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10   Reed stands during different water level periods: physico-chemical properties of the sediment and growth of

11   *Phragmites australis* of Lake Balaton

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19   Abstract

20   Water level fluctuations play a vital role in regulating macrophytes of shallow lakes. Morphology and growth

21   dynamics of *Phragmites australis*, together with physico-chemical parameters of the sediment, were studied at

22   stable (not degrading) and die-back (degrading) sites of Lake Balaton over an 8-year period that included low and

23   average water levels. Lower water level increased plant density and green leaf number, positively affecting

24   photosynthetically available leaf area. Nevertheless rhizome carbohydrate content was not influenced by water

25   level decrease. The physico-chemical parameters of the sediment did not vary greatly, although the nitrogen and

26   phosphorus content and the midsummer redox potential of the sediment were higher at the low water period.

27   During the transition from average to low water levels, the sediment shifted from severely anoxic to poorly

28   oxidised levels, with more favourable nutrient content while the amount of ammonia and sulphides decreased, too.

29   It was shown that lowering water levels could act on plants via increased redox potential of the sediment and could

30   counteract the die-back of *Phragmites*, suggesting the effectiveness of water level decrease as a management

31   practice to counter reed die-back.

32   Keywords: redox potential, morphology, growth dynamics, carbohydrates, water level changes

Introduction

Water depth is one of the crucial factors that controls zonation, distribution and progression of *Phragmites australis* within lakes (Coops et al., 1996; Vretare et al., 2001; Engloner & Papp, 2006; Tóth & Szabó, 2012). Numerous studies have shown that, due to specific cytological and biophysical features, common reed is able to tolerate high and prolonged inundation (Armstrong et al., 1994; Crawford & Braendle, 1996; Vartapetian & Jackson, 1997). A continuous gas space within the plant tissue called aerenchyma runs down from the aerial to the underground parts of the plant, channelling air from leaves to rhizomes and roots. This flux of atmospheric gases is driven by humidity-induced partial pressure differences between the air and the substomatal space (Armstrong & Armstrong, 1991). Without it, the reed could suffer complete or partial oxygen deprivation due to high microbial oxygen consumption within the sediment (Brinson et al., 1981; Crawford & Braendle, 1996). To survive anoxic conditions of the sediment the air from the aerenchyma is pressurised into the sediment surrounding reed roots via radial diffusion creating an oxygenated rhizosphere (Armstrong et al., 1991; Beckett et al., 2001). This mechanism cannot however compensate for effects of a severe or prolonged anoxia, which causes the temporary or permanent die-back of plants.

Reed die-back in Europe is a thoroughly discussed topic and several causes have been proposed (Den Hartog et al., 1989; Ostendorp, 1989; Crawford & Braendle, 1996; Fürtig et al., 1996; Kubín & Melzer, 1996; Brix, 1999; Armstrong & Armstrong, 2001). The simultaneous and general nature of this phenomenon (many sites) indicates that it could be caused by a widespread disturbance. In Lake Balaton, the process started in the 1970s (Kovács et al., 1989; Virág, 1997). The die-back was similar in many cases: the stands lost their homogeneity and the clumping of reed progressed with time, eventually leading to bands of clustered *Phragmites* at the affected sites. This phenomenon occurred predominantly at the maximal depth of reed penetration (i.e., at the lakeward side of the stands), suggesting the importance of water depth and thus the water level fluctuation. In all cases, plant density gradually decreased outside the clumps and eventually discrete reed clusters with high density were separated by increasingly large areas of open water until the last clump was tipped by the waves and washed away. *Phragmites* in these deeper waters can suffer from elevated levels of sulphides, organic acids, ammonia, as well as from direct hypoxia (Crawford & Braendle, 1996; Fürtig et al., 1996; Kubín & Melzer, 1996; Armstrong & Armstrong, 2001).

This paper presents the results of studies performed between 2000 and 2008 on the northern shore of Lake Balaton, in a bay with both stable and die-back *Phragmites* stands and characterized by slightly variable sediment physico-chemical parameters. The effect of water level on *Phragmites* growth and sediment characteristics was also assessed, since two distinctive water level periods were observed, characterised by low (2001-2003) and

63 average (2006-2008) water levels. The hypothesis that lake water level primarily affects the morphology and

64 growth dynamics (ecological status) of *Phragmites* via changes in the physico-chemical properties of the sediment

65 was tested. During this study, temporal and spatial dynamics of major biometric parameters of the *Phragmites*

66 (shoot height, diameter and density, leaf number) were recorded in combination with physico-chemical parameters

67 of the sediment of the studied stands.

68

69 ***Materials and methods***

70 *Study sites*

71 Lake Balaton is a large (596 km^2) and relatively shallow (average water depth 3.5 m) lake with a long shoreline

72 (240 km). In Lake Balaton, *Phragmites* is the stand forming helophytic perennial of the littoral zone and is

73 commonly found in extended, continuous populations along 112 km of the lake shoreline. The total area of reed

74 stands at Lake Balaton is approximately 12 km^2 and the majority (73% – ca. 9 km^2) concentrated on the windward,

75 northern shore. At the lakeward side of the reed stands the water is usually 1.5 m deep, indicating that water depths

76 might be the limiting factor in the majority of cases. Thus, an increase in water level may trigger die-back at the

77 maximal depth of progression, while a decrease in water level could induce an expansion of *Phragmites* stands.

78 A stable (46°58'3.11"N, 17°55'12.62"E) and a die-back (46°57'50.95"N, 17°55'0.28"E) reed stand on the

79 northern shore of the Lake Balaton were selected (Fig. 1). The stable sampling site was a monospecific stand

80 represented mainly by tall and thick plants, homogeneously distributed over the entire north-eastern side of the

81 Kerekedi Bay of Lake Balaton (Fig. 1). Shorter and thinner plants of the die-back stand on the western side of the

82 same bay were clumping, and were 430 meters from the stable stand (Fig. 1). The reed stands of the Kerekedi Bay

83 are considered to be quite old, since they are depicted already on the Krieger map of 1776 (Bendefy & Nagy,

84 1969). The stable and die-back reed stands were harvested last in 1997 and 1996, respectively. Both reed stands

85 were 140-150 meter long, and the lakeward 60-80 meters were covered with varying amount of water. Little

86 bathymetric differences were observed between the studied sites (Table 1).

87 All in situ measurements and sampling were made from elevated, 25 meter long narrow boardwalk built from

88 the lakeward edge of the reed stand toward the shore in a perpendicular direction: the sampling point at the edge

89 of the reed stand (labelled as "edge" in the text) was at the appearance of the first fully emerged reed plant in the

90 transect, while 20 meters from the edge of the reed stand, at the opposite end of the boardwalk was another

91 sampling point labelled as "20 m". In this study, low (2001-2003) and average water years (2006-2008) were

92 compared.

93   Publicly available daily water level data and precipitation data from Central-Transdanubian Water Authority
94   were used (http://www.kvvm.hu/balaton/lang_en/vizszintb.htm).

95

96   *Sediment analysis*

97   Sediment sampling was performed at the edge of the studied stands. Sediment samples were collected with 500
98   mm long, 60 mm (53 mm inner) diameter plastic tubes. The tube was filled with sediment, thus each time, three
99   at least 1 litre sediment cores were collected, and chemical and physical parameters of the sediment were studied
100 according to Hungarian standards (Buzás, 1988). The whole sediment core was homogenised and used. 50 grams
101 (fw) of the collected sediment was digested using a HNO_3-H_2O_2 mixture. Half of the resulting aliquot was used
102 for total phosphorus determination (ammonium-molibdate and ammonium-metavanadate colourimetric method),
103 while the other half of the aliquot was used for total potassium determination, with atomic absorption
104 spectrophotometer in emission mode. Another 50 grams (fw) of the sediment was digested using phenol-sulfuric
105 acid and total nitrogen was measured following the macro-Kjeldahl method. $CaCO_3$ content of the sediment was
106 measured through the CO_2 release after treatment with 10% hydrochloric acid. Humus content was measured on a
107 photometer following the sulfuric acid-potassium dichromate digestion of the organic C content after calibration
108 for glucose, and the humus content was calculated using the following equation: *humus=1.724*organic C*. Ignition
109 loss was determined gravimetrically following gradual heating to 550°C ($CaCO_3$ content of the samples was taken
110 into consideration). Water capacity of the sediment samples was measured as the upper limit of plasticity of the
111 dried and then re-watered samples with the following typical texture classes:

coarse sand < 25 ml 10^2 g^{-1} sediment

sand $25 - 30$ ml 10^2 g^{-1} sediment

sandy loam $31 - 37$ ml 10^2 g^{-1} sediment

loam $38 - 42$ ml 10^2 g^{-1} sediment

clay loam $43 - 60$ ml 10^2 g^{-1} sediment

clay $51 - 60$ ml 10^2 g^{-1} sediment

heavy clay $81 - 90$ ml 10^2 g^{-1} sediment

112 Pore water sulphide content was sampled with hollow plastic probes (100 mm long, 21 mm outer diameter, 10
113 mm inner diameter) covered with 21 mm diameter dialysis tubes (SERVAPOR 44144, SERVA) and filled with
114 distilled water. Each probe contained three separate 6 ml compartments. Probes were placed into the sediment at
115 the edge, at 10 m and at 20 m of sampling transect for 10 days at 50 cm depth. Upon the removal of the plastic

116 probes from the sediment its content was drained using a platinum coated needle into a 5 ml sterile glass syringes.

117 The samples were taken to laboratory within 10 minute and kept until sulphide determination in a cooler at 4°C.

118 Total sulphide content was determined using N,N'-diethyl-D-phenylenediamine at 670 nm (UV-VIS 1601,

119 Shimadzu, Japan) against a standard sodium sulphide solution.

120   The pH and the oxidation-reduction potential (ORP) of the sediment was determined at several points along

121 the boardwalk. ORP was measured with a platinum redox electrode mounted onto 1 meter long aluminium probe

122 (⌀ 12 mm), registering the data with a millivoltmeter (HI 98150, Hanna) against a saturated Ag/AgCl reference

123 electrode and related to the standard hydrogen electrode.

124

125   *Plant analysis*

126   *Phragmites* plants at both stable and die-back sites were sampled throughout the vegetation period (April-

127 October) at least once a month. During sampling, at least ten randomly chosen plants were cut at each sampling

128 point at their connection to vertical rhizomes (sometimes under the water level), and biometric measurements were

129 performed. Height of plants was determined from cut surface to the tip of the top leaf. Diameter in the middle of

130 the most basal internode of each cut reed stem was measured to the nearest 0.1 mm with a vernier calliper, and

131 both green and dry leaves of each plant were counted. Leaf area was measured indirectly by determining the dry

132 weight of leaves.

133   Reed shoots at the stable reed stand were counted within three randomly selected 0.25 m^2 quadrants at each

134 predefined sampling point. Due to the high spatial variance, the plants in the die-back site were counted on three

135 9 m^2 quadrants that contained at least two clumps.

136   Rhizomes were collected at the climax of the vegetation period (August-September). Internodes of horizontal

137 rhizomes were dried at 60 °C and the samples were then ground. Soluble carbohydrates and starch contents were

138 determined using the anthrone method (Dreywood, 1946).

139   The sources of GIS data were georeferenced digital orthophotos of Lake Balaton from 2000 (2000.06.02), 2003

140 (2003.08.15.), 2005 (2005.08.28.) and 2008 (2008.10.10.), available at a spatial resolution of 0.5 m on the ground.

141 Boundaries of the reed stands were traced as individual polygons based on these orthophotos. Within the selected

142 areas the movement of the reed stands at the lakeward side was tracked at 41 points. Vegetative spread was

143 quantified as the rate of expansion at the edge of the reed stand (expansion, m y^{-1}). Fragmentation of the reed stand

144 was estimated as a ratio of 200 m (i.e., full the length of the studied location) to the actual vegetated length of the

145 reed stand at the lakeward edge (edge length ratio - ELR). ELR changes between 0 (very fragmented) and 1 (fully

146 vegetated).

147

148 *Statistical analyses*

149 Stem length of *Phragmites* was fitted with a logistic, three parameter equation ($y=a/(1+e^{-b(x-x_0)})$) with P<0.01.

150 For each fit the following parameters were calculated:

151 •   date of the peak of the growth (**b** [day of the year]),

152 •   period of most intensive growth (**b·x_0/4** [days]),

153 •   and the intensity of growth (first derivative of the logistic equation [cm d^{-1}]).

154 Morphological data were analysed through ANOVA-GLM with reed morphological parameters as dependent

155 variables by reed ecological status (stable vs. die-back), water management period (average water vs. low water)

156 as conditional factors, and position within the reed stand and the date of sampling as continuous factors.

157 Assumptions of normality and homoscedascity were tested and, when necessary, data were transformed to attain

158 a normal distribution. Graphing and statistics were performed in SigmaPlot 12.5 and RExcel v.3.0.17 (Baier &

159 Neuwirth, 2007).

160

161 **Results**

162 *Precipitation and water level*

163 A decline in rainfall from the long term annual precipitation of 617 mm to 400-450 mm in the 2001-2003

164 period led to the significant decrease of Lake Balaton water level (Figure 2). The highest amplitude of water level

165 change in Lake Balaton was 87 cm from April of 2000 to October 2003, although the annual changes were

166 significantly lower. In 2007 the annual precipitation in the region increased to 734 mm, resulting in a 59 cm average

167 water level increase from 2.98 meters annual average in 2003 to 3.57 m in 2007 (Figure 2). This resulted in the

168 separation of our data into low water (2001-2003) and average water (2006-2008) periods.

169

170 *Sediment properties*

171 Although some of the parameters differed slightly, no large differences between the chemical properties of the

172 sediment from the different stands, or from the different water level periods, were found (Table 2). Differences

173 between the physical and chemical characteristics of the sediments of the stable and die-back sites were found

174 (Table 2): at the die-back site the organic C content during the average water level periods (t-test, P=0.041), the

175   clay content during the low water periods (t-test, P<0.001) and the soluble P content of the sediment during the

176   average water level periods (t-test, P=0.025) were significantly higher (Table 2). The water level change increased

177   (NO_3+NO_2)-N (t-test, P=0.004) and soluble P (t-test, P=0.007) content, and decreased NH_4-N (t-test, P=0.006),

178   concentration of the sediment at the stable reed stand, while the soluble P_2O_5 content of the die-back sediment was

179   smaller in the low water period (t-test, P=0.016) (Table 2).

180   The ORP of the sediment showed high vertical (depth profile of the sediment) (Figure 3), horizontal (along

181   transects of stands) and temporal (seasonal) (Figure 4) variations. The redox potential of the open water was stable

182   throughout the studied timespan (160-190 mV), although close to the sediment and inside the reed stands it

183   decreased rapidly (Figure 3).

184   During the average water periods at surface of the sediment, the ORP in the stable reed stand was around 60 −

185   70 mV, while in the die-back sites it varied between -80 and 16 mV (Figure 3). Deeper into the sediment, the redox

186   potentials decreased, stabilising at a certain depth (∼ 40 cm) (Figure 3). The ORP measured at 50 cm beneath the

187   sediment surface varied between -16 and -80 mV in the stable and -77 and -190 in the die back sites. Further into

188   the stands, the ORP tended to be 20 to 40 mV lower than at the lakeward edges (Figure 3). A decrease in water

189   level increased the absolute values of the ORP at 50 cm sediment depth in the edge by 20 to 30 mV and inside the

190   reed stand by 40 to 120 mV (Figure 3). Moreover, the decrease in water level diminished the differences between

191   the ORP values between the stable and die-back stands (two way ANOVA, P=0.188) (Figure 3).

192   Besides the vertical differences in ORP, there was a well-defined seasonal and spatial (horizontal) variability

193   both at the stable and die-back stands (Figure 4). The redox potential of the sediment in spring and autumn was

194   moderately hypoxic (0-60 mV), while at beginning of summer in the stable stand the ORP gradually decreased to

195   anoxic (−73±24 mV, Figure 4A) and in the die-back stand to severely anoxic (−170±20 mV, Figure 4B) conditions.

196   The amplitude of redox decrease was more pronounced within the reed stand (100 vs 148 mV decrease in the

197   stable and die-back stands, respectively), while at the edge the changes were less pronounced (Figures 4A and 4B).

198   The temporal (seasonal) and spatial gradients diminished at lower water levels (Figures 4C and 4D). Not only

199   did the redox potential increased throughout, but the specific seasonal pattern inside the reed stand disappeared

200   during all studied low water level years, both at the stable and the die-back sites (Figures 4C and 4D), although

201   there were no temperature differences between the studied years (data not shown, Mann-Whitney Rank Sum Test,

202   P = 0.114).

203   The seasonal pattern of sulphide content was more accentuated during the average water level periods in the

204   die-back reed stands, resulting in an increased sulphide concentration of up to 189±30 µg S^{-2} l^{-1}, while at the stable

205 reed stands, the maximal sulphide content was 30 ± 7 µg S^{-2} l^{-1} (t-test, P=0.003) (Figures 5A and 5B). The lower

206 water level significantly reduced the midsummer sulphide content of the sediment, to 4.8 ± 4.6 µg S^{-2} l^{-1} in the

207 stable (t-test, P=0.020) and to 59 ± 20 µg S^{-2} l^{-1} in the die-back sites (t-test, P=0.012) (difference during low water

208 period was also significant; t-test, P=0.028) (Figures 5C and 5D). The sulphide content during the average water

209 periods showed a strong correlation with temperature (R=0.83, P<0.001) and ORP of the sediment (R=-0.88,

210 P<0.001), while during the low water periods no correlations were observed (data not shown).

211

212 *Plant properties*

213 During the low water years the stable stand progressed at the lakeward side and regressed at the average water

214 level period, while the waterfront of the die-back stand regressed both at the low and average water level periods

215 (Table 3). Moreover, the progression of the reed stands was not uniform throughout the study areas, resulting in

216 decrease of the fragmentation in the low water period and transitional time (2003-2005) (Table 3)

217 Morphology of *Phragmites* plants in the studied area varied a lot, mostly between the stable and die-back sites,

218 but also between low water and high water periods. In general, plants of the stable stand were 15-31% higher, with

219 27-29% thicker stems as compared with plants from the die-back site (Tables 4 and 5). These morphological

220 parameters were not significantly affected by water level change (Table 5).

221 The differences between the morphology of *Phragmites* from stable and the die-back sites were observed not

222 only at the vegetation period climax, but throughout the whole vegetation period, thus affecting the growth

223 dynamics. During the low water period, young shoots at the stable stand appeared slightly earlier (data not shown),

224 but the growth of *Phragmites* peaked nearly at the same time in both the stable and the die back sites (between 8th

225 and 20th May) (Table 4). The maximal rate of growth at the die-back site was 60% higher than at the stable stand,

226 but lasted a significantly shorter period of time (Table 4). The intensity of plant growth was affected by increased

227 water level at both the stable and the die-back sites, decreasing it by 38 and 43% respectively, while the period of

228 intensive growth was prolonged by 25 and 27 days respectively, although due to interannual variations these

229 changes were not significant (Table 4). The difference in *Phragmites* density was not significant, although the

230 lower water level significantly increased the density of plants at the die-backs site (Tables 4 and 5). In the stable

231 reed stand the plants were homogeneously distributed around the whole stand, but at the die-back stand, the shoot

232 density had higher spatial variability (up to 300 m^{-2} within reed clumps, and 0 in between).

233 Carbohydrate reserves in the internodia of the horizontal rhizomes showed no signs of soluble carbohydrate

234 and starch depletion (Table 4). No recognisable seasonal pattern in the variability of the soluble carbohydrates and

235 starch were found (data not shown). Moreover, at the die-back site the plant rhizomes had slightly higher

236 carbohydrate levels as compared with the stable stand (Table 4). The only statistically significant difference was

237 detected for the starch content of the rhizomes during the average water level periods (Table 4). The difference in

238 water level did not affect the soluble carbohydrate, or the starch content of the horizontal rhizomes (Table 4).

239   To compare the different growth and morphological parameters of *Phragmites* Spearman's rank order

240 correlations between the rank order of physicochemical properties of the sediment, and various growth and

241 morphological parameters of *Phragmites australis* were calculated (Table 6). The NO_3-NO_2 N content of the

242 sediment correlated with the most morphological parameters studied (4), although the correlations were not strong.

243 Organic C content of the sediment also significantly influence 3 studied morphological parameters (Table 6). The

244 strongest negative correlation was observed between the NH_4-N content of the sediment and number of green

245 leaves, while the strongest positive was between the total P content of the sediment and basal diameter of the plants

246 (Table 6).

247

248 **Discussion**

249   *Phragmites australis* is a geographically widespread plant that can grow under a wide range of environmental

250 conditions. Its presence under such highly variable environmental conditions is related to its adaptability and high

251 tolerance. Nevertheless the plants have certain preferences. For example, the amount of litter (that was

252 approximated by the organic content of the sediment in this study) together with the high water table could

253 significantly influence reed growth and development (Clevering, 1997). In the presence of sufficient oxidisable

254 organic compounds (litter) and adequate microbial flora, oxygen, as the most preferential electron acceptor of

255 microbial respiration, is quickly depleted in the sediment which will eventually lead to anoxia. This study further

256 confirms that high organic carbon content of the sediment could be decomposed by the anaerobic bacteria leading

257 to chemical reduction of the sediment. During the average water level periods, the stable and the die-back sites

258 had similar seasonal patterns of redox potential changes originating from this microbial driven metabolism, with

259 significant differences in the seasonal amplitudes. The sediment of the stable reed stand was moderately anaerobic,

260 while the sediment of the die-back site was regularly anoxic. This difference in redox potential magnitude could

261 be associated with the difference in organic C content of the sediment.

262   ORP of the sediment increased quickly with lowering of the water level (after only one year – data not shown)

263 and this ORP increase could be explained by the lowered water level and the consequently facilitated oxygenation

264 of the sediment at both stable and die-back stands. The negative relationship between water level and ORP was

265 indirectly supported by the spatial pattern of ORP in the sediment. Due to the more extensive water movement and

266 higher reoxygenation in the lakeward edges higher (more oxidised) ORPs were always measured, while within the

267 reed stands under more stagnant water conditions the measured redox potentials were significantly lower. The

268 correlation of water level and the ORP of the sediment is not a highly discussed topic, but some direct and indirect

269 studies have shown that there is definitely a correlation between the above mentioned parameters (Fiedler &

270 Sommer, 2004; Dusek et al., 2008).

271 The current and other studies show that low redox potential can directly affect *Phragmites*, mostly via root

272 growth and functioning, translocation of root produced metabolites (hormones), and nutrient uptake (Blokhina et

273 al., 2003; Jackson, 2008; Parent et al., 2008). *Phragmites*' underground shoots are highly tolerant to anoxia

274 (Crawford & Braendle, 1996) due to the evolved avoidance of root anaerobiosis by means of extensive

275 underground oxygenation using pressurized gas flow (Vretare Strand & Weisner, 2002; White & Ganf, 2002;

276 Armstrong et al., 2006). Radial oxygen release from *Phragmites* roots (Vretare Strand & Weisner, 2002; White &

277 Ganf, 2002; Armstrong et al., 2006) ensures the survival of reed at less-favourable areas, but under some

278 environmental conditions it would not be able to fully compensate the highly anoxic ambient conditions of the

279 sediment, resulting in the reed plants' death.

280 Very low ORP values could also indirectly effect the reed. Decomposition of sediment rich in organic matter

281 could result in the production of phytotoxic materials, such as sulphides, ammonia or organic acids (Kubín &

282 Melzer, 1996; van der Putten, 1997; Armstrong & Armstrong, 2001). The sulphide content of the sediment at the

283 die-back site during the average water period was significantly higher than in the stable stand, but even at the peak

284 of their well recognisable seasonal and spatial pattern (inside die-back reed stand at the average water level

285 periods), the sulphide concentrations were not toxic (Dinka et al., 1995; Armstrong & Armstrong, 2001). The

286 ammonia content of the sediment of the die-back site was also higher than that of the stable stand during average

287 water periods, and could have caused the reed die-back. Nevertheless, the associated effect (i.e., deprivation of

288 carbon in the metabolism of the rhizomes and the possible ethanol fermentation (Kubín & Melzer, 1996)) was not

289 observed in Lake Balaton. The presence of the highly toxic undissociated forms of monocarboxylic organic acids

290 (Armstrong & Armstrong, 2001) in the sediment of Lake Balaton was highly unlikely due to the relatively alkaline

291 (~8.4) pH of the siliceous calcite-dolomite sediment of the Kerekedi Bay, and thus was not considered to be a

292 significant factor.

293 While water level decrease generated a quick positive, growth response of the *Phragmites*, the increase of

294 water level was not followed with a decrease of similar amplitude. Moreover, the effects of the lower water level

persisted for three more years. Only after this transitional period the reed regressed and the morphological parameters were altered.

Although the major sediment factors (nutrient content, pH, organic matter, etc.) were within the previously described tolerance ranges of *Phragmites* (Romero et al., 1999), and the amount of ammonia and sulphides in the pore water of the sediment was well below toxic level (toxic levels for S^{-2} is $\sim$ 2 mg l^{-1}, for NH_4 $\sim$ 10 g kg^{-1}) (Kubín & Melzer, 1996; Armstrong & Armstrong, 2001), the die-back process in the western part of the Kerekedi Bay was apparent. Plants from the stable reed stands were bigger by all studied parameters, while the ecological status of the plants also influenced the growth dynamics: intensity of growth of the die-back plants was higher, but the period of active growth was shorter, making them more susceptible to adverse environmental changes in this more limited period of time. The die-back plants contained significantly more carbohydrates than the rhizomes of the stable *Phragmites*, nevertheless the observed morphological differences between the die-back and stable, and low water and average water plants could not be connected to shortage of soluble carbohydrates in rhizomes. Morphological parameters of both stable and die-back *Phragmites* in Lake Balaton were well within those of European reed populations (Kühl et al., 1999; Paucá-Coománescu et al., 1999; Hansen et al., 2007).

A conceptual diagram (Figure 6) summarizes our findings about hypothetical relationships between water depth and plant growth. Briefly, I think that at average water level, bacteria associated with litter decomposition colonize the sediment, decreasing the redox of the sediment as a result of their metabolism. The lowered water level reoxygenizes the water above the sediment and increases the redox potential of the sediment. The redox affects plant growths both directly and indirectly.

This study identified a general effect of water level on morphology of *Phragmites* and the differences between the morphology of the stable and the die-back sites suggested the dependence on unique, locally effective disturbances. These site-specific differences could sway the direction and the amplitude of changes. The decrease of water level directly improves the ecological status of plants, mostly by increasing the assimilatory area of *Phragmites*: the plastic reaction of the plants to the lower water levels via increased green leaf number and plant density lead to increased leaf area index and consequent production. These morphological changes persisted for two more years, while the water level increased by 93 cm. The later higher and stabilised water level triggered the degradation of *Phragmites* in the studied areas.

Recreational stabilisation of the water level in major European lakes has had significant ecological drawbacks and one of them is the die-back of reed stands. This study indicated that both morphological parameters of *Phragmites* and the ORP of the sediment were directly influenced by the water levels in Lake Balaton. Thus,

325 changing conservative water management practices and artificially lowering the water level from time to time for

326 a 2-3 year periods could help the regeneration of the inner structure of reed stands.

327

332
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404
405 Tables
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407 **Table 1.** Water depth at the lakeward edge of the stable and die-back reed stands and 20 m from the edge of the

408 reed stand sites at the Kerekedi Bay of Lake Balaton during the low (2001-2003) and average water level periods

409 (2006-2008). Data are shown as three year averages ± SD (cm). The difference between the high water and low

410 water periods: t-test, t=14.2, P=0.0009. The difference between the stable and die-back sites: t-test, t=-5.7,

411 P=0.0026. The water level variability is represented as the difference between the maximal and minimal water

412 levels of the given three year period.

413

	stable		die-back		water level
	edge	20 m	edge	20 m	variability
low water	81±17	26±17	101±17	36±16	87 cm
average water	126±12	71±12	146±12	81±12	38 cm

414
415
416 **Table 2.** Chemical and physical parameters of the sediment in the stable and die-back reed stands of Kerekedi

417 Bay of Lake Balaton during low water and average water level periods (average ± SE, n=3). The differences

418 were assessed by Student's t-test. Significance of difference between the stable and die-back stands: [*] - P<0.05,

419 [***] - P<0.001. Significance of difference between the average and low water periods: [a] - P<0.05, [b] - P<0.01.

420

	stable		die-back	
	average water	low water	average water	low water
pH	8.4±0.1	8.3±0.1	8.4±0.1	8.4±0.1
humus (%)	5.4±0.1	5.5±0.1	5.9±0.1	5.4±0.1
water capacity (ml)	86±25	81±11	102±6	78±17
organic C content (%)	21±5	19±4	32±1 [*]	29±4
CaCO$_3$ (%)	17±11	15±4	34±3	19±12
clay content (%)	19±6	17±1	25±1	24±1 [***]
total N (g kg^{-1})	5.2±2.4	5.6±3.0	5.8±0.4	5.0±2.1
(NO$_3$+NO$_2$)-N (mg kg^{-1})	4.6±0.3	6.9±0.3 [b]	5.9±1.3	6.3±2.0
NH$_4$-N (mg kg^{-1})	96±4	68±5 [b]	101±8	87±15
soluble K$_2$O (mg kg^{-1})	153±68	87±5	99±13	176±46
soluble K (mg kg^{-1})	127±57	72±4	83±11	146±38
total K (g kg^{-1})	5.1±0.8	3.0±0.4	4.0±0.1	5.1±0.8
soluble P$_2$O$_5$ (mg kg^{-1})	153±38	171±48	245±25	137±23 [a]
soluble P (mg kg^{-1})	66±10	161±21 [b]	106±11 [*]	60±23
total P (mg kg^{-1})	333±95	398±21	268±54	237±69

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424 **Table 3.** Movement (mean±SD, m y^{-1}) and change in fragmentation (%) of the lakeward side of the reed stands

425 between 2000 and 2008 in the stable and die-back sites of the Kerekedi Bay of Lake Balaton. Positive movement

426 means progression, while negative values means regression in the lakeward front of reed. Positive values in

427 fragmentation means increase in fragmentation, while negative values mean homogenisation of the reed stand.

	stable			die-back		
	2000-2003	**2003-2005**	**2005-2008**	**2000-2003**	**2003-2005**	**2005-2008**
movement	0.9±1.5	1.4±1.5	−0.5±1.0	−1.3±2.0	0.2±0.9	−0.9±1.5
fragmentation	− 53	−40	17	−23	−35	52

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430 **Table 4.** Basic morphological parameters (stem length, basal diameter, number of green leaves, leaf area index

431 (LAI) and plant density), growth dynamics (maximal growth rate, date of maximal growth, length of growth) and

432 soluble carbohydrate and starch content of horizontal rhizomes of *Phragmites australis* at the investigated stable

433 and die-back stands in Kerekedi Bay of Lake Balaton at the low water (2001-2003) and high water (2006-2008)

434 periods. Growth dynamics (grey shading) were calculated from stem length of the given years, fitted with

435 logistic, three parameters equation. Each parameter is average±SE (morphology n~60, growth dynamics n=3,

436 carbogydrates n=35-45). Significance of Mann-Whitney Rank Sum Test between the stable and die-back stands:

437 *** - P<0.001. Significance of difference between the average and low water periods: [a] - P<0.05.

438

	low water		average water	
	stable	**die-back**	**stable**	**die-back**
stem length (cm)	310±11 ***	214±8	297±8 ***	250±10
maximal growth rate [cm day^{-1}]	3.7±1.1	5.8±1.1	2.3±0.1	3.3±0.5
date of maximal growth	14/May	08/May	20/May	10/May
length of growth (days)	74±18	44±2	99±4	71±11
basal diameter (mm)	8.4±0.4 ***	6.1±0.4	7.6±0.4 ***	5.5±0.1
number of green leaves	17.8±1.5	16.3±0.6	15.8±0.6	15.2±0.7
LAI (m^2 m^{-2})	12.4±1.5	11.4±3.6	9.4±0.3	6.6±1.2
density (m^{-2})	89±15	97±9	81±6	78±7 [a]
soluble carbohydrate (mg g[drw]$^{-1}$)	178.6±28.5	217.2±48.3	163.6±25.5	203.3±22.5
starch (mg g[drw]$^{-1}$)	94.7±13.2***	210.6±26.5	130.2±16.9	172.6±19.8

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Table 5. Results of ANOVA-GLM test [F^P] of reed morphological parameters (plant height, basal diameter, number of green leaves (leaves), leaf area index (LAI) and plant density) as dependent variables by reed status (stable or die-back), period (low water vs. high water) as conditional factors, position within the reed stand (0 or 20 m from the edge of the water) and date of sampling as continuous factors. For all tests the n is between 124 and 148, for plant density n=9. P: ns - $P \geq 0.05$, * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

	height	diameter	leaves	LAI	density
status	60.76 ***	226.48 ***	16.07 **	34.80 ***	2.43 ns
period	0.35 ns	3.41 ns	25.84 ***	13.10 **	18.14 **
position	1.45 ns	1.54 ns	1.73 ns	0.83 ns	1.10 ns
date	418.29 ***	47.13 ***	712.45 ***	633.61 ***	-

Table 6. Spearman's rank order correlation (r^P) between the rank order of physicochemical properties of the sediment, and various growth and morphological parameters of *Phragmites australis* of the stable and die-back stands. Significant correlations are marked with bold text, with the following significances: * - $P<0.05$, ** - $P<0.01$.

	stem length	maximal growth rate	date of maximal growth	length of growth	basal diameter	number of green leaves	LAI	density
pH	-0.64	0.03	-0.13	-0.06	-0.75	**-0.81***	-0.64	-0.21
humus	-0.15	-0.23	-0.37	-0.02	-0.58	-0.48	**-0.78***	-0.63
water capacity	-0.05	-0.50	-0.08	0.27	-0.55	-0.70	**-0.84***	**-0.85***
organic C content	**-0.76***	0.40	-0.76	-0.57	**-0.89****	**-0.71***	**-0.63***	-0.06
CaCO₃	-0.43	-0.10	-0.46	-0.13	**-0.82***	-0.74	**-0.89***	-0.56
clay content	**-0.90***	0.44	-0.73	-0.58	**-0.90****	-0.73	-0.60	-0.01
total N	0.35	-0.45	-0.07	0.24	-0.05	-0.03	-0.47	-0.64
(NO₃+NO₂)-N	-0.13	**0.62***	**-0.65***	**-0.67***	0.07	**0.66***	0.50	0.56
NH₄-N	-0.41	-0.29	0.01	0.19	-0.72	**-0.90****	**-0.88***	-0.58
soluble K₂O	-0.54	0.41	-0.03	-0.25	-0.25	-0.30	0.16	0.47
soluble K	-0.55	0.41	-0.03	-0.25	-0.26	-0.31	0.15	0.46
total K	-0.52	0.15	0.07	-0.05	-0.40	-0.60	-0.19	0.13
soluble P₂O₅	0.00	-0.37	-0.23	0.12	-0.47	-0.45	**-0.78***	**-0.72***
soluble P	0.59	-0.19	0.01	0.10	0.49	0.66	0.25	-0.11
total P	**0.86****	-0.53	0.65	0.60	**0.83***	0.70	0.43	-0.17

Figure captions

Figure 1. A. The map of Europe (grey) showing Hungary (dark grey) and Lake Balaton (black) within it. **B.** Lake Balaton with its smaller tributaries (blue lines) and its reed stands (green areas). The small rectangle shows the study area. **C.** The map of the study area (Kerekedi Bay) in the easternmost basin of Lake Balaton with reed (green areas) showing the stable (a) and die-back (b) sites. Areas not covered with reed are shown with blue (water of the lake) and grey (pastures, urban areas, etc.) colours.

Figure 2. Change of water level in Lake Balaton between 2000 and 2010. Red boxplots show the average water level in the low water (2001.01.01.-2004.01.01.) and average water level (2006.01.01.-2009.01.01.) periods. Boxes encompass the 25% and 75% quartiles of all the data, the central solid line represents the median, bars extend to the 95% confidence limits, and dots represent outliers. The dashed blue line is the average water level between 2000.01.01. and 2010.01.01. (3.46 m).

Figure 3. Example of change of oxidation-reduction potential (ORP) within the water column (positive numbers) and sediment (negative numbers) of the stable (green symbols) and die-back (brown symbols) reed stands of Kerekedi Bay, Lake Balaton during low water and average water periods (average ± SE, n~10). Dotted line represents the sediment level.

Figure 4. Contour graph of seasonal and spatial change of oxidation-reduction potentials at 50 cm depth of the sediment in the average-water (A and B) low-water (C and D) periods in the stable and die-back reed stands of Kerekedi Bay, Lake Balaton. On each figure 0 on the y-axis refers to the edge of the reed stand.
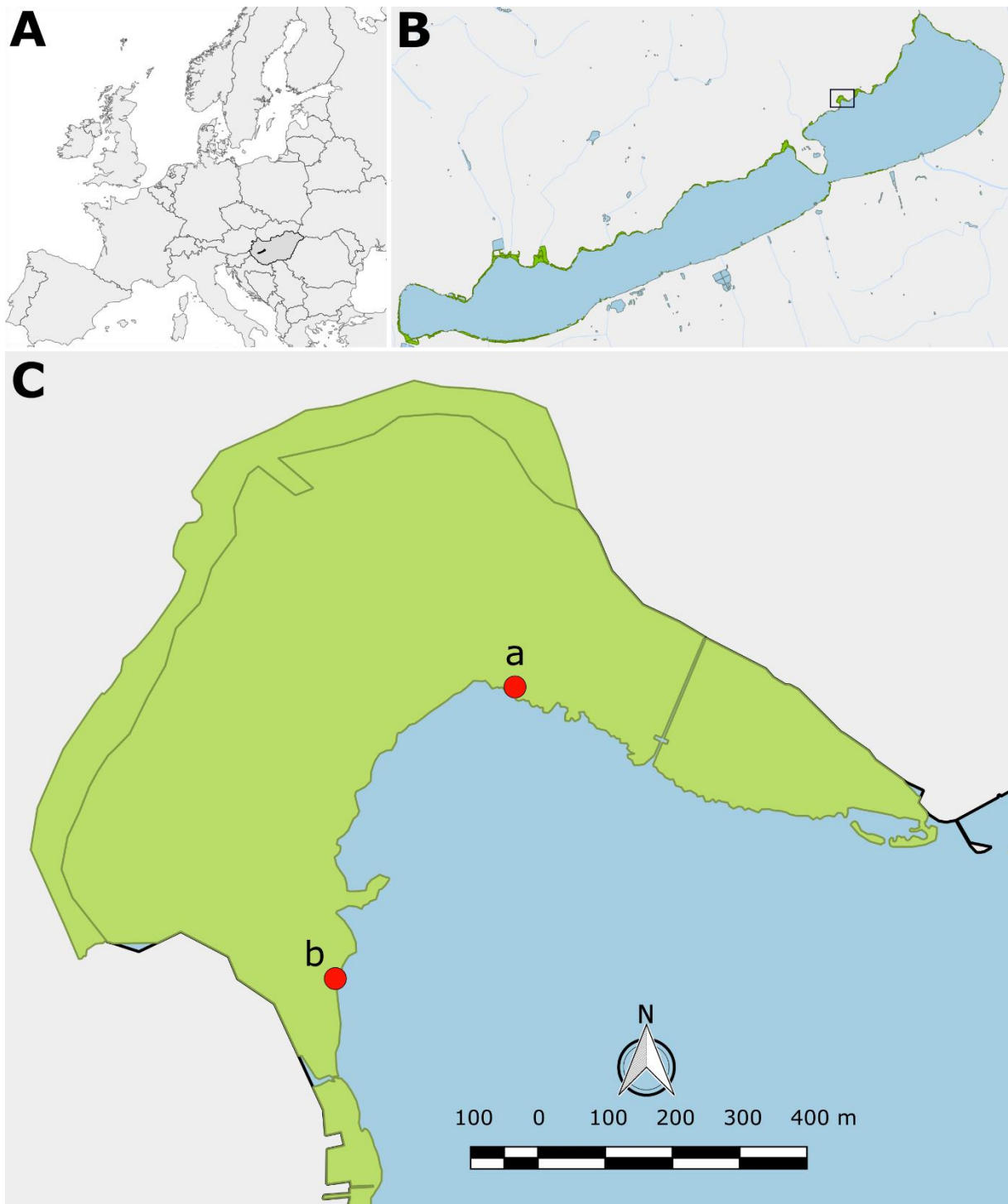
Figure 5. Sulphide (S^{2-}, µg l^{-1}) content at 50 cm depth of the sediment measured at the average water (A and B) and low water (C and D) periods in the stable and die-back reed stands of Kerekedi Bay of Lake Balaton.
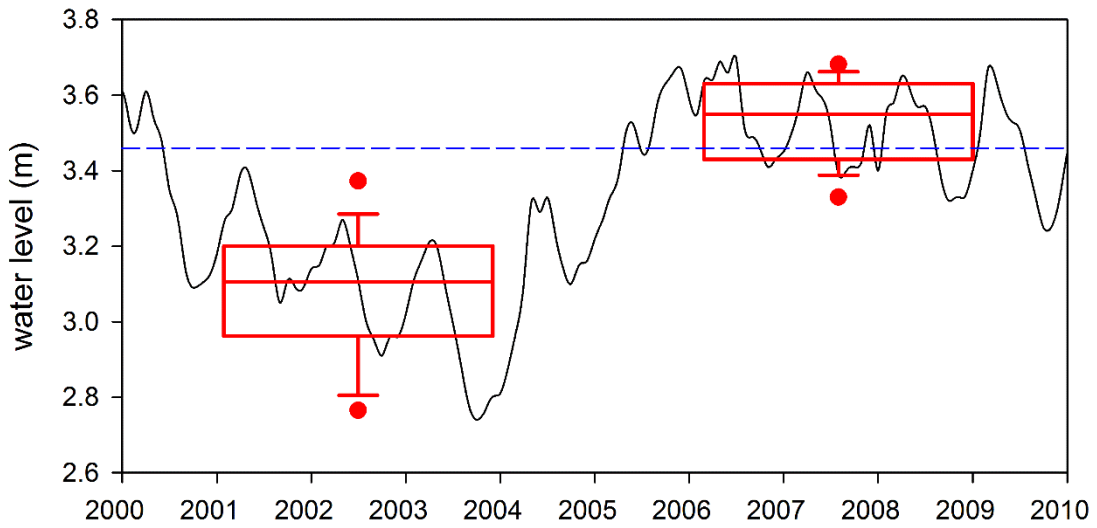
Figure 6. A flow chart representation of interactions within the water and sediment as a result of lowering water level.

484
485   Fig. 1.
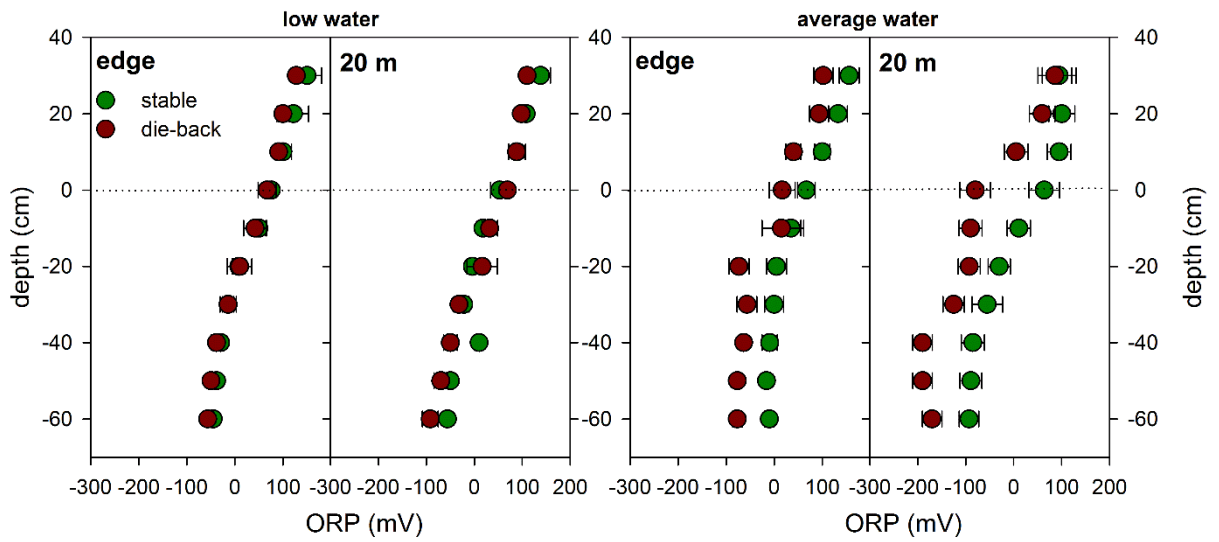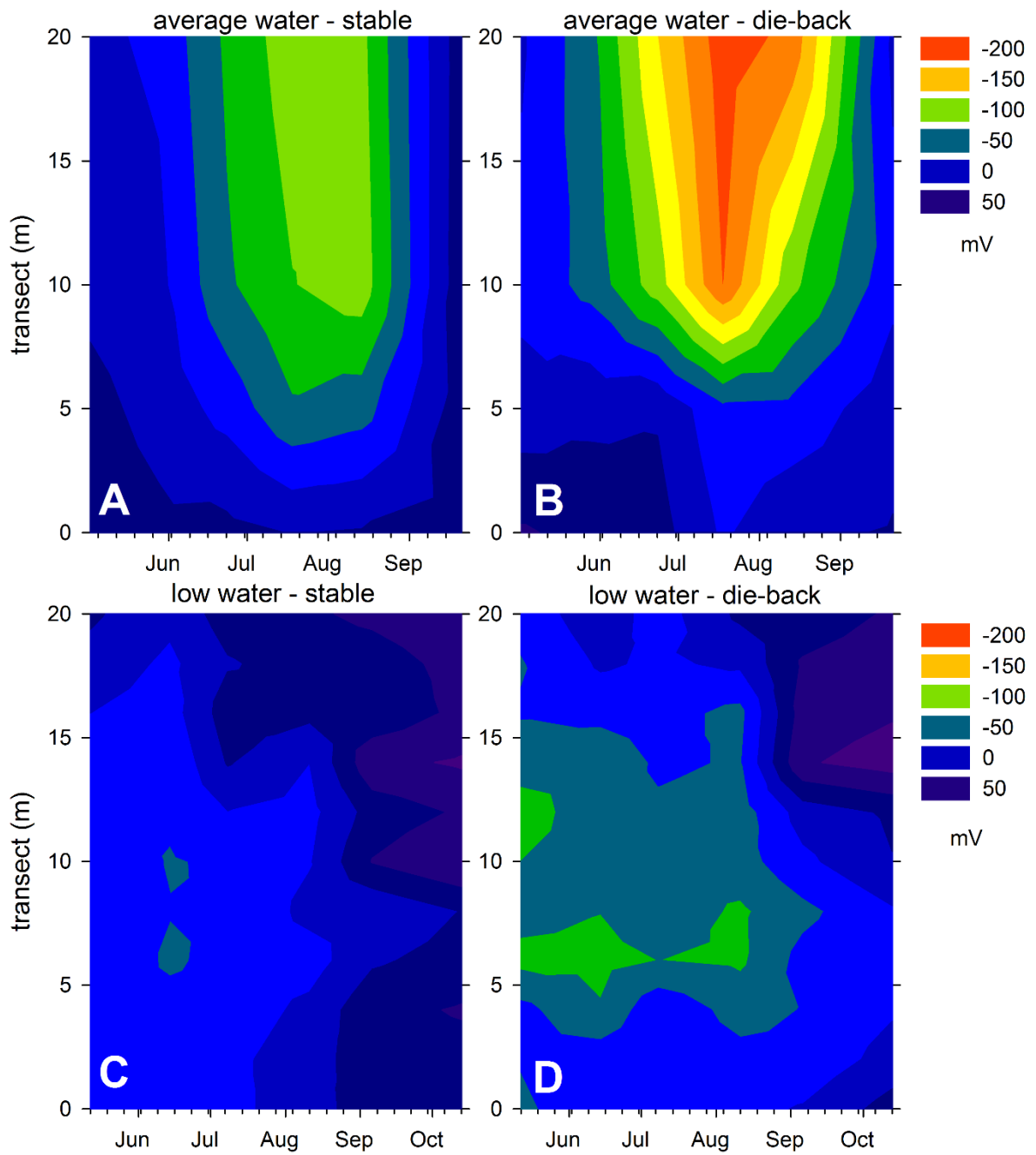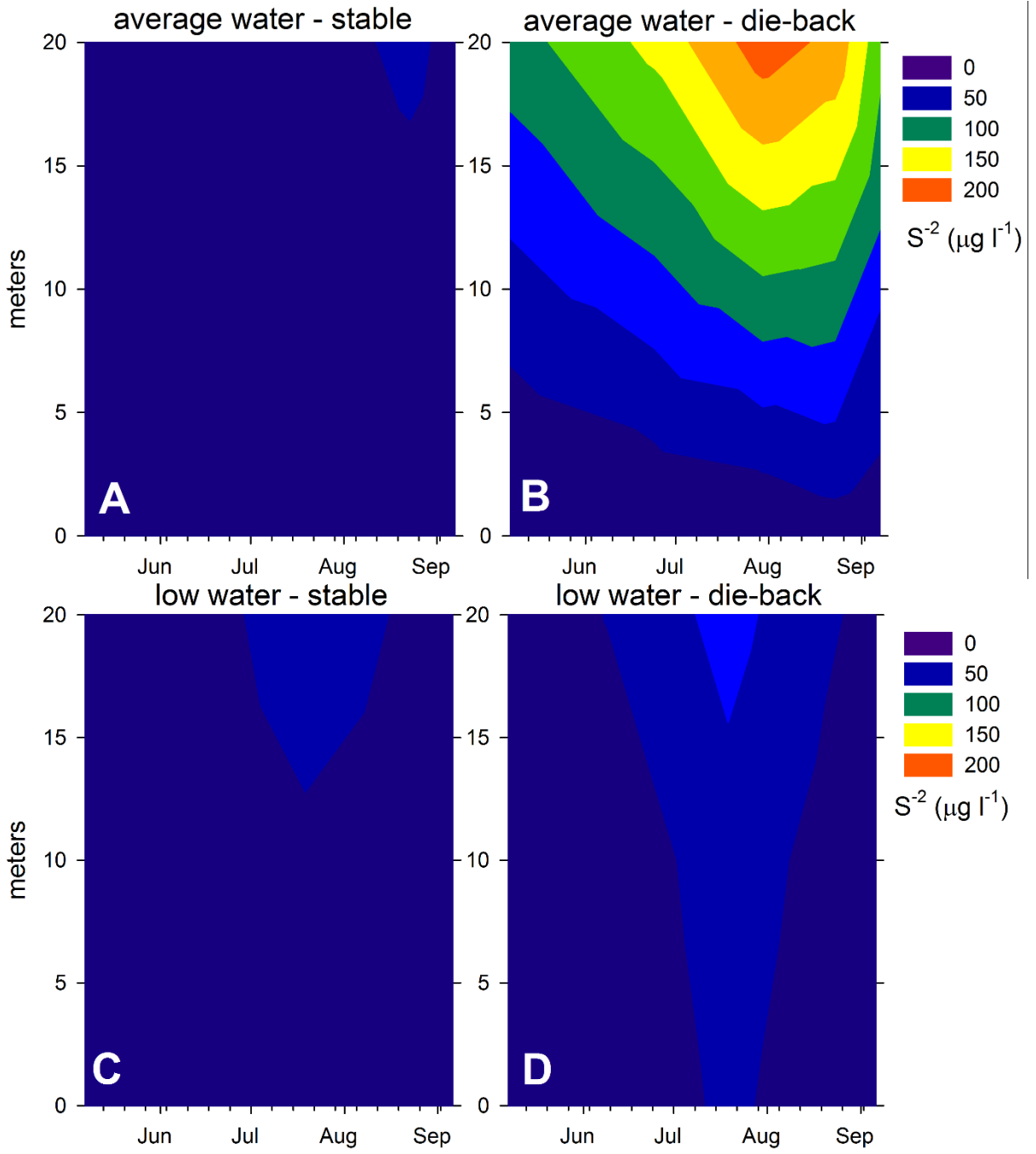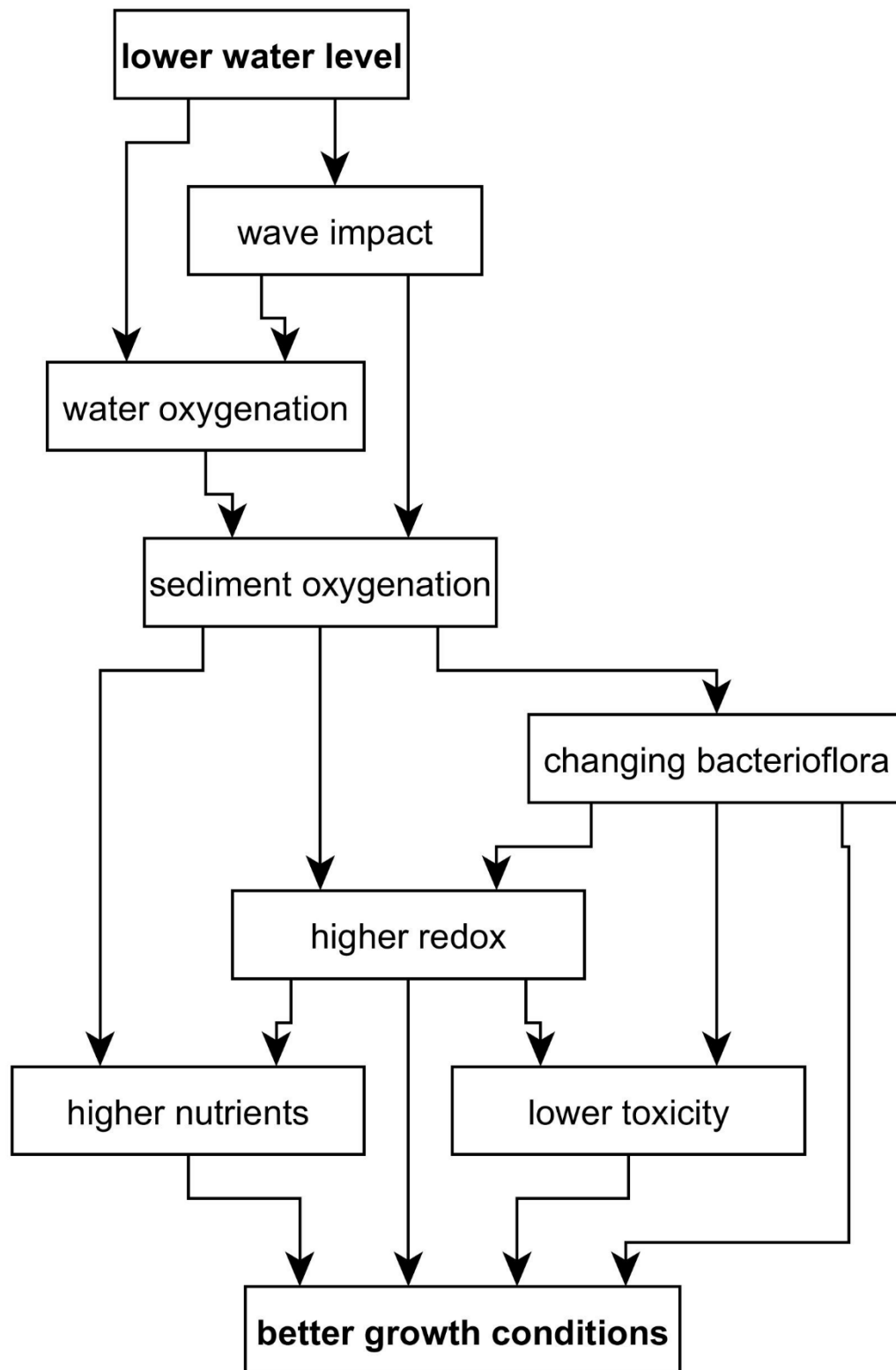
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