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3 **Investigating the role of water and sediment chemistry on growth potential of *Hydrilla***
4 **(*Hydrilla verticillata*) and *Cabomba* (*Cabomba caroliniana*) in two reservoirs of Austin, TX,**
5 **USA. Phase 2 report**

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7 **SR-16-08, August 2016**
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9 Portions of this report have been published as: Bellinger, B.J., Davis, S.L., 20XX. Investigating
10 the role of water and sediment chemistry from two reservoirs in regulating the growth potential
11 of *Hydrilla verticillata* (L.f.) Royle and *Cabomba caroliniana* A. Gray. *Aquat. Bot.* XX, XXX-
12 XXX.

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20
21 **Abstract**

Knowledge of aquatic system physicochemical characteristics can inform managers into growth potential of submerged plants. In a mesotrophic central Texas reservoir, Lake Austin, the exotic invasive *Hydrilla verticillata* (L.f.) Royle thrived for over a decade until management efforts achieved recent control. However, in the immediate downriver eutrophic reservoir, Lady Bird Lake, *H. verticillata* has been unsuccessful despite repeated introductions. Instead, the native plant *Cabomba caroliniana* A. Gray has recently colonized and spread. In this study we established mesocosms approximating each reservoir and tracked plant growth metrics to test the role of water chemistry and sediment chemistry and composition in inhibiting or supporting two internationally important species. Lake Austin had a significantly higher pH and lower nitrate concentrations in the water and sandy sediments compared to the eutrophic, silty reservoir. We observed higher growth rates and greater biomass of *H. verticillata* and *C. caroliniana* in the eutrophic reservoir treatments; the former species growth contrary to expectations. Between species, *H. verticillata* relative growth rates were nearly 4x higher, lengths 5–10x longer, and dry weights 2–5x greater than those for *C. caroliniana* within a given treatment. Concurrent with rapid growth rates in the eutrophic reservoir treatments, tissue phosphorus contents for both species increased. Our findings suggest that *H. verticillata* growth in the eutrophic reservoir has not been significantly impaired by the water and sediment attributes measured in this study. Conversely, our initial evidence corroborates the reduced growth potential of *C. caroliniana* in systems of relatively low nutrients and pH over 8.

22 Introduction

23 *Hydrilla verticillata* (L.f.) Royle is native to Asia and India and has successfully
24 colonized aquatic systems across the globe, often to the detriment of the native flora and physical
25 properties of the system (Kennedy et al. 2009; Sousa et al., 2011). Annually, significant effort
26 and resources are expended to control and reduce growth of *H. verticillata* using mechanical,
27 chemical, biological, and physical methods in infested aquatic systems, notably in the sub-
28 tropical southern United States (Langeland, 1996). *Cabomba caroliniana* is a native aquatic plant
29 to the southern United States and northern South America and is generally not actively managed
30 within its' native range (Wilson et al., 2007). However, primarily through the aquarium trade, *C.*
31 *caroliniana* has been introduced across the northern United States, Canada, Europe, and
32 Australia where it is recognized as an invasive exotic nuisance (Schneider and Jeter, 1982;
33 Wilson et al., 2007; June-Wells et al., 2013; Bickel and Schooler, 2015). Control of *C.*
34 *caroliniana* has been focused on biological and physical methods as chemical control agents
35 have been less effective (Wilson et al., 2007; Schooler, 2009).

36 In central Texas, USA, *H. verticillata* has an established and sometimes prolific presence
37 in the reservoirs and free-flowing rivers, negatively impacting recreational and flood control
38 functions (e.g., the Colorado River and reservoirs; Fig. 1) (for a full Texas distribution map see:
39 <http://www.texasinvasives.org/observations/mapping.php?species=HYVE3&search=go>; site
40 accessed 7/2016). However, a conspicuous exception to *H. verticillata*'s spread across central
41 Texas has been in a eutrophic reservoir in downtown Austin, TX (i.e., Lady Bird Lake; Fig. 1).
42 Despite repeated inadvertent introductions from the contributing reservoir over a decade and a
43 half period, *H. verticillata* has not yet become established (Gilroy, 2006; B. Bellinger, pers.
44 obs.). Rather, SAV was typically sparse in the small flow-through reservoir until 2011 when
45 *Cabomba caroliniana* A. Gray, colonized from a tributary source and quickly spread through the
46 upper reach of the reservoir (Magnelia and De Jesus, 2008; Farooqi and De Jesus, 2012). An
47 understanding of the physicochemical characteristics of each reservoir where the species have
48 been differentially successful will further our understanding of the attributes of aquatic systems
49 that contribute to plant spread, growth, and success.

50 The growth, species composition, and biomass of SAV are primarily influenced by
51 existing plant community composition and biomass, basin morphology, phytoplankton shading,
52 herbivore density, pH, and nutrient availability. When determining the susceptibility of a system
53 to successful colonization by an aquatic plant (desired or not), sediment composition and
54 chemistry and water chemistry are commonly evaluated (Koch, 2001; Bornette and Puijalon,
55 2011; Sousa, 2011; June-Wells et al., 2013; Matthews et al., 2013). *Hydrilla verticillata* has been
56 shown to be adaptable to oligotrophic through eutrophic lentic and lotic temperate and tropical
57 systems (Langeland, 1996; Sousa, 2011). However, *H. verticillata* has an apparent preference to
58 sediment organic matter content. Growth has been shown to be negatively affected by dense
59 inorganic sands or fine organic sediments (i.e., bulk densities <5% or >20%, respectively)
60 (Barko and Smart, 1986; Spencer et al., 1992; Sousa, 2011). While nutrient limitations to growth
61 influencing competition are a potential with inorganic sediments, growth inhibition in organic
62 matter-rich sediments may be related to phytotoxin concentrations (Barko and Smart, 1983;
63 Koch et al., 1990; Sousa, 2011). For example, Wu et al. (2009) observed reductions in *H.*
64 *verticillata* photosynthetic activity when sulfide was added to the root zone.

65 Conversely, *C. caroliniana* appears more restricted in ecological preferences. Preferential
66 physicochemical conditions include protected inlets or channels that have soft, loose, silty,
67 nutrient-rich sediments that are minimally impacted by wave energy or high currents due to a

68 shallow root system and fragile stems (Wilson et al., 2007; Schooler et al., 2009; Bickel, 2012).
69 *Cabomba caroliniana* was frequently found in eutrophic systems but has recently been shown
70 capable of spreading to oligotrophic waters (Wilson et al., 2007). Specific conductance has been
71 correlated with *C. caroliniana* occurrence (June-Wells et al., 2013), but pH appears to be one of
72 the most important determinants of success. Optimum growth occurs at a pH of 4–6 with
73 senescence at a pH over 8. The rationale for the decline in condition at an elevated pH is a
74 preference for CO₂ (Riemer, 1965; Schooler, 2009; Bickel, 2012; but see Matthews et al., 2013).
75 Occurrence of *H. verticillata* has been positively correlated with pH, but a pH < 7 may not be
76 detrimental through effective uptake of CO₂ and HCO₃⁻ (Sousa, 2011). Both species appear
77 capable of utilizing water and sediment nutrients (Langeland, 1996; Wilson et al., 2007), though
78 the latter have been shown more important to *H. verticillata* growth (Barko and Smart 1986;
79 Sousa, 2011).

80 In this study we evaluated the sediment and water characteristics of two reservoirs that
81 may have promoted or limited the growth of two potentially nuisance species in order to provide
82 managers with more information when evaluating system vulnerability or resistance to
83 colonization. We utilized a mesocosm study to approximate two central Texas reservoirs where
84 *H. verticillata* and *C. caroliniana* have had individual success and cross-planted each species in
85 order to track growth potential. By removing herbivory and interspecific competitive influences
86 on growth potential, we tested the hypotheses that: 1) physicochemical attributes of the
87 sediments in the eutrophic Lady Bird Lake reservoir have heretofore prevented invasion by *H.*
88 *verticillata*; and 2) an elevated pH coupled with lower water and sediment nutrients in the
89 mesotrophic Lake Austin reservoir would impair *C. caroliniana* growth and thus potential future
90 spread.

91 **Methods**

92 *Experimental design*

93 *Treatments*

94 Our mesocosm study was carried out in a greenhouse facility at the University of Texas
95 at Austin Brackenridge Field Laboratory (BFL; 30° 17' 04.6" N, 97° 46' 41.8" W). The facility
96 faces southwest and received unfiltered sunlight in the late morning through afternoon during the
97 study period of August – October, 2015. Greenhouse temperature (daytime 20–30 °C) was
98 moderated by an evaporative cooler. We established four treatments with five replicates for each
99 plant species for a total of forty experimental units in 19 liter (L) plastic buckets (approx. vol. of
100 24,439 cm³ each). Replicate treatment containers were placed in a water-filled basin (4 m x 2 m x
101 0.3 m deep) to further regulate treatment water temperatures. Treatment combinations and
102 abbreviations were: Lady Bird Lake water with Lady Bird Lake sediments (LBW/LBS); Lake
103 Austin water with Lake Austin sediments (LAW/LAS); Lady Bird Lake water with Lake Austin
104 sediments (LBW/LAS); and Lake Austin water with Lady Bird Lake sediments (LAW/LBS).
105 The LAW/LAS treatment represented the control for *H. verticillata* and the LBW/LBS treatment
106 represented the *C. caroliniana* control. The cross treatments of LBW/LAS and LAW/LBS were
107 used to establish if a particular matrix (water or sediment) more strongly affected plant growth
108 potential.

109 *Sediment collection and analyses*

110 Lake Austin sediments (top 10–15 cm) were collected on 6 August 2015 by shovel in 1–
111 1.5 m depth of water at an area accessed by boat that historically supported *H. verticillata* growth
112 (30° 20' 59.5" N, 97° 50' 54.8" W; Fig. 1). Lady Bird Lake sediments (top 10–15cm) were
113 collected on 5 August 2015 at a site accessed by boat in water 0.5–1.5 m deep and supporting
114 dense *C. caroliniana* growth (30° 15' 54.9" N, 97° 45' 25.9" W; Fig. 1). Each mesocosm was
115 filled with approximately 10 cm of intact sediment *in situ* during collection ($\approx 6,379 \text{ cm}^3$
116 sediment). Sediment nutrient chemistry and composition were characterized from six
117 concurrently collected samples from each reservoir in 500 mL glass jars and iced for transport to
118 the laboratory. Three of the samples were analyzed by the LCRA Environmental Laboratory
119 Services (Austin, TX, USA) for determination of total Kjeldahl nitrogen (TKN; US
120 Environmental Protection Agency [EPA] method E351.2), NO_x (USEPA method E300.0), TP
121 (USEPA method E365.3), SO_4^{2-} (USEPA method E300.0), and total organic carbon (TOC;
122 USEPA method SW9060A) content (i.e., mg kg^{-1}); and percent (%) clay (<0.002 mm), gravel
123 (>2.0 mm), sand (0.05–2.0 mm), and silt (0.002–0.05 mm; USEPA method 600/2-78-54). The
124 other three samples were sent to Analysys Laboratories (Corpus Christi, TX, USA) for
125 determination of total sulfide content (USEPA method 9034 & SM-4500S2E) and hydrogen
126 sulfide (H_2S) content (USEPA method SM-4500S2-H). The latter was estimated based on
127 sediment porewater conductivity, pH, and total sulfide content. Sediment total N (TN) content
128 was estimated by summing TKN and NO_x . Sediment total organic matter (OM) was determined
129 by multiplying TOC by 1.724 (NRCS, 2014).

130 At the end of the experiment, triplicate sediment samples were collected from only the
131 LBW/LBS treatment planted with *H. verticillata* and LAW/LAS treatment planted with *C.*
132 *caroliniana* to evaluate potential short-term changes in sediment characteristics should a plant
133 become established in the opposite reservoir. Sediment dry bulk density (g cm^{-3} ; $n = 3$) was
134 determined at the end of the experiment on triplicate sediment core samples (approx. 10 cm
135 depth; vol. = 166.2 cm^3) oven dried (60 °C for 48–72 h) to convert sediment nutrient contents
136 (mg kg^{-1}) to concentrations (g cm^{-3} ; Tolhurst et al., 2005).

137 *Water collection and analyses*

138 A total of 260 L of water was collected from each reservoir with 20 L polyethylene
139 containers to establish experimental treatments. Lake Austin water was collected on 6 August
140 2015 from shore approximately 8 km downriver of the sediment collection site (30° 20' 57.9" N,
141 97° 47' 52.2" W; Fig. 1). Lady Bird water was collected from shore on 5 August 2015
142 approximately 1 km upriver of the sediment collection site (30° 16' 12.6" N, 97° 45' 57.7" W;
143 Fig. 1). Water collection sites were well mixed in vegetation-free zones of about 1.5 m depth and
144 afforded dock access for weekly collections. At the BFL greenhouse, sediment-containing
145 buckets were filled with reservoir water to a depth of 20 cm ($\approx 13 \text{ L}$) and allowed to settle for 5 d
146 prior to planting.

147 Throughout the experimental period we attempted to maintain water quality conditions
148 reflective of the reservoirs by replacing approximately two-thirds of the water in each mesocosm
149 weekly with fresh reservoir water collected from the sites identified above. During weekly
150 morning water collections from each reservoir we measured *in situ* water temperature (°C),
151 dissolved oxygen (DO; mg L^{-1}), specific conductance ($\mu\text{s cm}^{-1}$), and pH with a Hydrolab
152 Datasonde (model # MSS; OTT Hydromet, Loveland, Colorado, USA). Water nutrient chemistry
153 was measured bi-weekly in each reservoir from a single surface (top 0.3 m) grab sample. Water

154 chemistry samples were kept on ice and delivered to LCRA Environmental Laboratory for
155 analyses. From a 250 mL unpreserved sample we determined TKN (USEPA method E351.2),
156 NO_x (USEPA method SM4500-NO₃-H), ammonia (NH₄⁺; USEPA method E350.1), TP (USEPA
157 method E365.4), and TOC (USEPA method SM5310D) concentrations. Ortho-phosphate (ORP;
158 mg L⁻¹; USEPA method E300.0) and sulfate (SO₄²⁻; mg/L; USEPA method E300.0)
159 concentrations were measured from a 250 mL H₂SO₄ acidified sample. For measurements below
160 accepted reporting limits, we used laboratory-suggested limits of detection. Total nitrogen (TN)
161 concentration was determined by summing TKN and NO_x concentrations.

162 *Plant collection and analyses*

163 *Hydrilla verticillata* plants were collected on 10 August 2015 from the Colorado River
164 below Lady Bird Lake (30° 14' 45.6" N, 97° 41' 19.9" W; Fig. 1). Sediment texture appeared
165 similar between the Lake Austin and Colorado River sites (i.e., silty sand; B. Bellinger, pers.
166 obs.). Aboveground biomass of plants was collected and kept in site-water filled coolers and
167 returned to the BFL for processing and same day planting. Initial biomass for each treatment was
168 standardized by cutting 80 healthy apical plant stems to an approximately 10 cm length with no
169 root material. Initial lengths and wet weight (WW; average of 1.2 g) of plants were recorded
170 prior to planting the lower ≈3 cm (or 3 leafy nodes) of four apical stems in each replicate
171 mesocosm equidistant from one another. *Cabomba caroliniana* above ground biomass was
172 collected from Lady Bird Lake on 10 August 2015 from the same location as the sediment
173 samples. Healthy apical plant stems of 80 plants with no root material were standardized at
174 approximately 19 cm length and WWs (average of 4.7 g) were determined prior to planting the
175 bottom ≈6 cm (or 3 leafy nodes) of four stems equally spaced in each replicate mesocosm.
176 Longer *C. caroliniana* initial stems were necessary due to greater inter-nodal spacing than
177 observed for *H. verticillata*.

178 The experimental period ended ten weeks after planting. Plant growth was tracked by
179 measuring total stem length (including branches and new growth from sediments) in each
180 mesocosm weekly. We stopped weekly plant length measurements in the LBS treatments planted
181 with *H. verticillata* after four weeks because stems had grown too dense and entangled to
182 efficiently measure stems and without damaging plants. Weekly measurements of total plant
183 length in the remaining treatments continued for another three weeks until plant stems in most
184 treatments were too dense for measurement. At the end of the experiment all plant material was
185 removed from each replicate container for determination of total plant length, WW, and dry
186 weight (DW; g) after oven drying plants for 24 h at 60 °C. Because we could not ensure all root
187 material was collected, we provide only approximate observed root lengths.

188 Initial and final plant nutrient chemistry (TC, TN, and TP) was determined on
189 approximately 5 g DW material by LCRA Environmental Laboratory Services using the methods
190 described above for sediments. Initial *C. caroliniana* TP contents were incorrectly assayed, so
191 we used the TP contents derived from *C. caroliniana* plants grown in the LBW/LBS treatment as
192 it represented control conditions. The analytical laboratory required the large dry mass of
193 material for analysis, necessitating compositing of plants from multiple replicate mesocosms,
194 thus reducing the final *n* within a treatment to two.

195 *Data analysis*

196 Differences in water chemistry between reservoirs across all sampling events were
197 evaluated with a student's *T*-test. Sediment composition and nutrient chemistry were compared

198 between reservoirs from initial collections and the *H. verticillata* LBW/LBS and *C. caroliniana*
199 LAW/LAS treatments collected at the end of the experiment using a one-way ANOVA. When
200 significant, pair-wise differences were identified with Tukey's honestly significant difference
201 (HSD) test. We evaluated only those two cross-treatments for potential short-term impacts on
202 sediment chemistry should a species colonize the opposite reservoir.

203 In order to compare changes in plant biomass (as DW) between experimental treatments,
204 we first established a predictive model of initial plant DW (Bellinger and Davis, 2016). Briefly,
205 from an additional fifty stems of each species we used simple linear regression to evaluate the
206 relationship between plant DW with length or WW. We found no significant relationship
207 between plant length and DW for either species, but the relationship between WW and DW was
208 significant for *H. verticillata* ($y = 0.10x - 0.007$, $r^2 = 0.76$, $p < 0.001$) and *C. caroliniana* ($y =$
209 $0.053x + 0.023$, $r^2 = 0.68$, $p < 0.001$). Therefore, we estimated initial plant DW in the growth
210 study from our regression equation based on measured WW.

211 From the growth study, descriptive and comparative statistics were based on the replicate
212 mesocosms ($n = 5$) for each treatment after summing plant measures within a mesocosm. Means
213 and 95% confidence intervals were derived using the SAS LSMEANS statement within PROC
214 GLIMMIX. We performed a generalized linear model (GLM) analysis using the SAS PROC
215 GLIMMIX with a gamma distribution to evaluate the main effects of reservoir water and
216 reservoir sediment on treatment differences in measured average weekly plant lengths and
217 estimated daily growth rates. Interaction effects were evaluated between subjects by *sediment *
218 water*, and within subjects by *sediment * time*, *water * time*, and *time * sediment * water*. We
219 also used GLMs to test for differences in final length, DW, dry matter content (DMC), and
220 relative growth rates (RGRs) due to reservoir water, sediment, and *sediment * water* interactions.
221 Pair-wise differences between treatments were made by comparing overlap in 95% confidence
222 intervals around the mean. Estimated daily treatment plant stem growth rates (cm d^{-1}) were
223 determined by: $(L_2 - L_1)/(t_2 - t_1)$, where L_2 and L_1 are the plant lengths at time t_2 and t_1 ,
224 respectively. Plant DMC (%) was determined by: $[\text{DW}/\text{WW}] * 100$ (Elger and Willby, 2003).
225 Final RGRs ($\text{mg g}^{-1} \text{d}^{-1}$) were based on changes in plant biomass (DW) between the beginning
226 and end of the experiment within a treatment by: $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_2 and W_1 are
227 plant weights at time t_2 and t_1 , respectively (Van et al., 1999). Initial (i.e., t_1) plant DWs (i.e., W_1)
228 were estimated from the predictive model described above. There were no significant differences
229 in plant length or biomass within a particular treatment at the onset of the study ($p > 0.05$; not
230 shown). Plant roots were not explicitly measured for length and so were not incorporated into
231 final plant stem lengths, but were included in mass and nutrient analyses (Barko and Smart,
232 1983, 1986). For all data, we evaluated normality with the Shapiro-Wilk test, data skewness ($> -$
233 1.0 or < 1), and kurtosis (≈ 3.0). Statistical tests were run with Systat 13 (v.13.1; Systat software,
234 Inc. San Jose, California, USA) and SAS (v.9.4; SAS Institute, Inc. Cary, NC, USA).
235 We descriptively assessed changes in plant nutrient chemistry between the beginning and end of
236 the experiment and among experimental treatments due to a lack of sufficient replication for
237 statistical analyses.

238 Results

239 *Reservoir water and sediment chemistry*

240 Over the study period the mesotrophic LAW had a significantly lower specific
241 conductance, pH, and concentrations of $\text{NO}_x\text{-N}$ and TN, and higher molar C: N ratio than in

242 LBW (t -test: $p < 0.05$; Table 1). Based on water pH, the proportion of CO₂ in LAW would have
243 been approximately 1% and HCO₃⁻ would have been near 99%, whereas in LBW CO₂ would
244 have been near 10% with 90% HCO₃⁻. Water temperatures in both reservoirs declined
245 approximately 6 °C over the three month study. Across sample events, ORP was below detection
246 limits (<0.01 mg L⁻¹) in both reservoirs; in LAW, NH₄-N and NO_x were also below detection
247 limits with the exception of an anomalous NO_x concentration of 112 µg L⁻¹ in late September.
248 Water molar C:N:P ratios indicated a P-imbalance in both systems (i.e., C:P > 258 and N:P > 22;
249 Hecky et al., 1993); only C:N significantly differed between reservoirs (Table 1).

250 Lady Bird Lake sediment had significantly less sand and greater silt than LAS (one-way
251 ANOVA: $p < 0.05$), contributing to a 44% greater bulk density in the former reservoir (Table 2).
252 Total OC and TN contents (mg kg⁻¹) and concentrations (mg cm⁻³) were significantly greater in
253 the eutrophic LBS (one-way ANOVA: $p > 0.05$). Sediment NO_x contents were near detection
254 limits in both reservoirs; sulfide concentration was significantly greater in LAS (one-way
255 ANOVA: $p > 0.05$; Table 2). Sediment molar C:P and N:P ratios were significantly higher in the
256 eutrophic LBS treatments (one-way ANOVA: $p < 0.05$).

257 We did not determine any significant changes in neither sediment texture nor chemistry
258 between the beginning and end of the experiment within reservoir treatments planted with *C.*
259 *caroliniana* or *H. verticillata* (Tukey's HSD > 0.05; Table 2).

260 *Hydrilla verticillata* growth and stoichiometry

261 *Hydrilla verticillata* mean plant lengths over the majority of the study period were longer
262 in the LBS treatments (Fig. 2A). Daily growth rates in LBS treatments increased for the first
263 month, and though they slowed by the end of the experiment, were still faster than in the LAS
264 treatments; daily growth rates in the LAS treatments were similar through time (Fig. 2B).
265 Between and within subjects, sediment significantly affected plant length and growth rates, but
266 there was also a sediment-type interaction with time due to greater expansion in the LBS
267 treatments (GLM: $p < 0.001$; Table 3). Mean final *H. verticillata* length (Fig. 2A), and DW,
268 DMC, and RGRs significantly differed among treatments (Fig. 3A, B, and C, respectively), with
269 sediment-type being the only significant influencing factor (GLM: $p < 0.001$; Table 4). Despite
270 only planting apical stems, harvested plants were observed to have roots growing from nodes in
271 contact with or below the sediment surface, with lengths in excess of 20 cm. Lateral runners
272 along the sediment surface also had observable root development.

273 Relative to initial average contents, final *H. verticillata* tissue C and P contents declined
274 by nearly 50% and 70%, respectively, in both LAS treatments (Table 5). Conversely, final P
275 content increased by approximately 49% and 83% in the LBW/LBS and LAW/LBS treatments,
276 respectively, from initial contents. *Hydrilla verticillata* TN contents declined by approximately
277 14–24% in all treatments. Lowest molar C:P and N:P ratios were observed for plants in the LBS
278 treatments (Table 5).

279 *Cabomba caroliniana* growth and stoichiometry

280 Longest average *C. caroliniana* plant lengths (Fig. 2C) and in general fastest growth rates
281 (Fig. 2D) were observed in the LBS (control) treatments; significantly shorter plants and lowest
282 growth rates were observed in the LAW/LAS treatment. Between subjects, sediment
283 significantly influenced *C. caroliniana* length and growth rates (GLM: $p < 0.001$; Table 3).
284 However, within subjects there were significant interaction effects among factors on lengths and
285 growth rates (Table 3, Supplemental Fig. 1). At the end of the experiment, the LAW/LAS

286 treatments had lowest DW (Fig. 3D) and slowest RGR (Fig. 3F). Plant DMCs were similar
287 across all treatments (Fig. 3E). Sediment had a significant effect on all plant metrics, but source
288 water also influenced DWs and RGRs, and there was a significant sediment \times water interaction
289 effect on DWs and DMC (GLM: $p < 0.05$; Table 4; Supplemental Fig. 2). We observed less root
290 growth from planted leaf nodes across treatments, commonly less than 20 cm from any given
291 subsurface node.

292 *Cabomba caroliniana* tissue C and N contents and molar ratios remained similar across
293 all treatments (Table 5). However, P contents declined by approximately 42% and 34% in the
294 LAW/LAS and LBW/LAS treatments, respectively. Conversely, TP contents increased 29% in
295 the LAW/LBS treatment. Concurrent with lower plant TP contents in LAS treatments, molar C:P
296 and N:P ratios increased relative to initial ratios (Table 5).

297 Discussion

298 As SAV continue to be dispersed across regions through anthropogenic activities,
299 increasing our understanding of the suitability of an aquatic system to support a potentially
300 nuisance species is critical for management. We rejected our hypothesis that sediment conditions
301 in a eutrophic reservoir have heretofore impeded successful colonization by *H. verticillata*.
302 Growth and biomass in our eutrophic Lady Bird Lake treatments were greater relative to our
303 mesotrophic Lake Austin reservoir treatments. In the latter system, *H. verticillata* had been
304 successful to the point of detrimental for over a decade, indicating other limiting factors in the
305 eutrophic Lady Bird Lake reservoir. In the eutrophic LBS treatments, we found that sediment
306 organic matter content was 11%, below the literature suggested threshold for *H. verticillata*
307 growth impairment of 20%, and instead was near the modeled growth optima (Barko and Smart,
308 1986; Silveira and Thomaz, 2015). We were also incorrect in our expectation of greater sediment
309 sulfide concentrations in the eutrophic LBS that could have impaired *H. verticillata* growth
310 during root development from planted apical stems (Sousa, 2011). Rather, we found sulfide
311 concentration in the LBS were less than half that from the mesotrophic LAS. Lower sediment
312 sulfide concentrations could be due to surface water nitrate sustaining sediment redox reactions
313 preferentially through the denitrification pathway. Additionally, an apparent lack of phytotoxin
314 impairment could be due to sulfides being bound to iron or the $\text{pH} > 7$ which favors the less toxic
315 form of reduced sulfur (i.e., $[\text{HS}^-] > [\text{H}_2\text{S}]$); (Brodeius and Smith, 1976; Reddy and DeLaune,
316 2002).

317 The negative impact of an elevated pH on *C. caroliniana* growth metrics appeared
318 evident in our mesotrophic reservoir treatments where pH remained above 8 (Riemer, 1965;
319 Wilson et al., 2007; Matthews et al., 2013). However, in the eutrophic Lady Bird Lake reservoir
320 we believe *C. caroliniana*'s successful colonization and spread has been possible not just
321 because of favorable water and sediment chemistry and alkalinity, but also related to
322 environmental and hydrological factors. Bickel and Perrett (2014) suggested *C. caroliniana* may
323 have a limited competitive potential relative to established vegetation, but instead thrives in un-
324 vegetated systems. Prior to establishment in 2011, total vegetative coverage in Lady Bird Lake
325 was minimal (e.g., $< 5\%$; Farooqi and De Jesus, 2012). In addition, the rapid spread after 2011
326 coincided with a decline in upriver discharges to the eutrophic reservoir (LCRA;
327 [http://www.lcra.org/water/water-supply/water-management-plan-for-lower-colorado-river-
328 basin/Documents/FINAL-WMP-AsApprovedbyTCEQ-Nov-2015.pdf](http://www.lcra.org/water/water-supply/water-management-plan-for-lower-colorado-river-basin/Documents/FINAL-WMP-AsApprovedbyTCEQ-Nov-2015.pdf); site accessed 7/2016).
329 Lower flows would have benefited *C. caroliniana* by reducing dislodging frequency due to weak
330 anchorage provided by a poorly developed root system in soft sediments (Wilson et al., 2007).

331 Indeed, large discharge events into the Lady Bird reservoir have been observed to precede rapid
332 declines in *C. caroliniana* areal coverage (B. Bellinger, unpubl. data), providing an effective
333 management tool during nuisance growth.

334 At the end of the experiment we observed *C. caroliniana* roots from fewer nodes and less
335 than half the length of roots from *H. verticillata*. *Cabomba caroliniana* can grow as a free-
336 floating mat or rooted through effective uptake of dissolved or sediment-bound nutrients, and is
337 typically observed lacking robust roots (Wilson et al., 2007). Use of nutrients from both sources
338 would have help offset sediment nutrient limitations in our mesotrophic reservoir treatments, and
339 may have contributed to our observed significant *water x sediment* interaction effects on biomass
340 and RGRs (Table 4). Studies of *H. verticillata* have suggested preferential utilization of sediment
341 nutrients through a robust root system (Barko et al., 1988, 1991), though leaf nutrient uptake is
342 common among SAV species (Madsen and Cedergreen, 2002), and must be carried out by *H.*
343 *verticillata* after fragmentation and as roots develop from leaf nodes. In our study, GLM results
344 confirmed the relative importance of sediment nutrients in promoting *H. verticillata* growth
345 (Tables 3 & 4; Barko and Smart, 1986). Though we only planted apical stems, dense root masses
346 were evident from all *H. verticillata* plants. Despite the abundant growth by *H. verticillata* in the
347 eutrophic sediments, we were unable to detect significant changes in sediment nutrient content at
348 the end of the experimental period as might be expected (*sensu* Barko et al., 1988; Racchetti et
349 al., 2010), possibly due to large variability in our data or plant-mediated sequestration of
350 nutrients into surface sediments (Barko et al., 1991).

351 Sediment N concentration has been suggested as an important predictor of *H. verticillata*
352 growth potential (Barko et al., 1988), whereas P concentrations have been linked to *C.*
353 *caroliniana* growth metrics (Bickel and Schooler, 2015). Between reservoirs, N concentrations
354 of sediments and water were significantly greater in the eutrophic Lady Bird Lake whereas P
355 concentrations were similar between the systems. Surprisingly, both reservoirs had an apparent
356 imbalance in sediment N relative to C (i.e., molar C:N >14), and Lady Bird Lake was also C:P
357 imbalanced (i.e., > 186) (Cleveland and Liptzin, 2007) suggesting that molar ratios may not
358 always accurately reflect nutrient availability to vegetation growth potential.

359 Across all treatments we observed *H. verticillata* RGRs approximately 3-4x higher,
360 biomass 2-5x greater, and total stem lengths 5-10x longer than for *C. caroliniana*. Bickel and
361 Perrett (2014), in a small mesocosm study, observed no significant effect of *C. caroliniana* on *H.*
362 *verticillata* growth when planted together, and our data suggest that growth rate-related
363 competition likely would have been a minor factor influencing the relative success of each
364 species in the eutrophic reservoir. *Cabomba caroliniana* is commonly described as a “fast
365 growing species” (e.g., Wilson et al, 2007; Bickel and Schooler, 2015). However, our measured
366 RGRs were only approximately one-third rates measured for *C. caroliniana* plants grown in
367 isolated beakers (0.04 to 0.06 g g⁻¹ d⁻¹; Huang et al., 2016). Our mesocosm conditions, even in
368 the “control” eutrophic Lady Bird Lake treatment, may not have been ideal for growth of *C.*
369 *caroliniana* by not bubbling CO₂ (*cf.* Riemer, 1965), though we did not monitor mesocosm pH
370 after the weekly water collections. Conversely, our measured RGRs for *H. verticillata* fit well
371 with previous studies. For example, our RGRs were comparable or greater than from *H.*
372 *verticillata* planted in sandy sediments supplemented with nutrients (200 to 318 mg g⁻¹ wk⁻¹;
373 Spencer and Anderson, 1986) or from a subtropical Brazilian reservoir (0.035 g g⁻¹ d⁻¹; Bianchini
374 et al., 2010), and were only marginally lower than *H. verticillata* grown in low and high
375 sediment fertility treatments (266 and 450 mg g⁻¹ wk⁻¹, respectively; Van et al., 1999).

376 Concurrent with greater growth of both species in the eutrophic Lady Bird Lake reservoir
377 treatments, we observed greater tissue P content resulting in lower molar C:P and N:P ratios. Our
378 findings thus fit the tenants of the growth rate hypothesis whereby comparatively rapid growth of
379 autotrophs positively correlates with tissue P contents, which is be driven by greater production
380 of P-rich molecules (e.g., nucleic acids, ribosomes) in order to sustain higher growth rates
381 (Sterner and Elser, 2002). Conversely, C- and N- rich cellular components (e.g, chloroplasts,
382 proteins, cells walls) may be produced at a relatively constant ratio regardless of growth rate,
383 resulting in an overall decrease in molar C:P and N:P ratios, and stable C:N ratios (González et
384 al., 2010; Racchetti et al., 2010; Sterner and Elser, 2002). However, tissue P contents from both
385 species were generally lower than critical contents observed from SAV species in nutrient
386 enriched systems (e.g., 0.23–0.75%); *C. caroliniana* more closely matches tissue P contents from
387 a nutrient-poor lake (e.g., 0.10–0.33%) (Gerloff and Kromholz, 1966). As such, our measured
388 molar C:N:P ratios from *C. caroliniana* (440–1,125:25–65:1) were generally greater than have
389 been reported for some SAV (e.g., 370–570:16–29:1; Fernández-Aláez et al., 1999; Demars and
390 Edwards, 2007; Xia et al., 2014), but better matches molar stoichiometry of other SAV species
391 (e.g., 500–1,500:20–70:1; Frost and Hicks, 2012). The imbalanced C:P ratios would be
392 consistent with the observed overall low growth rates. However, *H. verticillata* was even more
393 C:P and N:P imbalanced than *C. caroliniana*, despite faster growth rates. The RGRs we
394 measured for *H. verticillata* were similar or greater than for other SAV ($0.02\text{--}0.10\text{ g g}^{-1}\text{ d}^{-1}$; Li et
395 al., 2013; Richter and Gross, 2013), despite the seeming P-imbalance. While inclusion of root
396 material may disproportionately influence our final nutrient contents relative to initial contents as
397 SAV roots may have less C content but similar or greater P content than leaves (Smart et al.,
398 1994; Li et al., 2013), this fact does not explain the interspecies growth rate and C:P
399 discrepancies.

400 At the end of the experiment we observed declines in *H. verticillata* tissue C contents
401 only in the high pH LAW treatments. *Hydrilla verticillata* is purported to effectively utilize
402 bicarbonate when CO₂ is scarce (Van et al., 1976; Sousa, 2011), though growth has been shown
403 to be negatively influenced by low dissolved inorganic carbon concentrations (Smart et al.,
404 1994). Under suboptimal photosynthetic conditions plants may utilize intracellular C stores
405 (Sterner and Elser, 2002). However, because we do not have direct measures of water chemistry
406 within experimental treatments between weekly water changes, we cannot speculate further.

407 Our inability to show that sediments and water from our eutrophic reservoir had a
408 demonstrable negative impact on *H. verticillata* growth has led to the new hypothesis that
409 grazing pressure may be a significant regulating factor. Turtles, common carp (*Cyprinus carpio*),
410 triploid *C. idella*, and water fowl are common in Lady Bird Lake and have been found to have a
411 consumptive preference for *H. verticillata* among SAV species (Hardin et al., 1984; Pine, 1991;
412 Langeland, 1996; Hossain et al., 2010; Munscher et al., 2015). Indeed, herbivory tends to
413 increase as DMC decreases, and *H. verticillata* DMC measured in this study (7–10%) was lower
414 than for many SAV species previously quantified (7–20%; Elger and Willby, 2003; Lemoine et
415 al., 2009; Wong et al., 2010). Significant grazing pressure in eutrophic Lady Bird Lake, with the
416 conspicuous exception of *C. caroliniana*, is further inferred from our observations of aquatic
417 vegetation (e.g., *Vallisneria americana*, *Potamogeton* spp., *Nymphaea lutea*, *Pontederia*
418 *cordata*) being able to persist only when planted in herbivore exclusion pens (Lesniak, 2015; B.
419 Bellinger, unpubl. data). Future expansion of *H. verticillata* in the reservoir could be an
420 indication that losses or changes have occurred with the herbivore community.

421 The apparent lack of consumption of *C. caroliniana* in the eutrophic Lady Bird Lake is
422 surprising given the observed tissue molar C:N (15) and DCM (5%), though consumptive
423 ambiguity exists with this species (Wilson et al., 2007). The relationships between herbivore
424 consumption and DCM may weaken in the presence of allelochemicals (Kapusinski et al.,
425 2014). Morrison and Hay (2011) suggested increased production of intracellular compounds by
426 *C. caroliniana* due to an invertebrate grazer. More broadly, our observation of the apparent
427 aversion to consumption of *C. caroliniana* has management implications during nuisance
428 growth. Herbicides have also been shown ineffective in controlling *C. caroliniana* (Wilson et al.,
429 2007), thus potentially limiting management options to mechanical removal or flushing in a
430 reservoir system where stocked herbivores are ineffective.

431 **Further research**

432

- 433 • Determine *in situ* (biomass (DW m⁻²) of *H. verticillata* and *C. caroliniana*
- 434 • Determine *in situ* RGRs (mg g⁻¹ d⁻¹) for comparison with mesocosm results
- 435 • Quantify below ground biomass, root-to-shoot ratios
 - 436 ○ How rapidly do roots grow and what is their maximum length and biomass?
- 437 • Track tissue nutrient contents over a growing season
- 438 • Try and determine herbivore densities in Lake Austin and Lady Bird Lake
 - 439 ○ What are the differences in the herbivores and their densities between reservoirs?
- 440 • Try and determine velocities necessary to scour *C. caroliniana*, providing a management
441 option in the event of nuisance growth
- 442 • Quantify *in situ* DIC, CO₂, and HCO₃ concentrations
- 443 • Expand quantification of DMC content to other macrophytes in the reservoirs
- 444 • Test if DIC limitations in the mesocosms affected *C. caroliniana* growth

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447 **Monitoring**

- 448 • Continue to monitor areal extent and biomass of SAV in each reservoir
- 449 • Monitor herbivore densities in each reservoir
- 450 • Track SAV tissue nutrient stoichiometry

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454 **Recommendations**

- 455 • Ensure adequate signage at boat ramps about the importance of cleaning watercraft of any
456 and all potentially attached vegetation

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644 Table 1. Mean water chemistry \pm SD and ranges observed for each reservoir over the study
 645 period. Ortho-phosphorus not shown as all concentrations were below lab reporting limits. NS –
 646 not significant. Nutrient stoichiometry based on molar mass.
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Parameter	n	Lake Austin water		Lady Bird water		T-test
		Mean \pm SD	Range	Mean \pm SD	Range	T_{crit}
Temperature ($^{\circ}$ C)	10	28.5 \pm 2.1	25.6–31.4	27.4 \pm 2.0	24.5–30.9	1.2, NS
Specific conductance (μ s cm^{-2})	10	524.7 \pm 10.0	517.1–546.0	605.5 \pm 19.8	574.9–638.3	-11.5***
DO (mg L^{-1})	10	7.8 \pm 0.4	6.8–8.3	8.4 \pm 0.8	7.3–10.0	-2.1, NS
DO saturation (%)	10	102.3 \pm 7.8	86.0–113.0	108.6 \pm 14.1	88.7–137.0	-1.2, NS
pH	10	8.1 \pm 0.1	7.9–8.3	7.6 \pm 0.1	7.5–7.8	9.4***
SO ₄ ²⁻ (mg L^{-1})	5	30.5 \pm 2.2	28.5–34.0	35.9 \pm 4.8	30.5–43.1	-2.3, NS
TOC	5	4.4 \pm 0.3	4.1–5.0	3.8 \pm 0.9	3.1–5.3	1.5, NS
TP (μ g L^{-1})	5	13.3 \pm 7.3	8.0–112.0	22.9 \pm 11.7	8.0–40.8	-1.6, NS
TKN	5	462.2 \pm 106.4	321.0–544.0	583.4 \pm 167.3	422.0–859.0	-1.4, NS
NO _x -N	5	34.5 \pm 45.0	8.0–112.0	192.0 \pm 58.0	152.0–293.0	-4.8**
TN	5	496.7 \pm 99.1	329.0–572.7	775.4 \pm 174.2	598.0–1,015.0	-3.1*
C: N (molar)	5	10.8 \pm 2.3	8.8–14.7	5.9 \pm 1.2	4.4–7.0	4.2**
C: P	5	1,058.7 \pm 453.3	506.4–1,440.9	540.7 \pm 350.3	337.5–1,163.7	2.0, NS
N: P	5	98.6 \pm 42.5	57.3–150.4	89.8 \pm 43.9	55.0–165.3	0.3, NS

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655 Table 2. Sediment texture and chemistry mean \pm SD ($n = 3$) and ranges observed for each reservoir from the initial collection and at
 656 the end of the experiment for LAW/LAS treatments planted with *C. caroliniana*, and LBW/LBS treatments planted with *H.*
 657 *verticillata*. Abbreviations: LAW – Lake Austin water; LBW – Lady Bird water; LAS – Lake Austin sediments; LBS – Lady Bird
 658 sediments. Nutrient stoichiometry based on molar mass. Where significant 1-way ANOVA differences were observed, superscript
 659 letters indicate pair-wise differences based on Tukey’s HSD post hoc test.
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Parameter	<i>C. caroliniana</i>			<i>H. verticillata</i>	ANOVA (F _{3,8})
	LAS – initial Mean \pm SD	LAW/LAS Mean \pm SD	LBS – initial Mean \pm SD	LBW/LBS Mean \pm SD	
Clay (<0.002 mm) (%)	5.2 \pm 2.1	6.9 \pm 7.8	14.7 \pm 1.2	14.7 \pm 8.0	2.3, NS
Silt (0.002—0.05 mm) (%)	21.3 \pm 4.2 ^a	13.2 \pm 3.1 ^a	40.0 \pm 3.5 ^b	25.2 \pm 13.1 ^{ab}	7.2*
Sand (0.05—2.0 mm) (%)	73.1 \pm 4.5 ^a	75.8 \pm 9.5 ^a	41.9 \pm 2.7 ^b	53.2 \pm 15.6 ^{ab}	8.8**
Bulk density (g cm ⁻³)		1.4 \pm 0.1		0.9 \pm 0.1	
pH	8.1 \pm 0.1 ^a	7.9 \pm 0.1 ^a	7.4 \pm 0.1 ^b	7.5 \pm 0.2 ^b	28.1***
OM (mg kg ⁻¹)	20,280 \pm 11,513 ^{ac}	16,131 \pm 10,813 ^a	108,037 \pm 38,934 ^b	83,097 \pm 24,150 ^{bc}	10.7**
OM (mg cm ⁻³)	28.5 \pm 16.2 ^a	22.7 \pm 15.2 ^a	91.8 \pm 33.1 ^b	70.6 \pm 20.5 ^{ab}	6.6*
C (mg kg ⁻¹)	11,763 \pm 6,678 ^{ac}	9,357 \pm 6,272 ^a	62,667 \pm 22,584 ^b	48,200 \pm 14,008 ^{bc}	10.7**
C (mg cm ⁻³)	16.5 \pm 9.4 ^a	13.2 \pm 8.8 ^a	53.3 \pm 19.2 ^b	41.0 \pm 11.9 ^{ab}	6.6*
TP (mg kg ⁻¹)	153.4 \pm 55.0	242.7 \pm 27.8	272.0 \pm 67.8	257.3 \pm 52.2	3.1, NS
TP (μg cm ⁻³)	215.8 \pm 77.4	341.4 \pm 39.1	231.2 \pm 57.6	218.7 \pm 44.4	3.6, NS
TN (mg kg ⁻¹)	383.5 \pm 177.3 ^a	430.3 \pm 70.5 ^a	2,560.0 \pm 926.7 ^b	1,755.7 \pm 740.5 ^{ab}	9.4**
TN (μg cm ⁻³)	539.4 \pm 249.5 ^a	605.4 \pm 99.1 ^a	2,176.1 \pm 787.7 ^b	1,492.4 \pm 629.4 ^{ab}	6.7*
SO ₄ ²⁻ (mg kg ⁻¹)	80.1 \pm 33.3	52.9 \pm 7.8	116.0 \pm 19.9	107.6 \pm 48.6	3.0, NS
SO ₄ ²⁻ (μg cm ⁻³)	112.6 \pm 46.9	74.4 \pm 11.0	98.6 \pm 16.9	91.5 \pm 41.4	0.8, NS
Sulfide (mg kg ⁻¹)	21.3 \pm 3.1	21.3 \pm 7.8	7.4 \pm 6.4	10.0 \pm 8.8	3.5, NS
Sulfide (μg cm ⁻³)	30.0 \pm 4.3 ^a	30.0 \pm 10.9 ^a	6.3 \pm 5.4 ^b	8.5 \pm 7.5 ^b	9.2**
H ₂ S (mg kg ⁻¹)	1.6 \pm 0.5	2.1 \pm 1.3	2.3 \pm 2.0	2.6 \pm 2.2	0.2, NS
H ₂ S (μg cm ⁻³)	2.3 \pm 0.7	3.0 \pm 1.8	1.9 \pm 1.7	2.2 \pm 1.8	0.1, NS
C: N (molar)	36.0 \pm 16.6	25.5 \pm 17.5	28.6 \pm 1.5	34.0 \pm 7.2	0.4, NS
C: P	191.0 \pm 79.2 ^a	97.5 \pm 60.8 ^a	613.9 \pm 247.4 ^b	498.5 \pm 184.2 ^{ab}	6.9*
N: P	5.9 \pm 2.5 ^{ab}	3.9 \pm 0.3 ^a	21.4 \pm 8.4 ^b	15.9 \pm 8.8 ^{ab}	5.4*

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662 Table 3. Generalized linear model (GLM) output testing between and within subject effects of reservoir water and sediment, and time
 663 main factors and interactions on changes in plant lengths and daily growth rates (from Figure 1A and 1C). Significant differences ($\alpha =$
 664 0.05) indicated in bold italics. Abbreviation: Sed – sediment. Significant interaction effects are graphically displayed in Supplemental
 665 figure 2.
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Species	Metric	Factor	Source	df	F-ratio	p-value
<i>H. verticillata</i>	Length	Between Subjects	Water	1	0.06	0.80
			Sediments	1	149.77	< <i>0.001</i>
			Sed x Water	1	0.82	0.38
			Error	16		
		Within Subjects	Time	5	2203.42	< <i>0.001</i>
			Time x water	5	0.21	0.96
			Time x sed	5	114.77	< <i>0.001</i>
			Time x sed x water	5	0.74	0.59
	Growth Rate	Between Subjects	Water	1	0.04	0.84
			Sediments	1	158.51	< <i>0.001</i>
			Sed x Water	1	0.67	0.43
			Error	16		
		Within Subjects	Time	4	117.43	< <i>0.001</i>
			Time x water	4	1.03	0.40
			Time x sed	4	33.59	< <i>0.001</i>
			Time x sed x water	4	1.02	0.40
Error	63					

<i>C. caroliniana</i>	Length	Between Subjects	Water	1	2.05	0.17
			Sediments	1	18.44	< 0.001
			Sed x Water	1	3.97	0.06
			Error	16		
		Within Subjects	Time	8	1022.89	< 0.001
			Time x water	8	5.12	< 0.001
			Time x sed	8	18.56	< 0.001
			Time x sed x water	8	3.24	< 0.01
	Growth Rate	Between Subjects	Water	1	2.79	0.11
			Sediments	1	25.36	< 0.001
			Sed x Water	1	1.43	0.25
			Error	16		
		Within Subjects	Time	7	1.91	0.08
			Time x water	7	3.11	< 0.01
			Time x sed	7	4.24	< 0.001
			Time x sed x water	7	1.36	0.23
			Error	108		

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689 Table 4. Generalized linear model (GLM) output testing between and within subject effects of reservoir water and sediment main
 690 factors and interactions on changes in final plant length (from Figure 1A and 1C), and dry weight, dry matter content, and relative
 691 growth rate (from Figure 2). Significant differences ($\alpha = 0.05$) indicated in bold italics. Abbreviations: DW – dry weight; DMC – dry
 692 matter content; RGR – relative growth rate; Sed – sediment. Significant interaction effects are graphically displayed in Supplemental
 693 figure 3.
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Species	Metric	Source	df	F-ratio	p-value
<i>H. verticillata</i>	Final length	Water	1	0.01	0.94
		Sediment	1	216.74	< 0.001
		Sed x Water	1	0.31	0.59
		Error	16		
	Final DW	Water	1	1.11	0.31
		Sediment	1	59.07	< 0.001
		Sed x Water	1	0.99	0.33
		Error	16		
	DMC	Water	1	0.05	0.82
		Sediment	1	16.73	< 0.001
		Sed x Water	1	1.64	0.22
		Error	16		
	RGR	Water	1	0.05	0.82
		Sediment	1	67.10	< 0.001
		Sed x Water	1	1.12	0.31
		Error	16		

<i>C. caroliniana</i>	Final length	Water	1	3.39	0.08
		Sediment	1	21.68	< 0.001
		Sed x Water	1	3.22	0.9
		Error	16		
	Final DW	Water	1	5.62	0.031
		Sediment	1	5.80	0.028
		Sed x Water	1	6.98	0.018
		Error	16		
	DMC	Water	1	2.30	0.15
		Sediment	1	0.33	0.57
		Sed x Water	1	14.91	< 0.01
		Error	16		
	RGR	Water	1	8.45	0.01
		Sediment	1	9.26	< 0.01
		Sed x Water	1	3.1	0.097
		Error	16		

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722 Table 5. Plant initial mean \pm SD ($n = 3$) and treatment minimum-maximum ($n = 2$) plant nutrient contents and molar nutrient ratios.
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Plant	Metric	Initial	LBW/LBS	LAW/LAS	LBW/LAS	LAW/LBS
<i>H. verticillata</i>	C (mg g ⁻¹)	488.0 \pm 4.4	424.0 – 493	175.0 – 332	367.0 – 448.0	268.0 – 319.0
	N	33.3 \pm 14.2	26.8 – 28.4	19.5 – 36.5	27.9 – 29.2	24.6 – 25.8
	P	1.0 \pm 0.2	1.0 – 2.0	0.3 – 0.4	0.3 – 0.4	1.8 – 2.1
	C:N (molar)	19.2 \pm 7.4	17.4 – 21.1	5.6 – 19.9	14.7 – 18.7	12.1 – 15.1
	C:P	1,210.3 \pm 219.6	617.4 – 1,148.5	1,474.8 – 2,467.3	2,665.9 – 3,339.0	329.1 – 457.0
	N:P	74.3 \pm 43.8	29.2 – 66.0	124.3 – 263.8	178.3 – 181.9	27.2 – 30.2
<i>C. caroliniana</i>	C (mg g ⁻¹)	441.0 \pm 40.4	369.0 – 428.0	419.0 – 453.0	383.0 – 403.0	371.0 – 507.0
	N	34.8 \pm 6.2	25.2 – 29.7	31.0 – 32.6	29.4 – 29.4	34.5 – 48.9
	P	1.9 \pm 0.4 [†]	1.6 – 2.2	1.0 – 1.1	1.2 – 1.3	1.8 – 3.1
	C:N (molar)	15.2 \pm 3.7	16.8 – 17.1	15.0 – 17.0	15.2 – 16.0	8.8 – 17.1
	C:P	606.5 \pm 55.6	438.5 – 698.6	964.7 – 1,123.3	811.9 – 837.0	425.9 – 540.5
	N:P	41.0 \pm 7.3	25.7 – 41.6	64.4 – 65.9	50.8 – 55.1	24.9 – 61.1

[†]Initial TP content unavailable; contents based on *C. caroliniana* plants grown in LBW/LBS treatment

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Figures

Figure 1. Sampling locations for sediments (stars), water (squares), and plants (triangles) in the Lake Austin and Lady Bird Lake reservoirs along the Colorado River in central Texas, USA (inset). Note: *H. verticillata* was collected from the Colorado River below Lady Bird Lake due to a current absence in the Lake Austin reservoir.

Figure 2. Weekly average \pm 95% confidence intervals ($n = 5$) *Hydrilla verticillata* (left column) A) stem lengths and B) growth rates; and *Cabomba caroliniana* (right column): C) stem lengths and D) growth rates. Where final lengths and growth rates significantly differed, post hoc pair-wise differences based on 95% confidence intervals indicated by different letters. Note scale differences between *H. verticillata* and *C. caroliniana* metrics. Treatments abbreviations: Lady Bird water/Lady Bird sediments (LBW/LBS; closed circles); Lake Austin water/Lake Austin sediments (LAW/LAS; closed squares); Lady Bird water/Lake Austin sediments (LBW/LAS; open triangles); and Lake Austin water/Lady Bird sediments (LAW/LBS; open upside down triangles).

Figure 3. Mean + 95% confidence interval (whisker) *Hydrilla verticillata* (left column) A) dry weight (g); B) dry matter content (DW); and C) relative growth rates (RGRs; $\text{mg g}^{-1} \text{d}^{-1}$), and *Cabomba caroliniana* (right column) D) weight wet (WW; g); E) dry weight (DW; and F); and relative growth rates (RGRs; $\text{mg g}^{-1} \text{d}^{-1}$). Where significant differences in final metrics were found, post hoc pair-wise differences based on 95% confidence intervals indicated by different letters. Treatments abbreviations: Lady Bird water/Lady Bird sediments (LBW/LBS; circles); Lake Austin water/Lake Austin sediments (LAW/LAS; squares); Lady Bird water/Lake Austin sediments (LBW/LAS; triangles); and Lake Austin water/Lady Bird sediments (LAW/LBS; upside down triangles). Note scale differences between *H. verticillata* and *C. caroliniana* metrics.

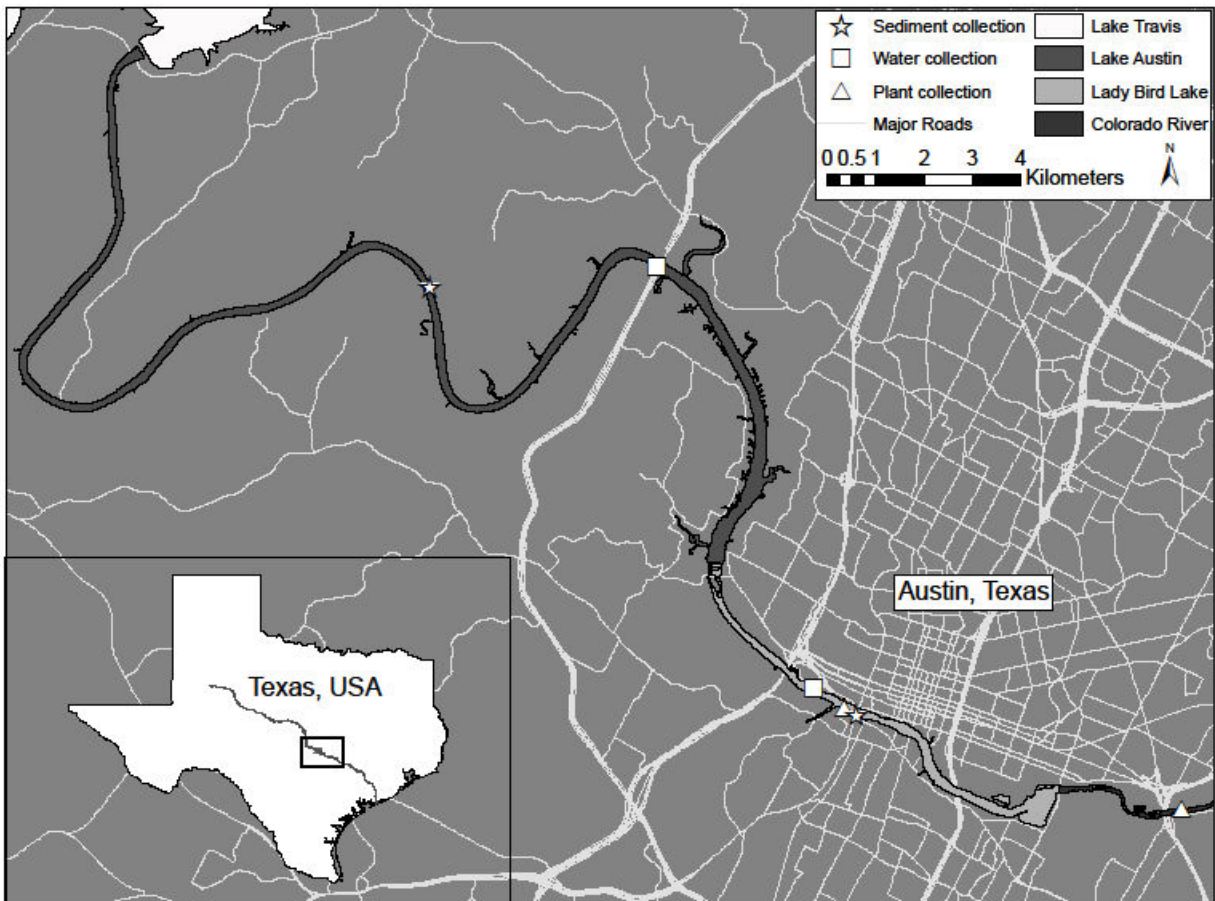


Figure 1

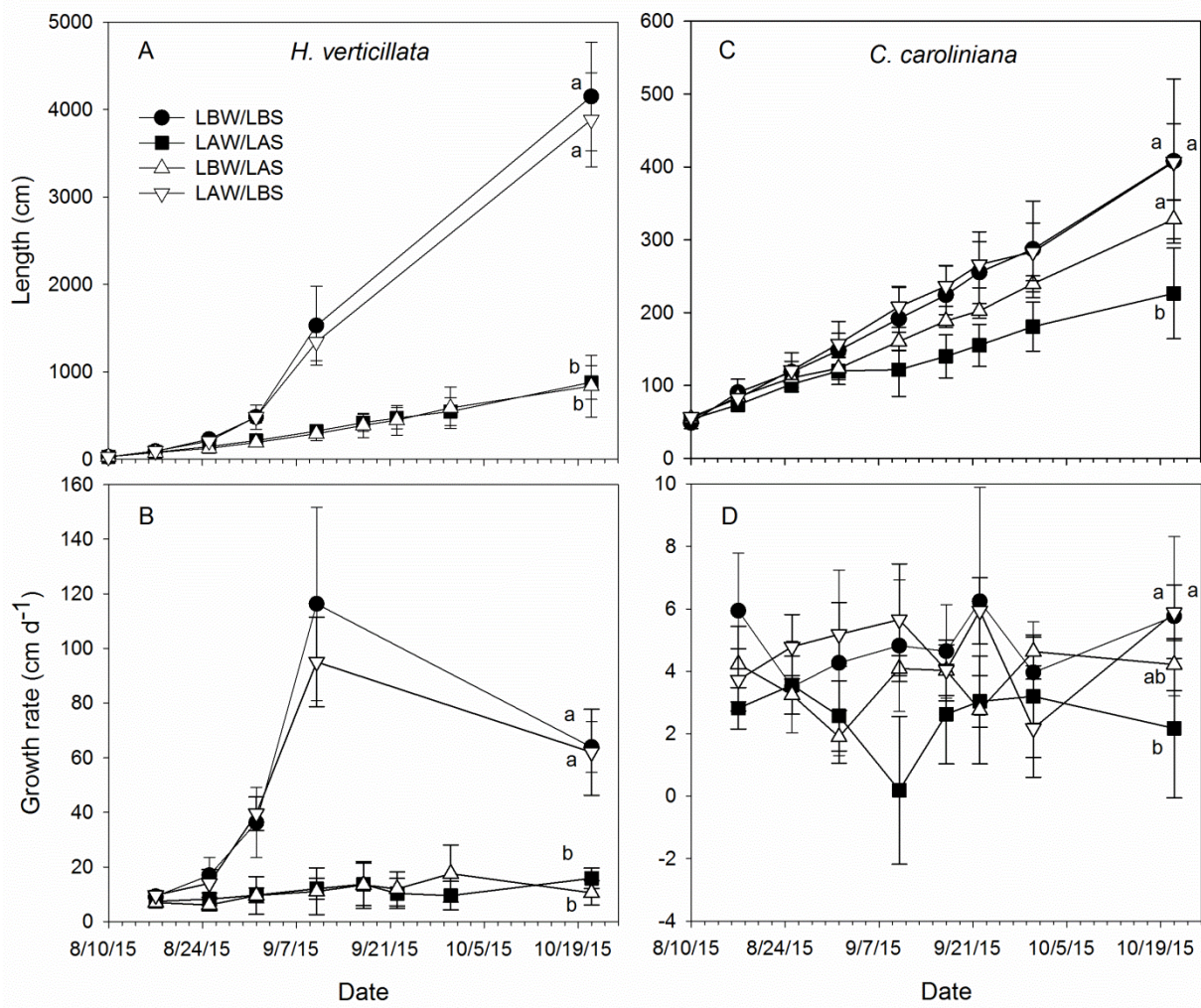


Figure 2

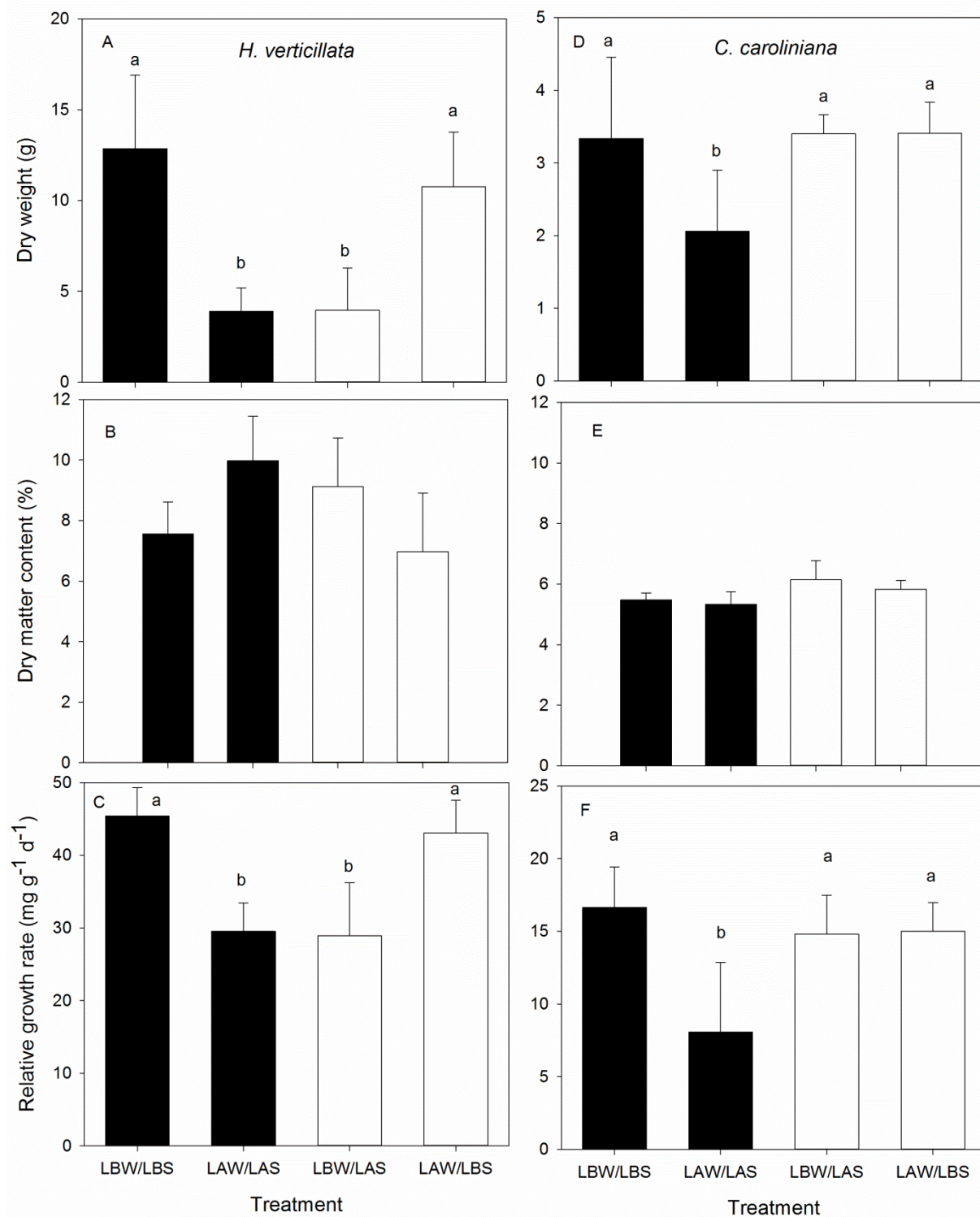
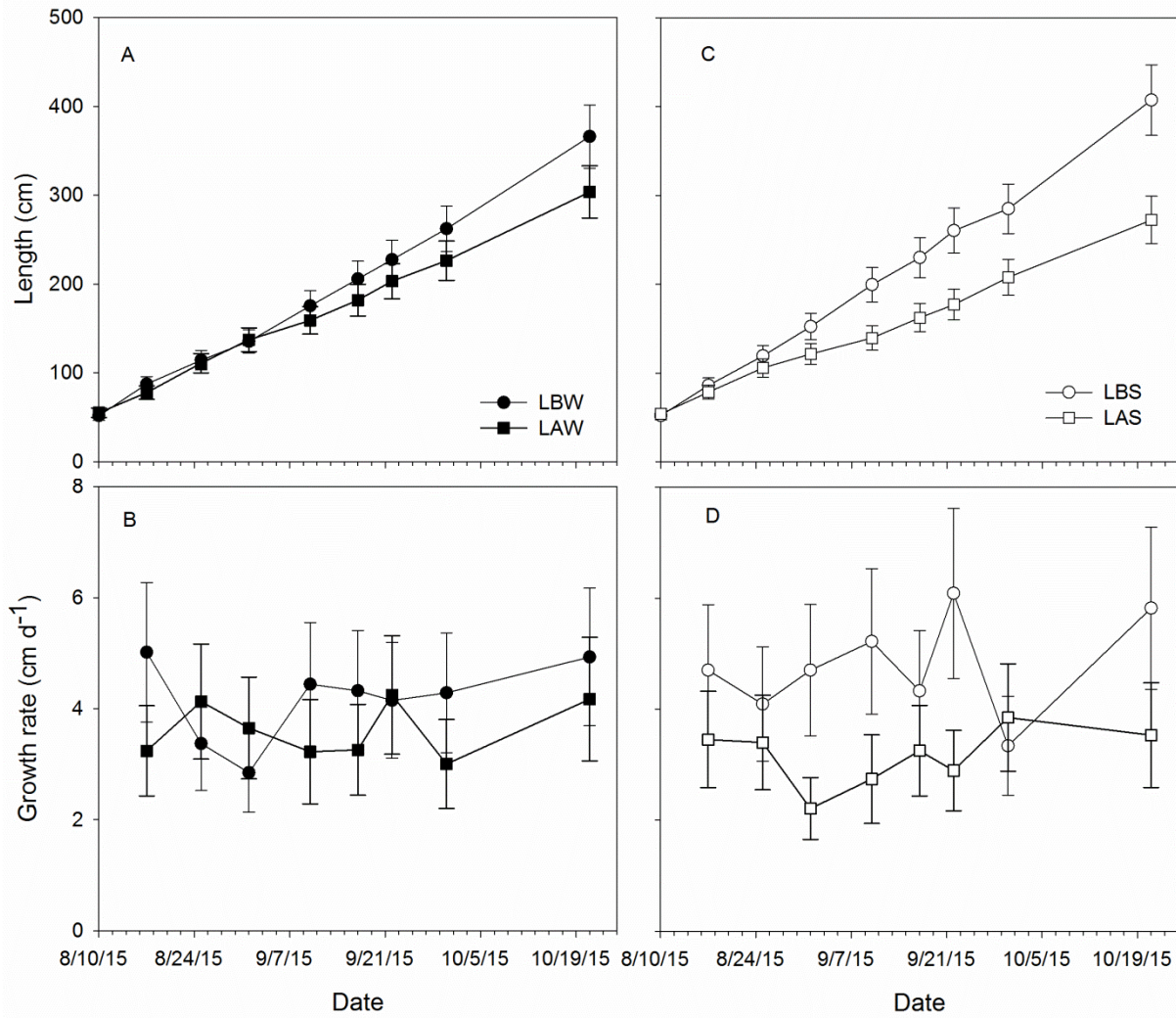


Figure 3

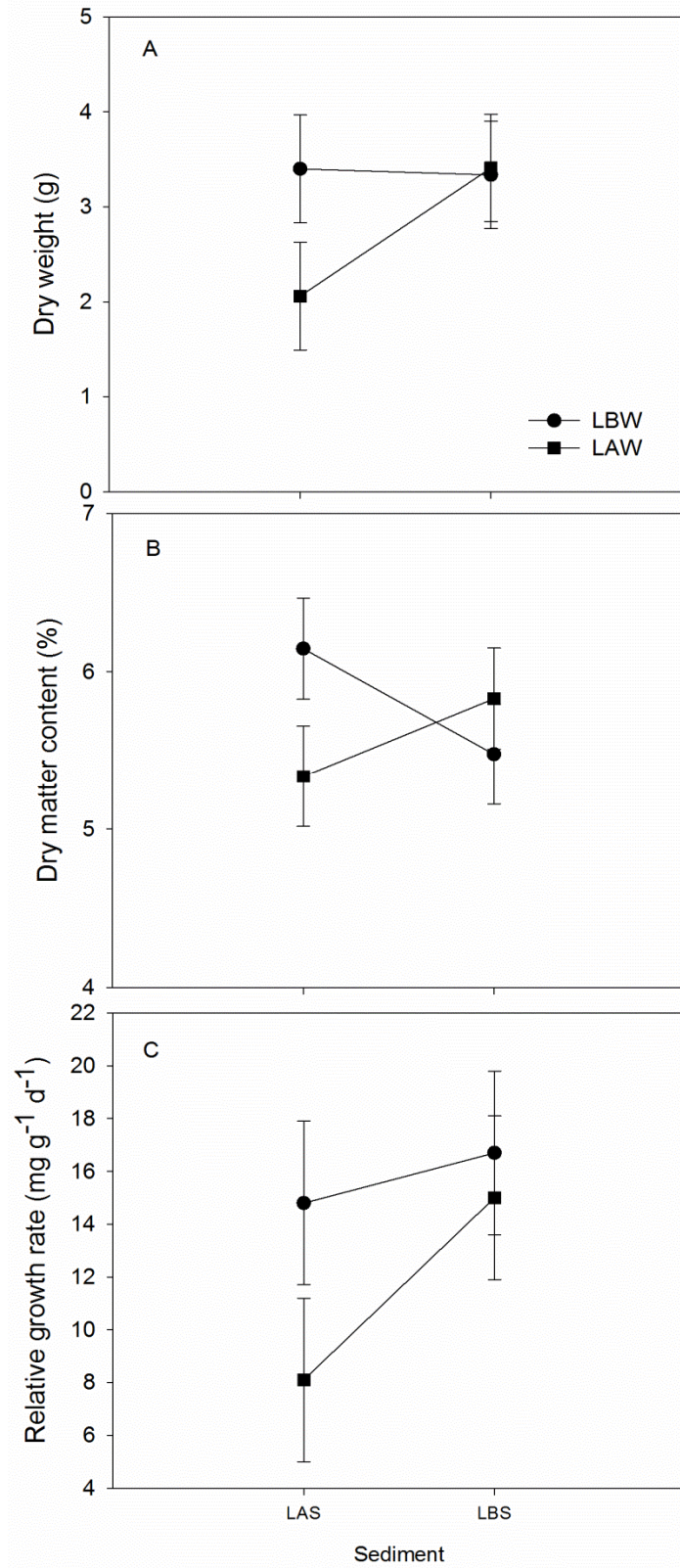
Supplemental Figures

Supplemental figure 1. Interaction effect of reservoir source water on *C. caroliniana* A) length and B) growth rate; and reservoir source sediments on *C. caroliniana* C) length and D) growth rate based on generalized linear model results in Table 3. Time interaction effects with both reservoir water and sediments are not shown.

Supplemental figure 2. Interaction effects of reservoir source water and sediments on *C. caroliniana* A) dry weight; B) dry matter content; and C) relative growth rate based on generalized linear model results in Table 4.



Supplemental figure 1



Supplemental figure 2