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Different morphology of **\*\*Nuphar lutea\*\*** in two contrasting aquatic environments and its effect on ecosystem engineering

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6

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18

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23

24 **Abstract**

25 Aquatic plants (macrophytes) can have a large effect on river hydraulics and  
26 geomorphology. However, the extent to what plant morphological plasticity actively  
27 influences these feedbacks has received little scientific attention. The nymphaeid  
28 macrophyte species *Nuphar lutea* (L.) Smith is characterised by a distinct leaf duality.  
29 Floating leaves shade most of the submerged leaves thereby limiting light  
30 penetration. Despite their apparent negligible photosynthetic role, submerged leaves  
31 of *N. lutea* remain intact during summer and contribute a significant part to the total  
32 biomass. Our results indicate that the submerged leaves are crucial in plant-flow  
33 interactions and hence in the engineering potential of the plant, i.e. the capacity to  
34 locally reduce flow velocities and to promote sedimentation, including organic matter  
35 deposition. Plant individuals growing in running river water were compared to  
36 individuals from adjacent oxbow lake water. The number and size of submerged  
37 leaves were significantly higher for river standing individuals and the accumulated  
38 sediment contained significantly more organic matter, total nitrogen and total  
39 phosphorus, and was characterised by a lower C/N ratio and a finer grain size. We  
40 therefore argue that the submerged *N. lutea* canopy in rivers has the ability to create  
41 a high-nutrient, low hydrodynamic environment, resembling the conditions found in  
42 oxbow lakes.

43

44 **Keywords:** Biebrza, scale-dependent feedbacks, morphological plasticity, bio-  
45 geomorphology, aquatic vegetation, nutrient dynamics, organic matter accumulation

46

47 **Introduction**

48 Multiple studies have demonstrated that plants can significantly affect river channel  
49 form and adjustment (Tal and Paola, 2007; Hicks et al., 2008; Larsen and Harvey,  
50 2010; Larsen and Harvey, 2011; Montakhab et al., 2012). There is a growing  
51 scientific interest in these plant-river interactions (e.g.: (Franklin et al., 2008; Gurnell  
52 et al., 2010; Zong and Nepf, 2010; Nepf, 2012), focusing mostly on riparian plant  
53 species, particularly shrubs and trees. However, true aquatic macrophytes can also  
54 affect the hydraulics and geomorphology of rivers (Gurnell et al., 2010; Bertoldi et al.,  
55 2013). Growing in patches, they can act as ecological engineers (Gurnell, 2014)  
56 meaning that they are capable of adapting the environment to their benefit, with  
57 positive and/or negative feedbacks. Flow velocity, for instance is reduced inside  
58 macrophyte patches, as friction is generated by the canopy (Vandenbruwaene et al.,  
59 2011; Schoelynck et al., 2012). Adjacent to patches, flow velocity is increased  
60 because of flow deviation around the patches (Schoelynck et al., 2012). As a  
61 consequence, shoots inside patches have a better survival chance and a larger  
62 primary production than shoots emerging between patches, where erosion, scouring  
63 and uprooting can limit here plant growth and patch expansion (Schoelynck et al.,  
64 2012). Macrophyte patches thus create spatial variability in stream velocity and  
65 induce geomorphological changes of the river including (i) changes in bathymetry  
66 (Cotton et al., 2006; Schoelynck et al., 2012; Schoelynck et al., 2013) and (ii) bank  
67 erosion leading to meandering (Gurnell (2014) and references therein).

68

69 Apart from river studies, knowledge of vegetation-hydrodynamics-geomorphology  
70 interaction is also rapidly emerging from studies in coastal and estuarine  
71 environments. Bouma et al. (2007), Temmerman et al. (2007), Van Wesenbeeck et

72 al. (2008) and Vandenbruwaene et al. (2011), for instance, clearly showed  
73 differences in stream velocity in and around vegetation patches of the tidal marsh  
74 grass *Spartina anglica* C.E.Hubb, causing increased sedimentation in the patches,  
75 and eroding gullies around the vegetation. Bouma et al. (2009) proposed a size-  
76 dependence of these these plant-flow interactions, with clear threshold values as  
77 they state that a minimum patch size and minimum organism density within the patch  
78 is needed before habitat modification can occur. This means decreasing flow  
79 velocities within the vegetation (i.e. positive feedback) and increasing flow  
80 acceleration alongside the vegetation patch (i.e. negative feedback). The  
81 combination of positive feedbacks within and negative feedbacks outside the  
82 vegetation are generally referred to as scale-dependent feedbacks (Rietkerk and Van  
83 de Koppel, 2008). Such feedbacks were recently also demonstrated to result in  
84 spatial self-organisation of riverine vegetation (Schoelynck et al., 2012).

85

86 The extent to which plant morphological plasticity can actively influence these scale-  
87 dependent feedbacks has received little scientific attention. The nymphaeid  
88 macrophyte species *Nuphar lutea* (L.) Smith (Fig. 1) is characterised by a distinct leaf  
89 duality. *N. lutea* is common in the temperate regions of the northern hemisphere  
90 (Heslop-Harrison, 1955): it occurs both in lakes with little hydrodynamic stress as well  
91 as in flowing streams. They prefer depths between 0.6 m and 2.4 m (Heslop-  
92 Harrison, 1955). Translucent, crumpled submerged leaves are produced in early  
93 spring; leathery floating leaves emerge later and reach the water surface in April and  
94 May. The occurrence of submerged leaves during the whole growing season is less  
95 explicitly found among other nymphaeid species (Smits et al., 1988b), and the reason  
96 for this summer presence is unstudied. Shoot density and leaf orientation in

97 vegetation are classically explained in relation to photosynthetic success (McMillen  
98 and McClendon, 1979; Binzer and Sand-Jensen, 2002). However, floating leaves  
99 covering most of the submerged leaves (Fig. 2) are likely to limit light penetration and  
100 the photosynthetic potential of the submerged leaves. Still, despite this hypothesised  
101 negligible photosynthetic role, submerged leaves of *N. lutea* remain intact during  
102 summer and contribute a significant part of the total biomass (Snir et al., 2006). Flow  
103 velocities may evoke strong hydrodynamic forces on the (submerged) shoots and  
104 leaves, obliging the plant to invest in energy-expensive tissue reinforcement to  
105 withstand them (Schoelynck et al., 2010): the presence of submerged leaves thus  
106 seems counterproductive. Other rooted, floating-leaved species like *Potamogeton*  
107 *natans* L. minimise their submerged biomass and concentrate all leaves at the water  
108 surface which maximises their photosynthetic success and minimises hydrodynamic  
109 forces (Bal et al., 2011).

110

111 We hypothesise that the submerged leaves are crucial in plant-flow interactions (Bal  
112 et al., 2011; Puijalon et al., 2011) and hence in the engineering potential of the plant,  
113 i.e. the capacity to alter flow velocities and to promote sedimentation including  
114 organic matter deposition. Higher sediment organic matter content may lead to higher  
115 nutrient and carbon availability (Brock et al., 1985; Webster and Benfield, 1986; Snir  
116 et al., 2006), improving plant productivity within the patches. This is especially  
117 important for an eutraphent species like *N. lutea* (Bornette and Puijalon, 2011).

118 By means of field measurements, we investigate two possible reasons for the  
119 presence of submerged leaves on *N. lutea* individuals at periods of peak biomass.

120 We hypothesise that:

- 121 i) *N. lutea* is an ecosystem engineer: the submerged leaves are efficient in  
122 reducing flow velocity thereby increasing organic matter deposition and hence  
123 nutrient availability. The efficiency of reducing the flow velocity depends on  
124 size and density of the patch: investing in submerged leaves is hence only  
125 valuable in running river water and not in still oxbow lake water, implying  
126 morphological differences between plants growing under different  
127 hydrodynamic regimes;
- 128 ii) floating leaves of *N. lutea* prevent light from reaching its submerged leaves,  
129 making the latter redundant for photosynthesis and should therefore not be  
130 retained as an explanation for the existence of submerged leaves.

131

132 **Materials and methods**

133 *Study site*

134 *Nuphar lutea* (L.) Smith is a common macrophyte in the Biebrza River, a tributary of  
135 the Narew River in north-eastern Poland. The river is approximately 160 km long, up  
136 to 80 m wide and has a catchment area of ca. 7000 km<sup>2</sup>. It runs through a sandy bed  
137 (median grain size D50 is 365 µm), it has an average annual discharge of ca. 30 m<sup>3</sup>s<sup>-1</sup>  
138 <sup>1</sup>, and it has an average water-surface slope of 0.016% between Sztabin and  
139 Goniądz. The acidity of the river water is neutral to slightly alkaline (Wassen et al.  
140 2006), which is favorable for the occurrence of *N. lutea* (Smits et al., 1988a). This  
141 species has a smaller ecological amplitude with respect to alkalinity in comparison to  
142 other nymphaeid species, and is also a typical eutraphent species which prefers a  
143 high nutrient availability (Bornette and Puijalon, 2011). This makes it abundant in  
144 typical nutrient rich lowland rivers. The floodplain is relatively undisturbed; the river  
145 has a natural channel pattern which is characterized by a single-thread meandering  
146 channel and small oxbow lakes. Due to the low agricultural fertiliser input the impact  
147 on nutrient cycles is low and a species rich flora still occurs in the Biebrza river and  
148 valley. Nutrient concentrations for 2008 in the upper catchment are: (NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>)-N  
149 = 0.18 ± 0.02 mg L<sup>-1</sup>; NH<sub>4</sub><sup>+</sup>-N < 0.08 mg L<sup>-1</sup>; PO<sub>4</sub><sup>3-</sup>-P = 0.04 ± 0.02 mg L<sup>-1</sup>. The  
150 macrophyte community in general can have a maximum biomass of 175 g DM m<sup>-2</sup> in  
151 the upper basin, for *N. lutea* specific this is up to 200 g DM m<sup>-2</sup> (personal  
152 observations in 2009). *N. lutea* has an average stem- and petiole density of 6 per m<sup>2</sup>  
153 ground surface and a total submerged leaf area of 0.22 m<sup>2</sup> per m<sup>2</sup> ground surface.  
154 Patches of *N. lutea* are generally a few meters long (2-10 m), but may extend up to  
155 30+ meters. The width of the patch is variable, and so is the blockage factor in the  
156 river (ratio patch width to river width). The patches we used in this study are

157 estimated to fill about 50-60% of the river width in the upstream sites, to less than  
158 10% in the most downstream site.

159 Five locations along the Biebrza river were selected on accessibility, presence of a  
160 nearby small oxbow lake and the presence of *N. lutea* patches in the river and in the  
161 oxbow lake (Fig. 3). The study was done in June of 3 consecutive years (2007 to  
162 2009) which had similar hydraulic conditions (Table 1) and similar vegetation  
163 conditions. For a more detailed description of the eco-hydrological functioning of the  
164 Biebrza River valley, see Wassen *et al.* (2006).

165

#### 166 *Vegetation sampling and biometric analysis*

167 The five locations along the Biebrza river were sampled in June 2008. On each  
168 location, one river patch and one lake patch were selected. Five *N. lutea* individuals  
169 were sampled in each of the selected river patches, and three in each of the selected  
170 lake patches. The entire plants were cut just above the roots. This resulted in total in  
171 25 riverine individuals and 15 lake individuals. The number of flowers and buds,  
172 stems, floating leaves, submerged leaves, petioles of floating leaves and petioles of  
173 submerged leaves of each individual were counted. Petioles are elliptically shaped  
174 (eye-shaped), and so the diameter of both the major and minor axes of the petiole  
175 was measured. Stems are circular and one diameter measurement sufficed.  
176 Diameters were determined using a digital calliper measuring petiole width (mm) on  
177 0, 25, 50, 75 and 100% of the length and averaged afterwards per petiole. All floating  
178 and submerged leaves were spread out and photographed on a grid to determine the  
179 leaf area (LA; m<sup>2</sup>) by digital image processing. The following characteristics were  
180 calculated per leaf type for each plant individual both from river and lake sampling  
181 locations:

- 182 i. mean leaf area ( $LA_{\text{mean}}$ ;  $\text{m}^2$ ): average LA per leaf type (floating or submerged)  
183 and per habitat (lake or river).
- 184 ii. mean total leaf area ( $LA_{\text{total}}$ ;  $\text{m}^2$ ): average total LA of an individual per leaf type  
185 and per habitat.
- 186 iii. mean total specific leaf area ( $SLA_{\text{total}}$ ;  $\text{m}^2 \text{kg}^{-1}$ ): average total SLA of an  
187 individual per leaf type and per habitat, with  $SLA = LA$  per unit leaf dry matter  
188 (Cornelissen et al., 2003)

189

#### 190 *Sediment sampling and chemical analysis*

191 In each of the selected patches (before the vegetation sampling), as well as in non-  
192 vegetated zones adjacent to the patches, five sediment cores ( $\varnothing$ : 0.06 m, depth: 0.20  
193 m of which the top 0.03 m was used) were taken with a sediment corer (Beeker,  
194 Eijkelkamp, Giesbeek, The Netherlands). Sediment cores adjacent to the patch were  
195 taken in zones with no vegetation at all (also no other species), yet as close as  
196 possible to the original patch (cross-stream, usually a few meters apart). Samples  
197 were dried for 48 h at 70 °C and sieved afterwards over a 1 mm mesh to remove  
198 larger particles and to obtain homogeneous samples (gravel removal from the  
199 mineral fraction and wood from the organic fraction). Total nitrogen and total  
200 phosphorus content were determined according to Walinga *et al.* (1989): samples  
201 were digested with  $\text{H}_2\text{SO}_4$ , salicylic acid and  $\text{H}_2\text{O}_2$  and subsequently analysed on a  
202 colorimetric segmented flow analyser (SAN<sup>++</sup>, Skalar, Breda, The Netherlands). The  
203 organic matter content was determined by loss on ignition (Heiri et al., 2001).  
204 Samples were heated to 105 °C for 2 h and weighed. Thereafter, samples were  
205 ignited at 550 °C for 4 h and weighed again. The difference between both gives an  
206 index of the organic matter present in the sample. Dividing organic matter by 1.8

207 gives the amount of carbon present (in mg/g) (Schlesinger, 1977; DIN38414/S3,  
208 1985). C/N ratios are a good predictor of the rate of organic matter decomposition  
209 (Taylor et al., 1989). Grain size distribution was determined using a laser diffraction  
210 unit (Mastersizer S, Malvern Instruments, Worcestershire, UK) and classified  
211 following the Udden (1914) and Wentworth (1922) scale.

212

### 213 *Flow and light measurements*

214 In June 2009, at the middle of the patch width, stream velocities were measured 0.3  
215 m upstream and 0.3 m downstream of the submerged canopy of 8 *N. lutea* patches  
216 with a different submerged canopy length (ranging between 1 and 7 m). The 5  
217 locations where this was done were equal to the 2008 sampling campaign sites  
218 (Fig. 3), but the patches were not necessarily the same, because we chose to focus  
219 on patches with a broad variety in length rather than to be able to directly compare  
220 the data from both years. Stream velocity was measured on 1/3 and 2/3 of the  
221 submerged canopy height (measured from the stream bed) using an Electromagnetic  
222 Flow Meter (EMF; Valeport model 801, Totnes, UK) over a sampling period of 60  
223 seconds at a sampling rate of 1 Hz and averaged afterwards. A reduction efficiency  
224 was calculated as the difference between the stream velocity upstream and  
225 downstream the patch at the same depth, divided by the respective upstream  
226 velocity. This way we were able to relate the blocking effect of a patch in a relative  
227 way to the submerged canopy length which was measured with a tape measure.  
228 Detailed flow and light conditions were measured in June 2007 on profiles through a  
229 *N. lutea* patch in the Sidra river, a channelized tributary to the Biebrza river near the  
230 village of Harasimowicze (Fig. 3). The selected patch was 7 m long, 2.5 m wide and  
231 growing in a stretch with an average width of 7.5 m and a maximal depth of 0.9 m.

232 This patch was also measured in the 2008 and 2009 campaigns. Measurements  
233 were made on four profiles of which three were inside the patch and one was at a  
234 non-vegetated location 3 m upstream of the patch. Inside the patch, one profile was  
235 measured at the upstream part of the patch where the flow velocity had pushed the  
236 floating biomass further downstream and hence only submerged biomass occurred.  
237 The other two profiles, one in the middle and one at the downstream end of the  
238 patch, went through a well-developed floating and submerged canopy. Profile depth  
239 interval was 0.1 m from the water surface until -0.7 m, and with an extra  
240 measurement at -0.05m. The total water depth was also recorded. Stream velocity  
241 was measured using an EMF (Nautilus C 2000, Ott Hydromet, Kempten, Germany)  
242 over a sampling period of 60 seconds at a sampling rate of 1 Hz and averaged  
243 afterwards. Light conditions were measured using an underwater LI-COR quantum  
244 sensor (LI-185B, LI-COR Biosciences, Lincoln, USA) at the same locations as the  
245 stream velocity measurements. The underwater quantum sensor measures quantum  
246 radiation in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ( $= 6.02 \cdot 10^{17}$  photons  $\text{m}^{-2} \text{s}^{-1}$ ). The sensor is used for  
247 measuring PAR in aquatic environments and has a 400-700 nm quantum response.  
248 Both the immersion effect and the cosine effect are accounted for by the  
249 potentiometer connected to the sensor.

250

### 251 *Statistics*

252 Statistical tests were performed in SAS 9.1 (SAS Institute inc., Cary, USA). One-way  
253 ANOVA followed by a post-hoc Tukey HSD correction was conducted to test mean  
254 differences in parameters between lake and river sediment samples and lake and  
255 river standing *N. lutea* individuals. A PCA analysis of variance was used to classify

256 grain size. A Spearman Rank correlation test was applied to test for relations  
257 between variables.

258

259 **Results**

260 Biometric data are summarised in Table 2. The number of submerged leaves and  
261 associated petioles was significantly higher for river standing individuals than for lake  
262 standing individuals ( $p < 0.001$ ). River submerged individuals had a mean leaf area  
263 and mean total leaf area that were significantly higher than those in lakes ( $p < 0.001$ ).  
264 This means that the river standing individuals have more and larger submerged  
265 leaves, resulting in more leaf area that can be in interaction with the flow. No  
266 difference of these parameters was found for floating leaves. For both leaf types, no  
267 difference in mean total specific leaf area was observed between river and lakes.  
268 Grouping both habitats, the mean total specific leaf area of submerged leaves was  
269 up to 2.7 times larger than that of floating leaves. All other biometric data (Table 2)  
270 did not show significant differences between both habitats except for stem length  
271 (+22% in river) and submerged petiole length (+27% in river).

272

273 Sediment taken within *N. lutea* patches in the river contained significantly more  
274 organic matter, and more total nitrogen and total phosphorus than sediment from  
275 non-vegetated locations in the river (Fig. 4a,b,c;  $p < 0.05$ ). For lake samples, no  
276 significant differences in sediment organic matter, total nitrogen and total phosphorus  
277 concentrations were observed between samples from the *N. lutea* stands and the  
278 non-vegetated locations. A comparison of the C/N ratio in all four groups of sediment  
279 samples (Fig. 4d) shows that only the C/N ratio in the sediment of non-vegetated  
280 river locations was significantly higher ( $p < 0.05$ ). Non-vegetated river samples had  
281 little very fine sand (63-125  $\mu\text{m}$ ) and fine sand (125-250  $\mu\text{m}$ ) but more coarse sand  
282 (500-1000  $\mu\text{m}$ ) compared to other samples ( $p < 0.0001$ ). This results in a larger D50  
283 grain size in non-vegetated river samples (calculated as the mean of the D50s of all

284 replicate samples), differing significantly from vegetated river samples and vegetated  
285 and non-vegetated lake samples (Fig. 4e).

286

287 Stream velocity in the river at the non-vegetated location upstream of the patch near  
288 Harasimowicze declines with depth (Fig. 5a). Profiles inside the patch are modified  
289 with lower velocities at the top 0.1 m layer if floating leaves are present (profiles (iii)  
290 and (iv)), higher velocities below the floating leaves and above the submerged leaves  
291 (all profiles) and strongly reduced velocities inside the submerged leaves (all  
292 profiles). This reduction generally causes lower flow velocities downstream of the  
293 patch, relative to the upstream flow velocity on both investigated depths (Fig. 6).  
294 Reduction efficiency is positively related to patch length ( $R^2 = 0.70$ ;  $p < 0.001$ ) with  
295 longer patches generally causing a more efficient reduction in velocity, sometimes up  
296 to 100%, which means the water is stagnant at the distal end of the patch.

297

298 Light intensity declines with depth at the non-vegetated location upstream the patch  
299 (Fig. 5b). The same was measured in profile (ii) above the submerged biomass, but  
300 as soon as the profile entered the biomass, light intensity declined drastically. Profiles  
301 (iii) and (iv), both shaded by a floating biomass, show a light intensity of nearly 0  
302  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at all depths.

303

304 **Discussion**

305 *N. lutea* individuals growing in running river water had significantly more submerged  
306 leaves with a larger total leaf area than individuals standing in the adjacent oxbow  
307 lakes. In running river water, the large submerged leaves of *N. lutea* reduced the flow  
308 velocity. This likely caused the increased amount of smaller sediment particles and  
309 organic matter found in the sediments within *N. lutea* patches relative to non-  
310 vegetated parts of the river bed, analogous to other studies on submerged  
311 macrophytes (Sand-Jensen, 1998; Cotton et al., 2006; Kleeberg et al., 2010).  
312 Organic matter concentration in the sediment of the riverine *N. lutea* patches was up  
313 to six times higher than the concentration found in non-vegetated zones of the river.  
314 Furthermore, the combination of a higher particulate nutrient stock (total nitrogen and  
315 total phosphorus) and a lower C/N ratio of the organic matter within riverine *N. lutea*  
316 patches indicates that the organic matter in the patches has the potential to break  
317 down rapidly into a large dissolved nutrient stock (Soetaert et al., 1996), so that  
318 nutrient availability can be higher within riverine *N. lutea* patches as compared to the  
319 non-vegetated river parts. This could be an advantage for the eutraphent *N. lutea* in  
320 the mesotrophic Biebrza river. Having a larger total submerged leaf area can  
321 therefore be considered as a benefit in the river and can fulfil the criteria required to  
322 be termed an ecosystem engineer (Jones et al., 1997). The engineering capacity is  
323 also size-dependent as the efficiency of the patch to reduce the flow was positively  
324 related to patch length.

325 In contrast, in the oxbow lakes, organic matter concentrations, particulate nutrient  
326 stocks and C/N ratios were equal inside and outside *N. lutea* patches, and equal to  
327 the values found inside river standing *N. lutea* patches. This indicates that organic  
328 matter deposition and nutrient availability is less spatially heterogeneous in stagnant

329 water, which reduces the need for *N. lutea* to engineer the environment. Moreover,  
330 the mechanism for this engineering is lacking as there is little to no water movement  
331 that can be slowed (apart from occasional wind wave induced currents, but these are  
332 expected to be of minor importance in the small oxbow lakes that we had  
333 investigated). Hence, there is no benefit for *N. lutea* of investing in a large total  
334 submerged leaf area in stagnant water.

335

336 We showed that light intensity underneath a floating canopy is close to zero, making  
337 photosynthetic benefit from a submerged biomass only relevant in early spring when  
338 the floating canopy has not yet developed. Other evidence also points towards the  
339 negligible role of submerged biomass for photosynthetic purposes in summer. The  
340 photosynthetic efficiency of submerged leaves under saturating irradiance is only 5%  
341 of that of the floating leaves, and it is saturated at lower irradiance levels (200 and  
342  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  respectively), making floating leaves by far the main photosynthetic  
343 tissue of *N. lutea* (Snir et al., 2006). Submerged leaves of *N. lutea* are only able to  
344 use  $\text{CO}_2$  as water-dissolved inorganic carbon source (Snir et al., 2006). The main  
345 supply of  $\text{CO}_2$  comes from decomposition of organic material, respiration and  
346 liberation from sediment. Increased organic matter deposition will possibly enhance  
347 the available carbon concentration, but it still remains suboptimal compared to the  
348 floating biomass that has access to atmospheric  $\text{CO}_2$  (Snir et al. (2006) and  
349 references therein). Moreover, submerged leaves have a minimal number of  
350 undifferentiated cell layers, lacking a cuticle and having their stomata degenerated  
351 and functionless (Maberly and Spence, 1989).

352

353 Based on these field measurements, we have strong indications that patches of *N.*  
354 *lutea* can be considered as ecosystem engineers. It depends on size (patch length)  
355 and density (total submerged leaf area) of the patch and is induced by habitat  
356 variation (presence or absence of a strong water flow). We can therefore accept  
357 hypothesis 1. We acknowledge that we did not take into account the 'causality effect':  
358 what if *N. lutea* seedlings in flowing waters preferentially establish in regions of the  
359 bed with finer sediment composition and higher nutrient content? This issue can only  
360 be tackled with an experimental approach which was beyond the scope of our field  
361 observations. However, this alternative is implausible because (i) vegetative  
362 propagation by extension of the rhizome system is the most important dispersal  
363 mechanism, and (ii) if the sediment is very loose and easily resuspended in water the  
364 seeds sink into the sediment to a depth from which seedling emergence is not  
365 possible (Barrat-Segretain, 1996).

366 Despite the potential contribution to early season photosynthesis, during the majority  
367 of the growing season, the submerged leaves of *N. lutea* in rivers are shaded by the  
368 floating leaves. They therefore only contribute very limited to the total photosynthesis  
369 of the plant, leading to the acceptance of hypothesis 2.

370

371 It is also unlikely that the observed differences are caused by genetic differences  
372 between the individuals in oxbow lakes and rivers. Reproduction in *N. lutea* is mostly  
373 vegetative and yearly winter flooding causes abundant exchange of seeds, plant  
374 fragments, or parts of rhizomes between the river and the oxbow lakes (Brock et al.,  
375 1987), and individuals in both environments likely derive from the same gene pool.  
376 The amount of flowers and flower bearing stems was also similar in both habitats  
377 implying an equal reproductive success (at least potentially since fertility

378 measurements were not performed). Further, no differences in stem and petiole  
379 diameters were found, also consistent with an equal development of these organs.  
380 The difference in stem and petiole lengths in the different habitats (not significant for  
381 floating leaf petioles) probably reflects the difference in water depth on the different  
382 sampling sites (Brock et al., 1987; Paillisson and Marion, 2006).

383

384 The ecological engineering capacity of the submerged leaves could also impact the  
385 geomorphology of the river. Submerged leaves of *N. lutea* in lowland rivers such as  
386 the Biebrza decelerate the stream flow inside vegetation patches. We showed that  
387 this could be linked to an accumulation of smaller sediment particles inside patches,  
388 which is in accordance with other studies (e.g. (Sand-Jensen, 1998; Cotton et al.,  
389 2006). Since stream velocity is related to bed shear stress (the driving force for  
390 sediment transport), and sediment texture is a measure for shear strength of the  
391 sediment bed (the resisting force against sediment transport), it could be expected  
392 that the patches will have an effect on the sedimentation and erosion patterns, and  
393 hence on the geomorphologic changes of the river bed. The river bed was indeed 15  
394 to 20 cm more elevated on profiles inside the patch near Harasimowicze compared to  
395 the profile upstream of the patch. These values are of the same order as found in  
396 other studies. Sand-Jensen (1998) and Schoelynck et al. (2012) for instance showed  
397 a 5 to 15 cm difference in mean elevation of the sediment surface between vegetated  
398 and non-vegetated zones in submerged macrophyte dominated lowland rivers.  
399 Although vegetative propagation of *N. lutea* is a slow process (Barrat-Segretain,  
400 1996), its rhizomes can remain in the same location for many decades (even more  
401 than a century in cultivation; (Heslop-Harrison, 1955)), producing new shoots each  
402 year. A systematic and long term influence of vegetation is therefore expected on

403 local stream flow magnitude and direction, both laterally and longitudinally, which will  
404 induce local bathymetric changes.

405

406 *Conclusion*

407 *N. lutea* had a significantly higher total submerged leaf area in running river water  
408 than in oxbow lake water. In running water, the benefit of having submerged biomass  
409 can be high, as this reduces the flow velocity, which likely increases the deposition of  
410 organic matter and improves nutrient availability relative to non-vegetated parts of the  
411 river bed. In oxbow lake water, where submerged biomass would not result in similar  
412 beneficial habitat modification, such dense and costly submerged biomass was  
413 absent. Our field measurements strongly support the hypothesis that submerged  
414 leaves in rivers engineer the environment: they trap organic matter and particulate  
415 nutrients and create oxbow lake-like conditions even in a river with relatively high  
416 stream velocities. On the long term this could have an impact on the local bathymetry  
417 (through sedimentation processes) and on local nutrient dynamics (through organic  
418 matter accumulation).

419

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433

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574

575

576

577 **Table 1**

578 Basic hydraulic data of 3 years (June) of the Biebrza river on five locations relevant  
 579 for this study. Discharge is measured using a tape measure for river width and depth,  
 580 and a propeller (OTT C31-87200) to measure the stream velocity. Distances to the  
 581 Belarus border are calculated in GIS.

		<b>2007</b>	<b>2008</b>	<b>2009</b>
<b>Sidra</b> Distance from Belarus border = 29 km	River width (m)	7.5	n.a.	n.a.
	Maximum river depth (m)	0.9	n.a.	n.a.
	Discharge (m <sup>3</sup> s <sup>-1</sup> )	(0.24)*	n.a.	n.a.
<b>Sztabin</b> Distance from Belarus border = 71 km	River width (m)	19.7	22.0	17.8
	Maximum river depth (m)	2.1	2.1	2.1
	Discharge (m <sup>3</sup> s <sup>-1</sup> )	0.97	0.86	1.06
<b>Jagłowo</b> Distance from Belarus border = 91 km	River width (m)	16.3	12.0	12.2
	Maximum river depth (m)	1.5	1.4	1.4
	Discharge (m <sup>3</sup> s <sup>-1</sup> )	1.08	1.14	1.44
<b>Dolistowo stare</b> Distance from Belarus border = 104 km	River width (m)	25.9	23.0	29.4
	Maximum river depth (m)	2.6	2.1	2.1
	Discharge (m <sup>3</sup> s <sup>-1</sup> )	5.28	3.30	6.62
<b>Goniądz</b> Distance from Belarus border = 122 km	River width (m)	44.8	57.7	60.3
	Maximum river depth (m)	2.5	3.0	3.4
	Discharge (m <sup>3</sup> s <sup>-1</sup> )	6.24	5.01	7.08

582 \* Actual discharge was not measured in 2007 at Sidra. The value given is an  
 583 indicative value from 2000, when hydraulic conditions were comparable to the 2007  
 584 situation.

585

586 **Table 2**

587 Biometric data of lake and river standing *N. lutea* individuals. Data are averages of 25  
 588 river individuals and 15 lake individuals, over five different locations along the  
 589 downstream gradient of the river with standard deviation (SD). # = number per  
 590 individual, l = length (m),  $\varnothing_a$  = smallest diameter (m),  $\varnothing_b$  = largest diameter (m)  
 591 perpendicular on  $\varnothing_a$ ,  $LA_{mean}$  = mean leaf area (m<sup>2</sup>),  $LA_{total}$  = mean total leaf area (m<sup>2</sup>),  
 592  $SLA_{total}$  = mean total specific leaf area (m<sup>2</sup> kg<sup>-1</sup>). Significant differences are calculated  
 593 with a two-way ANOVA, followed by post-hoc Tukey's HSD correction); p:  
 594 0.05 > \* > 0.01 > \*\* > 0.001 > \*\*\*

		Location Lake		Location River		2-way ANOVA
		Mean	SD	Mean	SD	p
Flowers	#	1.7	0.9	1.7	0.9	
Stems	#	1.6	0.8	1.7	0.6	
	l	0.63	0.17	0.77	0.26	**
	$\varnothing_{a=b}$	0.0079	0.0013	0.0080	0.0011	
Petioles of submerged leaves	#	4.6	2.3	7.3	3.2	**
	l	0.49	0.21	0.62	0.27	***
	$\varnothing_a$	0.0055	0.0012	0.0058	0.0010	
	$\varnothing_b$	0.0085	0.0018	0.0087	0.0013	
Petioles of floating leaves	#	5.5	2.3	4.0	2.1	
	l	0.67	0.31	0.73	0.30	
	$\varnothing_a$	0.0066	0.0015	0.0065	0.0011	
	$\varnothing_b$	0.0095	0.0020	0.0094	0.0014	
Submerged leaves	#	4.6	2.3	8.4	3.3	***
	$LA_{mean}$	0.0347	0.0260	0.0527	0.0331	***
	$LA_{total}$	0.15	0.06	0.44	0.04	***
	$SLA_{total}$	37.9	8.7	37.7	6.3	
Floating leaves	#	5.5	2.3	4.8	2.5	
	$LA_{mean}$	0.0299	0.0181	0.0330	0.0148	
	$LA_{total}$	0.17	0.04	0.15	0.02	
	$SLA_{total}$	11.7	2.7	15.1	4.0	



595

596 **Fig. 1**

597 *Nuphar lutea* (L.) Smith individual from the Biebrza National Park (Poland). Picture  
598 was taken outside the water lying on a white background. Starting from a rhizome, six  
599 translucent, crumpled submerged leaves (1-6), three leathery floating leaves (a-c)  
600 and one flower bearing stem originate.

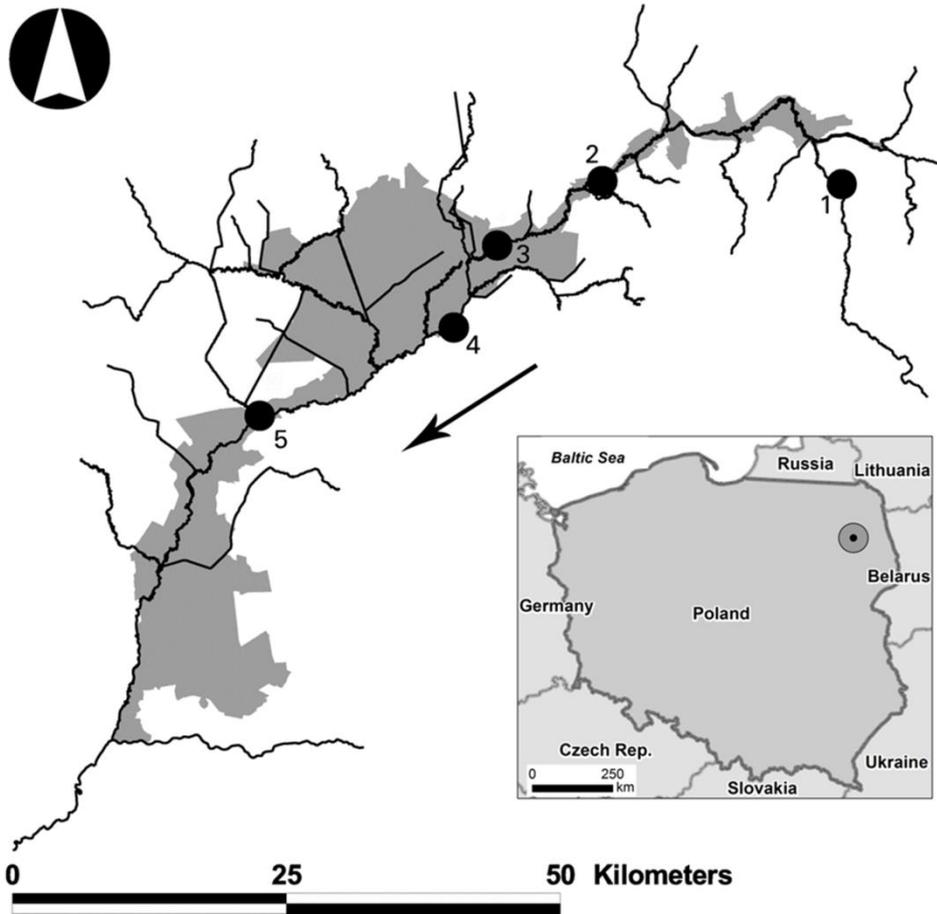


601

602 **Fig.2**

603 Picture of a *Nuphar lutea* patch in the river Sidra, near the village of Harasimowicze,  
604 which is location 1 in figure 3. This patch is representative of all patches measured in  
605 the river in this study, though blockage factor (ratio patch width to river width) may  
606 vary among the different locations. Floating leaves cover most of the water surface  
607 and shade the submerged leaves to a great extent. To the right of the patch, ripples  
608 are visible on the water surface, probably resulting from flow acceleration adjacent to  
609 the patch and flow deceleration inside the patch.

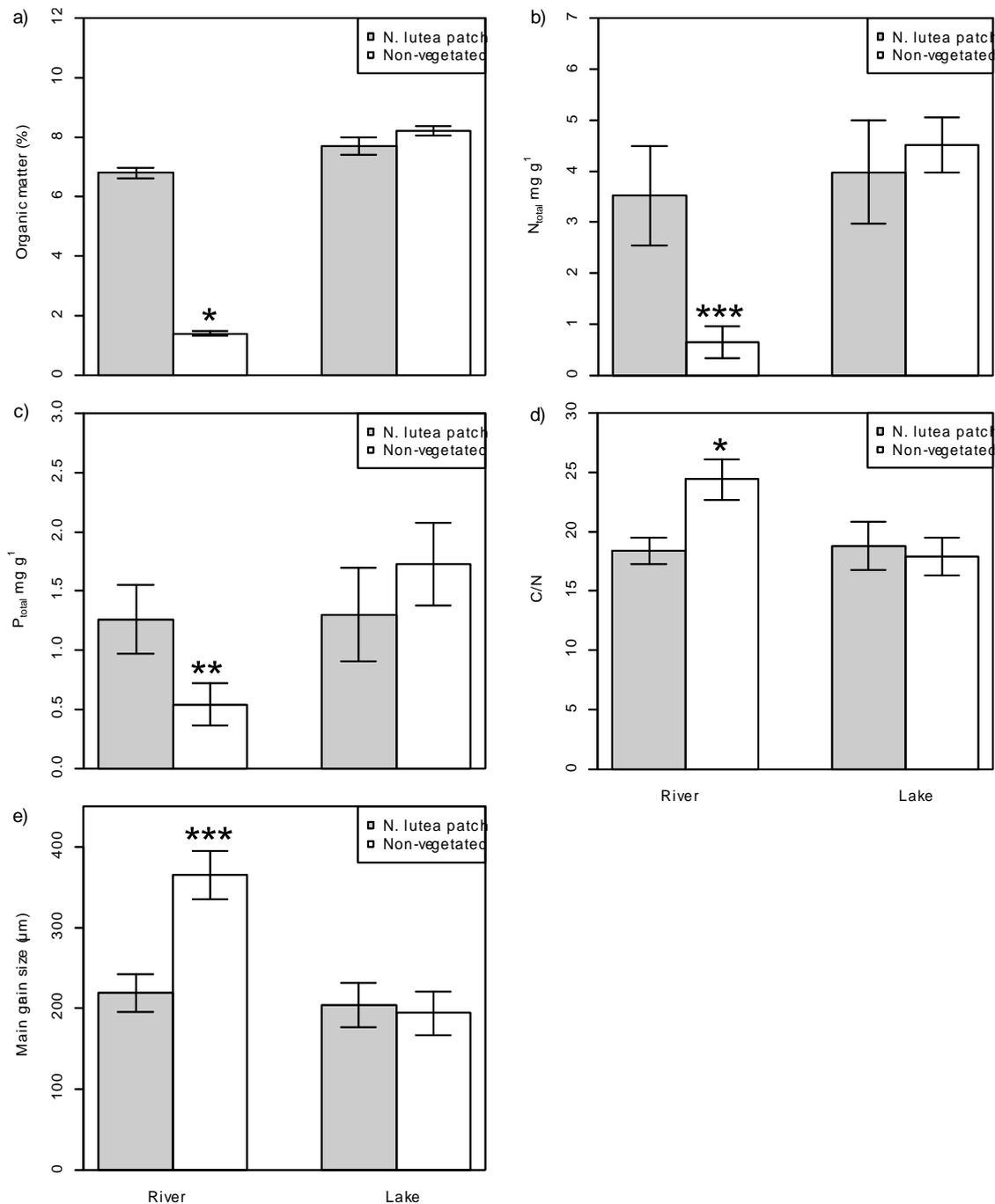
610



611

612 **Fig. 3**

613 Map of the Biebrza river in the Biebrza National Park, with park borders indicated in  
 614 grey. The arrow indicates the main water flow direction. The park is located in the  
 615 North-Eastern part of Poland. A country map is inserted with the exact location of the  
 616 National Park indicated with a ⊙ symbol (park headquarters at N53.449001,  
 617 E22.626008). Vegetation and sediment samples were taken at different sites along  
 618 the river and in adjacent oxbow lakes, located less than a few 100 m from the main  
 619 channel. Sample locations, from upper towards middle basin, were situated nearby  
 620 the following villages: Harasimowicze (on Sidra, tributary of Biebrza (1)), Sztabin (2),  
 621 Jagłowo (3), Dolistowo Stare (4) and Goniądz (5). Velocity and light climate were  
 622 measured on profiles through a *N. lutea* patch in the Sidra river, near the village of  
 623 Harasimowicze (1).



624

625 **Fig. 4**

626 (a) Mean organic matter content ( $\text{mg g}^{-1} \pm \text{SE}$ ), (b) total nitrogen content ( $\text{mg g}^{-1} \pm$

627 SE) of the entire sample, (c) total phosphorus content ( $\text{mg g}^{-1} \pm \text{SE}$ ) of the entire

628 sample, (d) C/N ratio of the organic matter ( $\pm \text{SE}$ ) and (e) mean D50 grain size ( $\mu\text{m} \pm$

629 SE) of sediment samples ( $<1\text{mm}$ ) taken from *N. lutea* patches and from non-

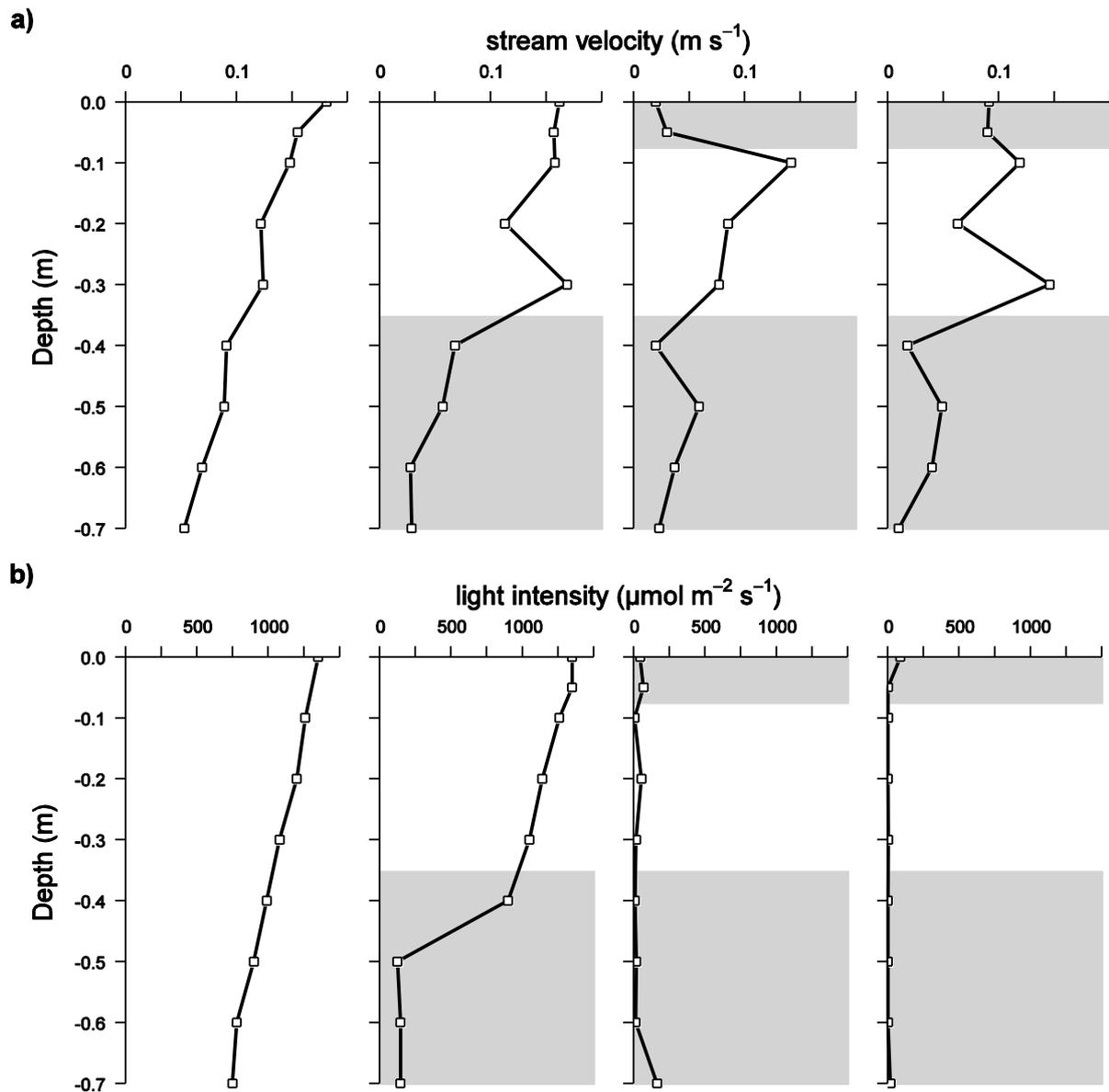
630 vegetated locations compared between lake and river. Significant differences are

631 calculated with a two-way ANOVA, followed by post-hoc Tukey's HSD correction and

632 preceded by a log<sub>10</sub> transformation in panel (a); p: 0.05>\*>0.01>\*\*>0.001>\*\*\*.

633 Sample size (n) = 25 in the river and 15 in the lakes.

634



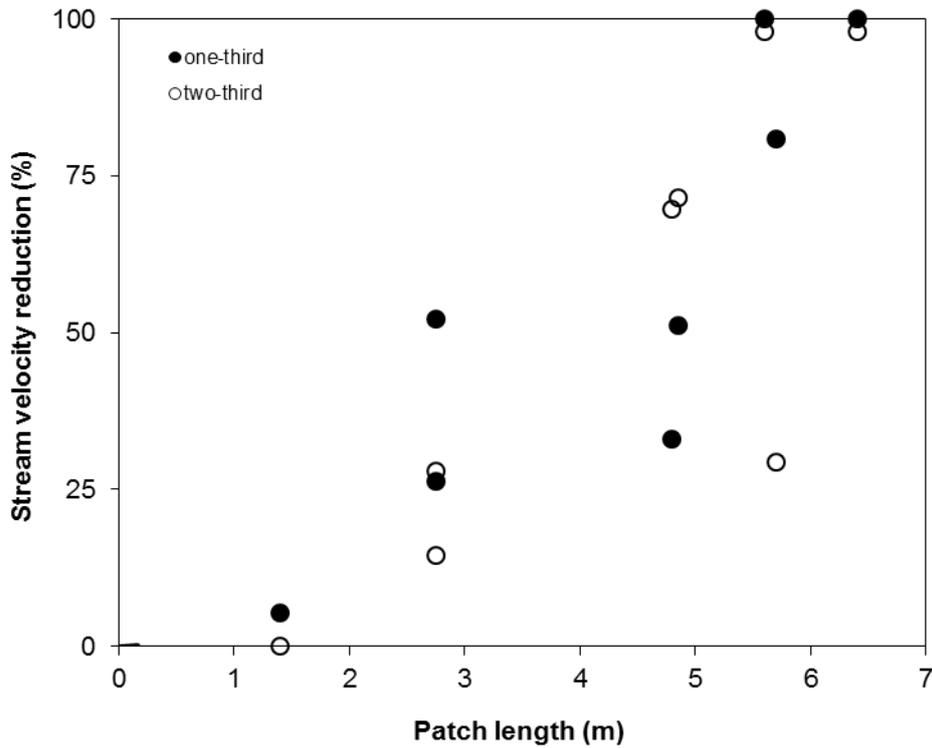
635

636 **Fig. 5**

637 Velocity and light climate were measured on profiles through a *N. lutea* patch in the  
 638 Sidra river, near the village of Harasimowicze (site (1) in figure 3). (a) Stream velocity  
 639 profiles and (b) light intensity profiles in the river on a non-vegetated location (first  
 640 profile (i), located 3 m upstream of the patch) and through a *Nuphar lutea* patch  
 641 (profiles (ii) to (iv) in the upstream- middle-, and downstream part of the patch). Total  
 642 water depth differed per profile (dark grey background). The light grey background  
 643 indicates the presence of leaf biomass: floating leaves in the top layer and

644 submerged leaves near the bottom. Standard deviations were not recorded. EMF  
645 velocity measurements typically have an error of about 10%. Light measurements  
646 have an error smaller than 5%.

647



648

649 **Fig. 6**

650 Relation between patch length of the submerged biomass (m) and flow velocity  
 651 deceleration efficiency which is based on the relative difference between the patch'  
 652 upstream and downstream stream velocity (%). Stream velocities are measured on  
 653 1/3d and 2/3d of the submerged canopy, measured from the bottom. Relation is  
 654 significant: Spearman Rank test,  $R^2 = 0.70$ ;  $p < 0.001$ ;  $n = 16$ ). Note that the patch  
 655 length measurements have an inherent uncertainty of a few decimetres because of  
 656 the continuous movement of the plants in the current.