed to determine whether
459 this has any significant effect on litter breakdown in the Okavango Delta.

460
461 Due to meandering and anastomosis of the channels, the water does not necessary flow along the
462 channels only from upstream to downstream reaches. Especially during high floods, water in the
463 channels also comes from, and flows into, seasonally inundated floodplains, where a large
464 amount of DOC and particulate organic matter is produced by the highly productive emergent
465 vegetation (Mladenov et al. 2005). This bulk organic matter is likely partly stored in the
466 floodplains themselves, and partly transported downstream within the channels. In these
467 channels, some of it accumulates in the sediments of the macrophyte patches in the upstream
468 reaches: organic matter concentration is generally higher at the upstream end of the Delta than at

469 the distal end. As set out above, the conditions for mineralization are likely suboptimal. By
470 accumulating and concentrating the organic matter in the sediments below the patches,
471 macrophytes are likely able to locally forestall a deficiency of nutrients. We hypothesize that few
472 nutrients can diffuse from the sediment to the Okavango surface water as those that are produced
473 are likely to be immediately taken up again in vegetation: a very short spiralling length in the
474 Telescoping Ecosystem Model of Fisher et al. (1998) (i.e.: a very tight recycling loop; Fig. 5).

475
476 Part of the organic matter is further transported downstream and is likely involved in one or more
477 cycles of entrapment into channel vegetation patches and flanking vegetation retaining materials
478 in the Delta. With this process, there is a net consumption of oxygen, and the refractory organic
479 matter is stored until only few particles remain to leave the Delta through the outlets. This may
480 explain the occurrence of the increased P and Si layers at the depth of -15 to -20 cm where P may
481 start to precipitate, especially in the downstream regions due to dry fallout (Humphries et al.
482 2014; a similar phenomenon was found in The Everglades, Wetzel et al. 2005). Meanwhile, N –
483 the limiting nutrient in this ecosystem – is likely being recycled as efficiently as possible.

484
485 We conclude that macrophyte patches in the Okavango Delta play an important role in the
486 entrapment and accumulation of particulate organic matter that is transported through the
487 channels. This entrapment is likely crucial for the macrophytes' survival because it may provide
488 a key source of the essential nutrients which the plants cannot obtain in sufficient quantities
489 directly from the nutrient poor water. By engineering the ecosystem as such, the channel
490 vegetation is, just like the floodplain vegetation, another step in retarding the transfer of the
491 elements and nutrients to island groundwater flow. These retention processes are key to

492 explaining why the Okavango Delta has such high productivity and which makes it unique
493 among its kind.

494

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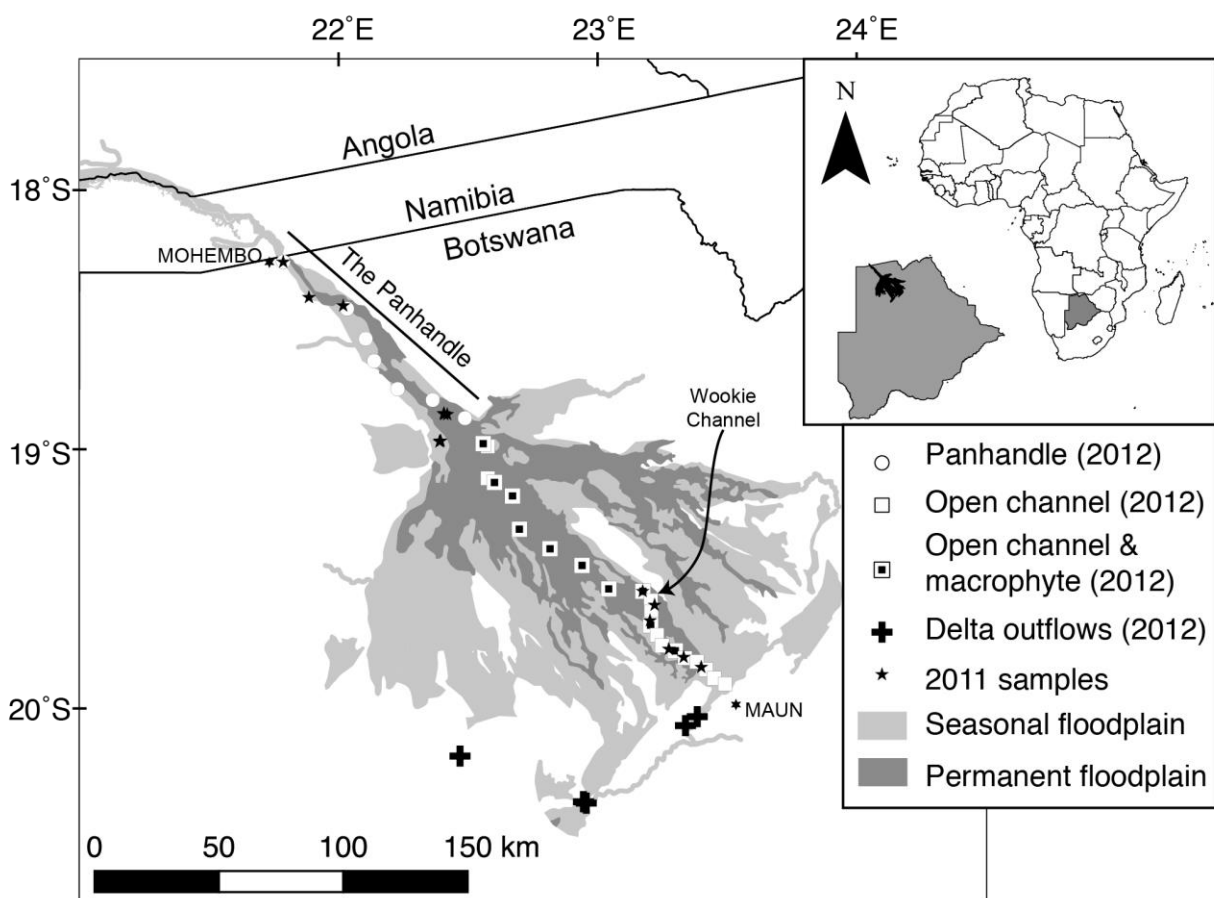
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725 **Table 1** Alphabetical list of all macrophyte species that were found during the 2012 sampling campaign in the Delta. Growth form is indicated: E = emergent, S
 726 = entirely submerged, F = partly submerged with floating leaves. The respective species composition in the sampled patches throughout the Delta and in the 100
 727 m transect (Wookie Channel) is indicated with '×'. All species were sampled and analyzed for C, N, P and BSi and the N/P and C/N mass ratio is given. Biomass
 728 and coverage were only measured in Wookie Channel. Biomass is expressed as g dry matter m⁻² vegetated channel bed. With totally around 50 % vegetation
 729 coverage, biomass should be divided by 2 to obtain biomass data representative for the entire channel bed. *Oxycaryum cubense* was not sampled.

<i>Species in the sampled patches</i>	<i>Growth form</i>	<i>Patch 1</i>	<i>Patch 2</i>	<i>Patch 3</i>	<i>Patch 4</i>	<i>Patch 5</i>	<i>Patch 6</i>	<i>Patch 7</i>	<i>Patch 8</i>	<i>Patch 9</i>	<i>Patch 10</i>	<i>Wookie channel</i>	<i>Coverage (%)</i>	<i>Biomass (g DM m⁻²)</i>	<i>N (mg g⁻¹)</i>	<i>P (mg g⁻¹)</i>	<i>C (mg g⁻¹)</i>	<i>BSi (mg g⁻¹)</i>	<i>N/P ratio</i>	<i>C/N ratio</i>
<i>Aldrovanda vesiculosa</i>	S												(-)	(-)	19.8	1.6	413.7	11.6	12	21
<i>Brasenia schreberi</i>	F												(-)	(-)	16.3	1.2	428.4	0.90	14	26
<i>Caldesia reniformis</i>	F											×	1	22	23.2	2.8	481.7	2.16	8	21
<i>Ceratophyllum demersum</i>	S	×		×				×	×			×	1	20	9.9	1.8	498.9	1.27	6	51
<i>Cyperus articulatus</i>	E											×	3	48	5.4	1.6	520.6	9.96	3	96
<i>Cyperus papyrus</i>	E			×	×								(-)	(-)	6.4	0.6	451.0	17.8	10	70
<i>Eleocharis dulcis</i>	E											×	2	306	13.0	2.0	492.8	26.9	7	38
<i>Lagarosiphon ilicifolius</i>	S			×					×			×	6	68	20.7	3.1	445.6	3.53	7	22
<i>Najas pectinata</i>	S	×				×		×	×		×		(-)	(-)	12.6	1.8	368.1	11.0	7	29
<i>Nymphaea nouchali var. caerulea</i>	F	×	×	×	×	×	×		×			×	15	48	14.4	1.9	502.8	0.67	8	35
<i>Nymphoides indica</i>	F												(-)	(-)	13.7	1.1	427.6	0.71	12	31
<i>Ottelia muricata</i>	S	×	×		×								(-)	(-)	10.2	1.8	351.0	3.32	6	34
<i>Ottelia ulvifolia</i>	S	×		×	×		×	×	×	×	×	×	15	221	8.3	1.1	453.3	2.28	8	55
<i>Oxycaryum cubense</i>	E											×	3	(-)	(-)	(-)	(-)	(-)	(-)	(-)
<i>Potamogeton thunbergii</i>	F												(-)	(-)	16.6	1.4	430.3	0.99	12	26
<i>Potamogeton schweinfurthii</i>	S												(-)	(-)	10.1	0.5	424.9	10.1	20	42
<i>Rotala myriophylloides</i>	S					×					×		(-)	(-)	11.4	0.6	392.7	3.04	19	34
<i>Schoenoplectus corymbosus</i>	E										×	×	4	298	8.5	1.3	504.4	10.1	7	59
<i>Trapa natans</i>	F	×											(-)	(-)	13.3	2.2	413.2	1.59	6	31
<i>Typha capensis</i>	E												(-)	(-)	7.9	0.9	454.8	0.22	9	58



731

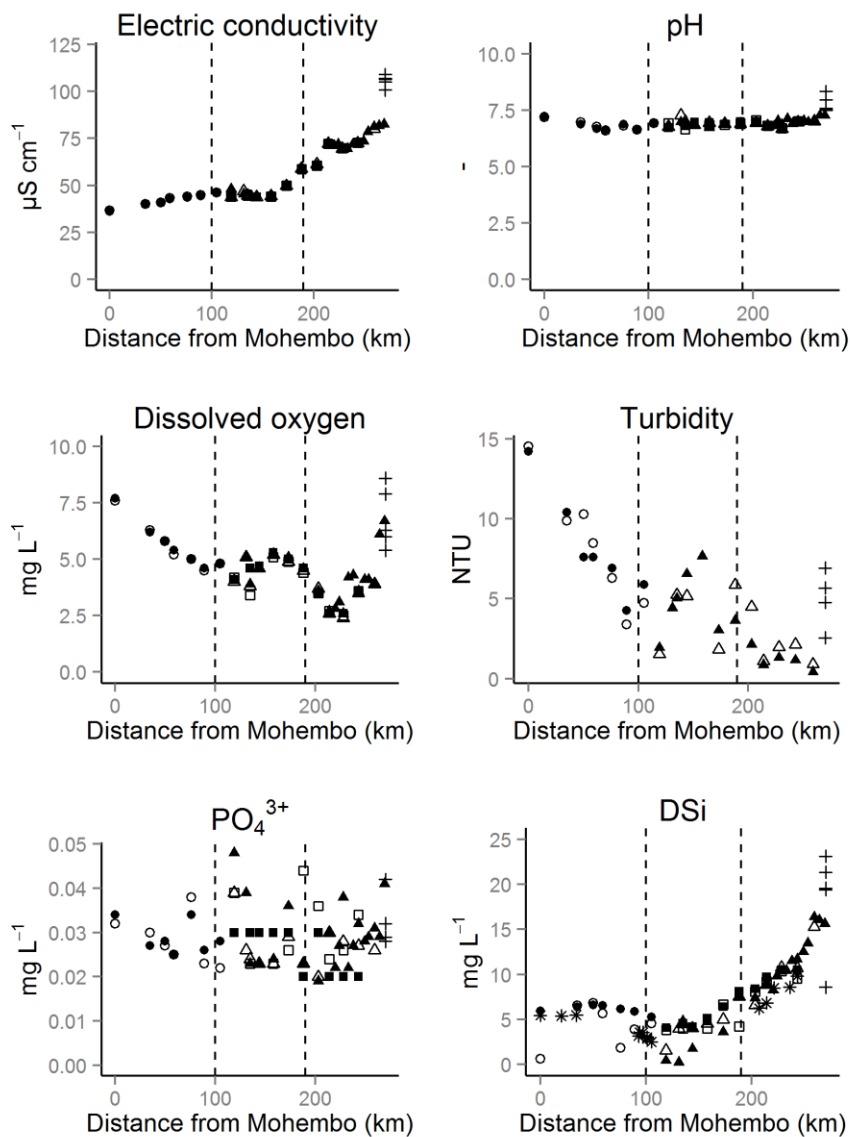
732 **Figure 1** Map of the Okavango Delta with location of sample stations, and the flooding regime.

733



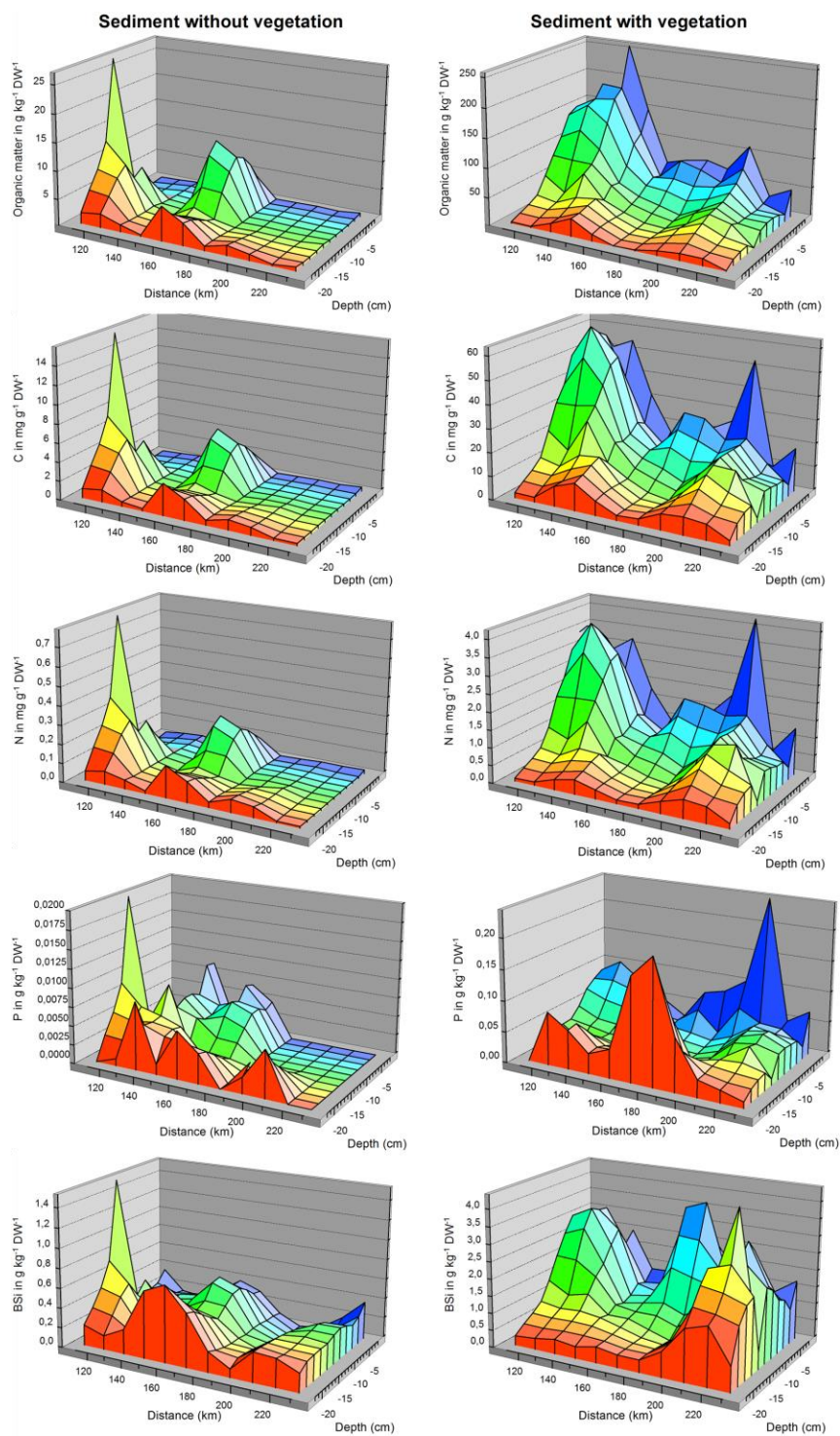
734

735 **Figure 2** (a) Large pieces of dead organic matter blocking a channel in the permanent swamp dominated by *Cyperus*
 736 *papyrus*. (b) Fine particulate organic matter deposited on the leaves of *Ottelia ulvifolia* in the seasonal swamp. (c)
 737 Comparison between sediment from vegetated river bed (left, black) and from non-vegetated sediment (right, white).
 738



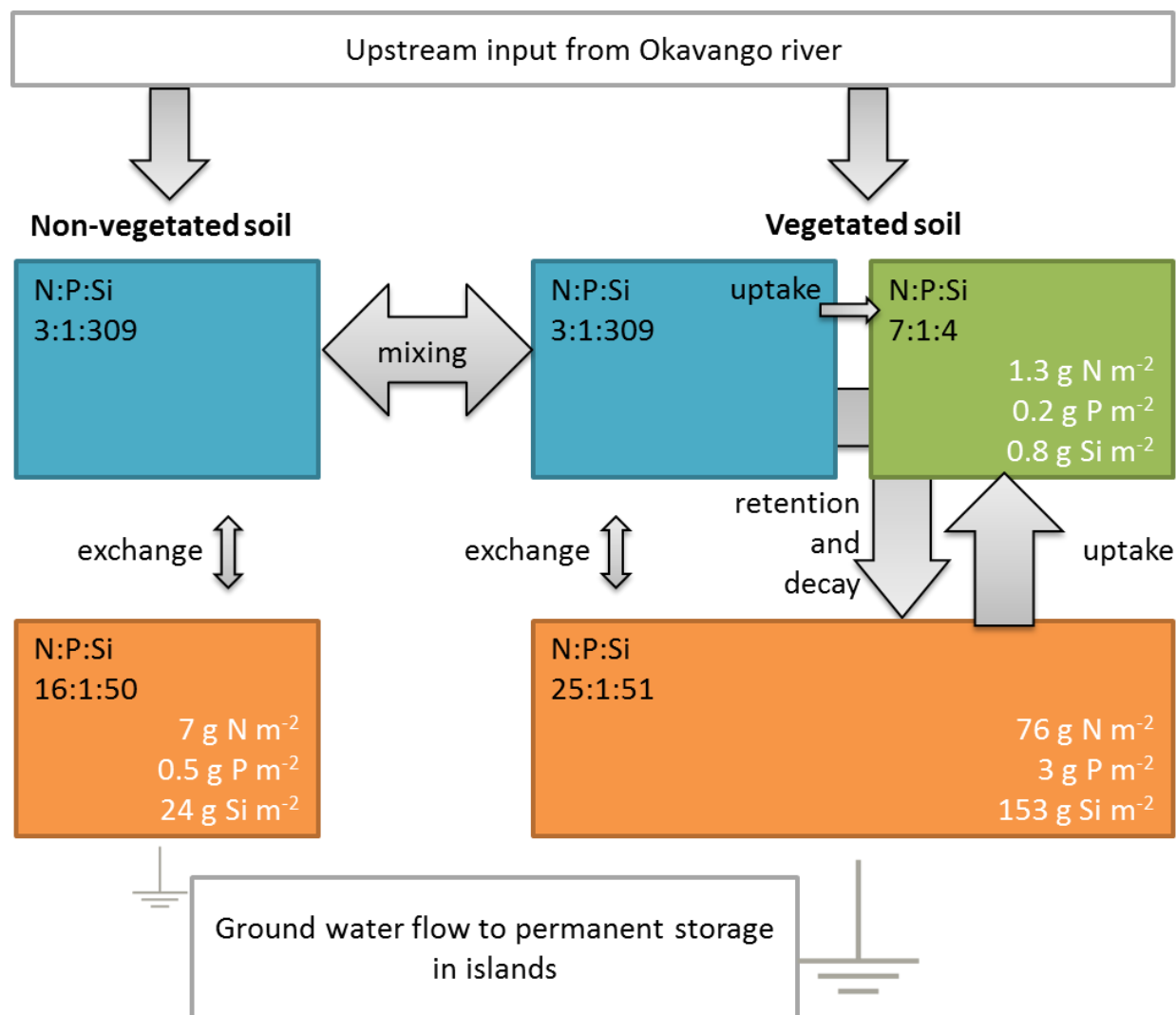
739

740 **Figure 3** Distributions of abiotic parameters and nutrient concentrations in the Okavango Delta channel water.
 741 Vertical dashed lines indicate the theoretical borders between Panhandle – Permanent Floodplain – Seasonal
 742 Floodplain. Panhandle surface water samples (●) and deep water samples (○), floodplain open channel surface
 743 water samples (▲) and deep water samples (△), floodplain macrophyte patch surface water samples (■) and deep
 744 water samples (□), and outlets (+) were sampled in 2012 and analyzed for electric conductivity ($\mu\text{S cm}^{-1}$), pH (-),
 745 dissolved oxygen (mg L^{-1}), turbidity (NTU), PO_4^{3-} (mg P L^{-1}) and DSi (mg Si L^{-1}). Surface water samples from 2011
 746 were also analyzed for DSi (*). Results for NO_3^- and NH_4^+ (2011 and 2012) are not displayed because they were all
 747 below detection limits.
 748



749

750 **Figure 4** Results of analysis of sediments from the Okavango Delta channels (permanent and seasonal floodplains)
 751 with and without vegetation: organic matter, C, N, P and BSi ($\text{g kg}^{-1} \text{DW}$). Data are interpolated linearly with depth
 752 (indicated by contour colour) and with distance downstream. Note the difference in vertical scales between
 753 vegetated and non-vegetated plots of the same element.
 754



755

756 **Figure 5** Nutrient ratios in (i) water column (blue) and stocks and ratios in (ii) vegetated and non-vegetated soils
 757 (orange), and (iii) macrophyte biomass (green). Stocks are given in g m⁻² and written in white, nutrient ratios are
 758 written in black. Main hypothesized interactions of particulate and dissolved nutrients are indicated with grey arrows
 759 of which the size reflects the relative hypothesized importance of each interaction. We hypothesize that the majority
 760 of interactions takes place at vegetated locations: organic matter (from upstream regions) is retained in macrophyte
 761 patches and stored in the sediment. Nutrients that dissolve from this decaying organic matter are either transported
 762 by the ground water flow, or are taken up by the vegetation above. Likely only a little amount is exchanged with the
 763 water column. When the plants become litter, this is transported downstream in the water column (mixing between
 764 water above vegetated and non-vegetated soil) before it is trapped again in vegetation patches further downstream.