

1 Root biomass and production of mangroves surrounding a karstic
2 oligotrophic coastal lagoon

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18 **Abstract**

19 Root production influences a range of belowground processes, such as soil
20 accretion, carbon sequestration and nutrient acquisition. Here, we measured biomass
21 and root production of mangroves surrounding a karstic oligotrophic lagoon that spans a
22 nutrient and salinity gradient. We also measured forest structure and soil
23 physicochemical conditions (salinity, bulk density, carbon, nitrogen (N) and phosphorus
24 (P)) in order to determine factors associated with root production. We tested the
25 following hypotheses: 1) root biomass and production increase at low soil P and N in
26 order to maximize resource utilization, and 2) root biomass and production increase with
27 high interstitial salinity. Root biomass ($947 - 3040 \text{ g m}^{-2}$) and production ($0.46 - 1.85 \text{ g m}^{-2}$
28 d^{-1}) increased where soil P and interstitial salinity were relatively high. Thus, we
29 rejected the first hypothesis and confirmed the second. The larger root fraction (5 - 20
30 mm) was the major contributor to root biomass and production. Our findings suggest that
31 root production and thus capacity for belowground carbon storage in karstic regions,
32 where P is often limiting, is greater where interstitial salinity and P are higher. This
33 contrasts with past assessments indicating that P-deficiency stimulates root growth,
34 suggesting wide variation in belowground responses in mangroves.

35

36 **Keywords:** phosphorus, nitrogen, salinity, belowground production, karst.

37

38 **Introduction**

39 Information on root biomass and production is extremely valuable for
40 understanding ecological processes that occur within mangroves. Root production is
41 associated with soil formation and vertical accretion, and thus the ability of mangroves to
42 keep pace with sea level rise (McKee et al. 2007). Additionally, root production is related
43 to belowground carbon stocks and sequestration rates (Alongi 2011). Field
44 measurements of root biomass and production in different regions and conditions will
45 advance our understanding of belowground dynamics and the response of mangroves to
46 a changing environment.

47
48 Mangrove root production has rarely been investigated under natural conditions,
49 partly due to logistical complications of field measurements (Clough 1992). Coarse root
50 biomass can be estimated using allometric equations (Matsui 1998; Komiyama et al.
51 2005), but direct field measurements of coarse root biomass and production remain
52 extremely challenging. However, the biomass of roots of less than 20 mm in diameter
53 can be measured with relatively simple methods (Vogt et al. 1998). Roots of this size
54 account for more than 50% of the total root biomass (Komiyama et al. 1987) and can be
55 used to estimate root production (Clark et al. 2001) and to investigate its response to
56 environmental factors (e.g. McKee et al. 2007; Castañeda-Moya et al. 2011).

57
58 Mangrove root biomass and production are sensitive to nutrient availability
59 (McKee 2001; Feller et al. 2003; McKee et al. 2007). When nutrients are limited,
60 mangroves can allocate up to 60% of their biomass to root production in order to

61 maximize the capture of limiting nutrients (Komiya et al. 2000; Naidoo 2009).
62 Mangroves growing in phosphorus (P)-depleted soil ($< 0.10 \text{ mg cm}^{-3}$) have higher root
63 biomass compared to sites where soil P is higher (Castañeda-Moya et al. 2011).
64 Nitrogen (N) concentrations can also influence root production; where N is abundant,
65 mangroves reduce root production and invest carbon in stem growth (Lovelock et al.
66 2006a). In soils with a heterogeneous distribution of nutrients, mangroves can invest in
67 root production in nutrient-rich patches compared to nutrient-poor patches (McKee 2001).
68 Therefore, mangroves where nutrients are limited tend to have higher root biomass and
69 production, particularly in soil patches where nutrients are relatively high.

70

71 Mangrove root biomass and production also vary with interstitial salinity, although
72 results are somehow conflicting (Krauss et al. 2013). For example, in trees of *Ceriops*
73 *decandra* and *C. australis* root biomass decreases as salinity increases (Ball 2002). In
74 contrast, trees of *Avicennia marina* and *Aegiceras corniculatum* allocate more carbon in
75 roots relative to shoots with increasing salinity, suggesting an increased root biomass in
76 these species when salinity is high (Ball 1988; Ball et al. 1997). However, increments in
77 root relative to shoot biomass can be interpreted as either an increase in root production
78 or as a decrease in aboveground production (Saintilan 1997). Although it is believed that
79 increments in root production benefit mangroves by increasing water uptake in saline
80 conditions (Ball 1988), this response appears to be variable among mangrove species
81 and environmental conditions (Krauss et al. 2013).

82

83 In this study, we measured biomass and production of live roots (< 20 mm
84 diameter) of mangroves surrounding a coastal lagoon that spans a natural gradient of
85 nutrients and salinity in the Yucatan Peninsula, Mexico. The Yucatan Peninsula has a
86 karstic substrate with a large groundwater discharge and soil that is poor in P, limiting
87 aboveground production (Adame et al. 2012). Mangroves from the inner lagoon are
88 predominately flooded by fresh groundwater (which has low salinity, < 3 ppt), mangroves
89 from the mid portion of the lagoon are flooded by a mixture of marine and fresh
90 groundwater (~ 23 ppt), and mangroves at the mouth of the lagoon are mainly flooded by
91 marine water (~ 34 ppt) (Herrera-Silveira 1996). Different floodwater sources are likely to
92 result in different nutrient inputs and nutrient soil concentrations, which in turn affect
93 mangrove structure and production (Zaldívar-Jiménez et al. 2004; ArandaCicerol et al.
94 2006; Adame et al. 2013). Following the natural environmental gradient, we sampled
95 root biomass and measured annual root production in mangroves from the inner, mid
96 and mouth of the lagoon (Fig. 1). In this study we hypothesized that: 1) Root biomass
97 and production would increase where soil P and N concentrations are low in order to
98 maximize resource utilization; and 2) Root biomass and production would increase in
99 soil with high interstitial salinity. Highest root biomass and production are expected in
100 sites where soil nutrients are low and interstitial salinity is high.

101

102 **Methodology**

103 *Study site*

104 Celestun is a coastal lagoon in the northwest coast of the Yucatan Peninsula (20°
105 42' N; 90° 15'W) (Fig. 1). The lagoon is part of a Biosphere Reserve that includes 81,462

106 ha, of which 19,261 ha are mangroves. The lagoon is connected in its southern portion
107 to the Gulf of Mexico by a 460-m-wide mouth. The substrate of the area is karstic, rich in
108 carbonates and highly permeable. There are no superficial rivers in the area, though
109 numerous springs discharge freshwater into the lagoon, mostly in the northern region
110 (Perry et al. 2009). Celestun has relatively low human disturbances, except for shrimp
111 and crab fishing, and eco-touristic activities (Zaldívar-Jiménez et al. 2004).

112
113 The climate of the region is hot and semi-arid with an annual mean temperature
114 of 28.5°C (mean monthly range of 21 to 35°C) and an annual mean rainfall of 760 mm
115 (García and Mosiño 1992). Three main seasons are recognized: a dry season (March to
116 May; 0-50 mm of rainfall), a rainy season (June to October; > 500 mm) and the north
117 trade wind season locally known as “nortes” (November to February). “Nortes” season is
118 characterized by strong winds (> 80 km h⁻¹), low rainfall (20 - 60 mm) and relatively low
119 temperatures (< 22°C) imposed by low-pressure air masses arriving from the north.
120 Hurricanes also occur in the region, with sixteen storms with winds exceeding 200 km
121 h⁻¹ recorded in the past century (Caribbean Hurricane Network, NOAA, 2011).

122
123 Mangrove forests were selected from the inner, mid and mouth of the lagoon,
124 following the natural salinity gradient (Herrera-Silveira 1996) (Fig. 1). The mangrove
125 forest from the inner lagoon comprises relatively tall trees (~ 13 m) of *Laguncularia*
126 *racemosa* and *Rhizophora mangle*. The forest from the mid lagoon is dominated by
127 medium sized trees (~ 8 m height) of *R. mangle* and *Avicennia germinans*. Finally, the

128 mouth of the lagoon has smaller *R. mangle* and *A. germinans* trees (~ 5 m height). Two
129 plots, parallel to the lagoon, were established at each site (N = 2). Each plot was 20 m x
130 30 m (600 m² per plot) at the inner and mid lagoon; at the mouth of the lagoon, the plot
131 size was smaller due to higher tree density (10 m x 30 m, 300 m² per plot). For each plot,
132 interstitial salinity, soil physicochemical characteristics (bulk density, P, carbon, and N),
133 forest structure, root biomass, and annual root production were measured as described
134 below.

135

136 *Interstitial salinity and soil characteristics*

137 Interstitial salinity was measured monthly during 2006 - 2007. Interstitial water
138 was extracted from the ground at a depth of 30 cm using a syringe and an acrylic tube.
139 The syringe was rinsed twice before obtaining a clear water sample from which salinity
140 was measured using an YSI-30 multiprobe sensor (YSI, Xylem Inc. Ohio, USA).

141

142 At each plot, two soil cores were taken (N = 12 cores) using a stainless-steel
143 hand corer of 10 cm in diameter and 35 cm in length. The soil core was divided in 4
144 subsamples according to depth (0 - 10 cm, 10 - 20 cm, 20 - 30 cm, 30 - 35 cm).
145 Samples were oven-dried at 60°C for 5 days and weighed. Bulk density was measured
146 as the dry weight of the sample divided by its volume. Soil total inorganic P was
147 determined as orthophosphates following the methods described by Aspila et al. (1976)
148 and Parsons et al. (1984). Briefly, 0.2 g of dry soil was combusted at 550°C for 2 h,
149 followed by an extraction with 1N HCl for 16 hours at 150 rpm. After extraction, samples
150 were filtered and read at 885 nm using the colorimetric method from the reaction of

151 ortophosphates with ammonium-molybdate. Soil N and carbon were measured with an
152 Elemental Analyzer (FlashEA 1112, Thermo Quest, Milan, Italy).

153

154 *Forest structure*

155 Species composition, tree density, and basal area were quantified through
156 measurements of species and diameter at breast height (1.3 m) of all trees rooted within
157 each plot (Cintrón and Schaeffer Novelli 1984). For trees of *R. mangle*, the diameter was
158 not measured at breast height, but at the main branch above the highest prop root,
159 following guidelines by Dahdouh-Guebas and Koedam (2006). Forest density (trees ha⁻¹)
160 was extrapolated according to plot size.

161

162 *Root biomass*

163 Four cores were taken within each plot (N = 24) with a stainless steel-corer in a
164 similar way as cores taken for nutrient analyses (see above). The cores were 10 cm in
165 diameter and 35 cm in depth. Each core was kept cold and taken to the laboratory
166 where it was rinsed with fresh water through a 1mm-sieving mesh to separate roots from
167 soil and other particulate matter. Roots were submerged in freshwater; floating live roots
168 were handpicked from sinking dead roots as suggested by Castañeda-Moya et al.
169 (2011). Live roots were separated in three fractions: fine (< 2 mm diameter), medium (2 -
170 5 mm diameter), and large (> 5 mm diameter) and weighed before and after being oven-
171 dried at 60°C (Castañeda-Moya et al. 2011). Using this technique, we measured
172 biomass of live roots with a maximum diameter of 20 mm from the shallow root zone (0 -
173 35 cm), which is the largest and most active portion of the roots (Castañeda-Moya et al.

174 2011). Data on root biomass are shown as grams of dry biomass per meter square (g m⁻²).
175

176

177 *Root production*

178 To measure annual root production, we used the in-growth core technique (Vogt
179 et al. 1998), which was modified for application to mangroves (McKee et al. 2007).

180 Briefly, in-growth cores of 10 cm x 35 cm made of flexible synthetic mesh and with a

181 mesh size opening of 5 mm were filled with pre-sieved sphagnum peat moss. The

182 commercial peat had similar characteristics of mangrove soils at Celestun, such as bulk

183 density (0.14 g cm⁻³ in Celestun vs. 0.15 g cm⁻³ in the commercial peat) and total N (1.3

184 vs. 1.7 mg cm⁻³); however, total carbon was lower at Celestun (32 vs. 71 mg cm⁻³). The

185 prefilled cores were buried in holes dug with the stainless steel corer. At each site, 16 in-

186 growth cores were installed (8 per plot; N = 48) (April to May, 2006). Half of the cores (4

187 from each plot) were harvested after 6 months (T1) (December, 2006) and the other half

188 after a year (T2) (July, 2007). Root production was measured as the difference in

189 biomass between T0 and T1, and between T1 and T2. Similar to the determination of

190 root biomass (see above), roots were sieved, submerged in freshwater, and floating live

191 roots were handpicked from sinking dead roots. Root turnover (yr⁻¹) for each root size

192 class was measured as root productivity divided by biomass, and root longevity (yr) as

193 the inverse of root turnover (Castañeda-Moya et al. 2011). Root production is shown as

194 grams of dry biomass per meter square of soil per day (g m⁻² d⁻¹).

195

196 *Statistical analysis*

197 A two-way analysis of variance (ANOVA) was used to determine significant
198 differences for soil characteristics among sites (inner, mid and mouth of the lagoon) and
199 depths (0 -10 cm, 10 -20 cm, 20 - 30 cm, 30 - 35 cm). Two-way ANOVA was also used
200 to determine differences in root biomass, root production and turnover rates among sites
201 and size classes (< 2 mm, 2 - 5 mm, > 5 mm). For ANOVA analyses, site, depth and
202 size class were fixed factors, and plots were nested within site. Differences in salinity
203 measured for two years were tested using repeated measures ANOVA, where site was
204 the repeated measurement over time (2006 and 2007). Due to violations on the
205 assumption of sphericity required for repeated measurement ANOVA, we used the
206 Greenhouse-Geisser correction (Grieve 1984). Normality was assessed using probability
207 plots, histograms and Shapiro-Wilk tests. When significant differences were found, pair-
208 wise comparisons were explored using Bonferroni post-hoc tests. Linear regression
209 analyses and stepwise multiple regression analyses were performed in order to test the
210 relationship between root biomass/production with salinity and soil physicochemical
211 characteristics. For regression analyses, plots were used as separate experimental units
212 to increase sample size. Additionally, a multivariate analysis of variance (MANOVA) was
213 performed to assess the relationship between root biomass and root production with
214 salinity and soil physicochemical characteristics. Analyses were performed with Prism
215 ver 5.0 (GraphPad Software, La Jolla, CA, USA) and the R software package, functions
216 *glm* and *manova* (R Development Core Team 2008). For all statistical analyses, we
217 used a significance value of $\alpha < 0.05$. Throughout the results, all values are shown as
218 mean \pm standard error.

219

220 **Results**

221 *Interstitial salinity and soil physicochemical characteristics*

222 Interstitial salinity was significantly different among sites with 26.9 ± 0.6 ppt, 37.1
223 ± 0.6 ppt and 50.2 ± 0.9 ppt for the inner, mid and mouth of the lagoon, respectively
224 ($F_{1,39, 65.5} = 295.7, p < 0.0001$) (Table 1, 2). Bulk density was lower in the inner lagoon
225 ($0.10 \pm 0.01 \text{ g cm}^{-3}$) compared to the mid ($0.14 \pm 0.01 \text{ g cm}^{-3}$) and mouth of the lagoon
226 ($0.14 \pm 0.02 \text{ g cm}^{-3}$) ($F_{2, 36} = 4.05, p = 0.02$) (Table 1, 2).

227
228 The mean carbon concentration of the soil profile (0 - 35 cm in depth) was similar
229 among the inner ($27.0 \pm 1.22 \text{ mg cm}^{-3}$), mid ($29.3 \pm 2.84 \text{ mg cm}^{-3}$) and mouth of the
230 lagoon ($32.9 \pm 2.36 \text{ mg cm}^{-3}$) ($F_{2,36} = 2.31, p = 0.11$). Among sites, carbon values were
231 significantly lowest in the soil horizon between 30 - 35 cm deep ($F_{3, 36} = 5.24, p = 0.004$)
232 (Table 1, 2).

233
234 Mean soil N (0 - 35 cm in depth) was $1.34 \pm 0.11 \text{ mg cm}^{-3}$, with similar values
235 between the inner ($1.04 \pm 0.08 \text{ mg cm}^{-3}$), mid ($1.75 \pm 0.34 \text{ mg cm}^{-3}$) and mouth of the
236 lagoon ($1.41 \pm 0.19 \text{ mg cm}^{-3}$). N was not significantly different among soil horizons
237 (Table 1, 2).

238
239 Finally, mean soil P (0 - 35 cm in depth) was $0.11 \pm 0.01 \text{ mg cm}^{-3}$. Surface soil P
240 (0 -10 cm) at the mouth of the lagoon was significantly different from the surface soil P at
241 the inner and mid lagoon (Site: $F_{2, 36} = 6.40, p = 0.004$; Depth: $F_{3, 36} = 4.50, p = 0.008$;

242 Site x depth: $F_{6, 36} = 2.81$, $p = 0.023$). See Supplementary Materials (Table S1) for
243 minimum and maximum values of all soil physicochemical characteristics.

244

245 *Forest structure*

246 The forest from the inner lagoon had the tallest trees (12.3 ± 0.8 m), largest basal
247 area (40.5 ± 1.0 m² ha⁻¹) and lowest density ($1,108 \pm 75$ trees ha⁻¹), and was dominated
248 by *L. racemosa* (55%) and *R. mangle* (35%). The forest in the mid lagoon had
249 intermediate values of tree height, basal area and tree density (7.7 ± 0.2 m; 23.6 ± 0.1
250 m² ha⁻¹; $1,467 \pm 117$ trees ha⁻¹, respectively) and was mainly composed of *R. mangle*
251 (45%) and *A. germinans* (35%). Finally, the forest at the mouth of the lagoon had the
252 shortest trees (5.3 ± 0.0 m), moderate basal area (29.2 ± 1.4 m² ha⁻¹) and high density
253 of trees ($2,450 \pm 750$ trees ha⁻¹) of *R. mangle* (52%) and *A. germinans* (31%).

254

255 *Root biomass*

256 Mean root biomass was $1,705.6 \pm 669.2$ g m⁻². Total biomass was significantly
257 different among sites and between size classes, with highest biomass of roots > 5mm
258 measured at the mouth of the lagoon (Site: $F_{2, 27} = 7.98$, $p = 0.0019$; Size class: $F_{2, 27} =$
259 11.3 , $p = 0.003$; Site x Size class: $F_{4, 27} = 4.14$, $p = 0.009$) (Fig. 2a; Table 3).

260

261 *Root production*

262 After six months of field deployment, root production was not significantly different
263 among sites. However, after one year, root production was significantly different among
264 sites and size class with highest root production in roots > 5mm from the mouth of the

265 lagoon (Site: $F_{2,27} = 19.3$, $p < 0.0001$; Size class: $F_{2,27} = 23.2$, $p < 0.0001$; Site x Size
266 class: $F_{4,27} = 3.65$, $p = 0.016$) (Fig. 2b; Table 3 and 4). Root production was significantly
267 correlated with root biomass ($R^2 = 0.69$, $p = 0.04$).

268

269 *Turnover rates and root longevity*

270 Mean turnover rates were $0.38 \pm 0.10 \text{ yr}^{-1}$ in fine roots, $0.19 \pm 0.04 \text{ yr}^{-1}$ in medium
271 sized roots and $0.33 \pm 0.06 \text{ yr}^{-1}$ in large roots, which corresponds to longevities of $6.1 \pm$
272 1.7 yr , $1.2 \pm 2.9 \text{ yr}$ and $5.9 \pm 2.4 \text{ yr}$, respectively. When comparing among sites, root
273 turnover rates were $0.39 \pm 0.08 \text{ yr}^{-1}$, $0.19 \pm 0.04 \text{ yr}^{-1}$ and $0.33 \pm 0.10 \text{ yr}^{-1}$ for the inner,
274 mid and mouth of the lagoon, respectively. Root longevity was $6.08 \pm 1.17 \text{ yr}$, $11.01 \pm$
275 2.24 yr and $6.71 \pm 1.64 \text{ yr}$ for the inner, mid and mouth of the lagoon, respectively.
276 However, differences in turnover rates and root longevity among size class or sites were
277 not significant (Table 3).

278

279 *Root biomass and production vs. forest and soil characteristics*

280 Root biomass significantly increased with soil P ($R^2 = 0.75$, $p = 0.02$, Fig. 3a),
281 interstitial salinity ($R^2 = 0.66$, $p = 0.04$, Fig. 3b) and forest density ($R^2 = 0.81$, $p = 0.01$,
282 Fig. 3c). Thus, highest root biomass was measured at dense forests with soils rich in P,
283 with relatively high interstitial salinity. Root biomass exhibited no relationship with soil N
284 ($R^2=0.15$, $p=0.40$, Fig. 3d).

285

286 Similarly, root production was positively correlated with soil P ($R^2 = 0.89$, $p =$
287 0.004 , Fig. 4a) and interstitial salinity ($R^2=0.92$, $p=0.002$, Fig. 4b). Multiple regression
288 demonstrated that P and salinity explained 96% of the variation in root production (Root
289 production = $-1.69 + 1.40 \times 10^5 P + 3.42 \times 10^{-5}$ Interstitial salinity; $p < 0.05$ for each
290 coefficient). The MANOVA, in which root biomass and root production were grouped as
291 one response variable, demonstrated a significant effect for P in the soil profile ($p =$
292 0.02), however no significant effects were detected for salinity or N.

293

294 **Discussion**

295 Coarse root biomass and production (> 5 mm diameter) in mangroves
296 surrounding the karstic oligotrophic Celestun Lagoon were higher at the mouth of the
297 lagoon compared to the mid and inner lagoon and were associated with increased soil P,
298 increased interstitial salinity and high tree density.

299

300 The positive relationship between root biomass and production with P increments
301 rejects the first hypothesis that predicted that root biomass and production would
302 increase at low nutrient concentrations in order to maximize resource utilization. This
303 hypothesis was partly based on a study of mangroves in The Everglades, Florida, where
304 highest root biomass was found in soils poor in P ($< 0.25 \text{ mg cm}^{-3}$; Castañeda-Moya et
305 al. 2011). Soil P concentrations in Celestun are similar to those in The Everglades,
306 ranging from 0.03 to 0.20 mg cm^{-3} . However, the combination of high soil P and high
307 salinity at the mouth of the Celestun Lagoon may account for the differences found in
308 root production of mangroves at this location compared to those at The Everglades.

309 Additionally, mangroves from the Everglades have a distinct hydroperiod that may
310 influence soil P directly and root production indirectly. High root production is a
311 mechanism for tolerating stress associated to highly saline conditions (Chapin 1991).
312 For example, trees of *Avicennia marina* increase root production when water demand
313 increases, thereby maintaining water uptake at high salinity (Ball 1988). Additionally, P
314 increases the hydraulic conductivity of mangrove stems when growing under highly
315 saline conditions (Lovelock et al. 2006a, 2006b). Therefore, high root biomass and
316 production may be facilitated by soil P and might be necessary to maintain appropriate
317 water uptake in mangroves from the mouth of the lagoon where salinity is relatively high
318 (> 50 ppt).

319
320 Our results from Celestun Lagoon, interpreted in the context of other studies,
321 support the idea that root production in mangroves responds to multiple variables acting
322 synergistically, from which nutrients, salinity, and tidal inundation appear to be
323 particularly important (McKee et al. 2007; Castañeda-Moya et al. 2011). For example, P
324 additions in mangroves in Twin Cays, Belize caused an increase in root production
325 (similar to our results) but only in interior, not fringing, mangroves (McKee et al. 2007).
326 Interior forests have infrequent tidal inundation and high salinity, conditions similar to
327 those observed at the mouth of Celestun Lagoon. The mangroves at the mouth of
328 Celestun Lagoon are inundated for less hours and at lower depths (mean depth of 3 cm),
329 compared to mangroves from the mid and inner lagoon (7 and 9 cm, respectively)
330 (Herrera-Silveira et al. 2010). Therefore, mangroves that are seldom inundated and have
331 high salinity may be more sensitive to P concentrations than forests that are frequently

332 inundated and have lower salinity.

333

334 Contrary to P, root biomass and production did not exhibit a significant response
335 to N increments; however, root biomass decreased with increased soil N in some sites.
336 Fertilization with N typically causes higher investment in shoots compared to roots;
337 therefore, trees growing under high N conditions are more vulnerable to hydraulic failure
338 when salinities are high (Lovelock 2009). In Celestun Lagoon, mangrove soils from the
339 mid portion of the lagoon, where N concentration is highest, had low root biomass and
340 production. These trees are close to the town of Celestun (population of 6,269), which
341 produces sewage effluent rich in nitrates that leach into the mangroves (Herrera-Silveira
342 and Morales-Ojeda 2009). However, the effect of soil N was not evident in all of our sites,
343 supporting the notion that root production responds stronger to P than to N increments
344 (Nye and Tinker 1977; McKee 2001). N exhibits larger diffusion coefficients ($10^{-5} - 10^{-7}$
345 $\text{cm}^2 \text{s}^{-1}$) compared to P ($10^{-9} \text{cm}^2 \text{s}^{-1}$) and thus, is strongly adsorbed in the soil and is
346 less available for plant uptake. Finally, soil nutrient concentrations might have a different
347 influence in root production compared to pore water nutrients, which represent a more
348 readily available source of nutrients to plants. Future studies, including pore water
349 nutrient concentrations, might clarify the importance of N loads on root production in
350 Celestun mangroves.

351

352 Root biomass and production were clearly influenced by forest structure, with the
353 highest values measured in dense forests. Similar results have been observed in
354 Thailand, where the highest root biomass was found within a dense *Rhizophora* spp.

355 forest, compared to that of less dense *Bruguiera* spp. and *Sonneratia* spp. forests
356 (Komiya et al. 1987). The production of roots may be a strategy to acquire limited
357 resources (water and nutrients) where high density of trees and competition occurs
358 (López et al. 1998). On the other hand, species composition, which is a determinant of
359 root production in some locations (Gleason and Ewel 2002), was not a primary factor in
360 our study. Stands of different species composition (i.e. the mid lagoon was dominated by
361 *A. germinans* and *R. mangle* and the inner lagoon by *L. racemosa* and *R. mangle*) had
362 similar root production. Forest structure, including tree density, in Celestun is a reflection
363 of the environmental variability within the lagoon (Zaldívar-Jiménez et al. 2004). In
364 addition to salinity and nutrients, the hydroperiod and storm exposure directly influence
365 the forest structure within Celestun (Herrera-Silveira et al. 2010), and thus, root biomass
366 and production.

367

368 Root production ($0.46 - 1.85 \text{ g m}^{-2} \text{ d}^{-1}$) in Celestun was within the ranges of
369 oligotrophic mangrove sites. In comparison, root production was $0.71 - 1.28 \text{ g m}^{-2} \text{ d}^{-1}$ in
370 The Everglades, Florida (Castañeda-Moya et al. 2011), $0.11 - 1.10 \text{ g m}^{-2} \text{ d}^{-1}$ in Twin
371 Cays, Belize (McKee et al. 2007) and 0.05 to $3.14 \text{ g m}^{-2} \text{ d}^{-1}$ in Southwest Florida (McKee
372 and Faulkner 2000). Differences in root production across regions will affect processes
373 within mangroves, with higher belowground carbon accumulation, increased soil
374 respiration, and heightened capacity to adjust to sea level rise in sites with higher root
375 production (Lovelock et al. 2006c; McKee et al. 2007). It must be noted that the in-
376 growth technique used to estimate root production has known limitations. For example,
377 physically and chemically reconstructing the root-free soil environment is challenging

378 and determining how root production might differ in a root-free zone from that already
379 occupied by roots is difficult (Vogt et al. 1998). Nevertheless, the in-growth core
380 technique has proven successful for estimating root production and for comparing
381 production rates across different environmental settings (e.g. Gleason and Ewel 2002;
382 Cahoon et al. 2003; Castañeda-Moya et al. 2011).

383
384 Large roots (> 5 mm diameter) were the most abundant size class observed at
385 Celestun Lagoon. Longevity and turnover rates were similar among sites and size
386 classes. Similarly, Castañeda-Moya et al. (2011) found a major contribution of larger
387 root size class (> 5 mm diameter) to total root biomass in The Everglades. They also
388 found that root turnover rates varied across sites, and attributed these differences to soil
389 P and inundation frequency, both of which affect root decomposition rates (Poret et al.
390 2007). This hypothesis may imply that while production of roots > 5 mm is highest at the
391 mouth of Celestun Lagoon for this size class, decomposition is also high, resulting in
392 similar turnover rates across the Lagoon. Finally, root turnover rates in the Everglades
393 decreased with larger size class, suggesting that larger roots in mangroves are less
394 vulnerable to stresses and exhibit slower metabolic rates than finer ones. Our data do
395 not support this hypothesis. Results from Castañeda-Moya et al. (2011) were obtained
396 during a 3-year period, and it is possible that longer periods of time (> 1 yr) allow for
397 more precise measurements to test differences among longevity and turnover rates
398 among size classes.

399
400 We conclude that in Celestun Lagoon, tree density, salinity and soil P can explain

401 root biomass and production. Higher root biomass and production in soils with relatively
402 high P may allow trees to tolerate stresses imposed by saline conditions. Root biomass
403 and production were less sensitive to soil N, although this nutrient might affect
404 production where loads are very high, such as forests close to sewage effluents.
405 Aboveground productivity of mangroves in Celestun Lagoon and across the Yucatan
406 Peninsula is P limited (Adame et al. 2012); our results show that belowground
407 production also appears to be highly sensitive to changes in soil P concentrations.

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418

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548 **Tables**

549 **Table 1.** Soil physicochemical characteristics of fringe mangroves from the inner, mid
 550 and mouth of Celestun Lagoon, Yucatan, Mexico. C = carbon; N = nitrogen; P =total
 551 phosphorus. Interstitial salinity was measured at a depth of 30 cm.

Site	Salinity (ppt)	Depth (cm)	Bulk			
			density (g cm ⁻³)	C (mg cm ⁻³)	N (mg cm ⁻³)	P (mg cm ⁻³)
Inner	26.9 ± 0.6	0-10	0.12 ± 0.03	31.7 ± 3.32	1.26 ± 0.31	0.09 ± 0.01
		10-20	0.10 ± 0.01	28.6 ± 0.05	1.12 ± 0.05	0.09 ± 0.01
		20-30	0.11 ± 0.06	27.4 ± 6.43	0.92 ± 0.38	0.09 ± 0.04
		> 30	0.07 ± 0.01	19.3 ± 0.09	0.78 ± 0.10	0.06 ± 0.00
		Mean	0.10 ± 0.01	27.0 ± 1.22	1.04 ± 0.08	0.08 ± 0.00
Mid	37.1 ± 0.6	0-10	0.10 ± 0.02	26.2 ± 3.15	1.96 ± 1.03	0.09 ± 0.00
		10-20	0.16 ± 0.04	34.7 ± 9.87	1.33 ± 0.65	0.12 ± 0.01
		20-30	0.17 ± 0.01	28.6 ± 2.76	1.72 ± 1.10	0.10 ± 0.01
		> 30	0.15 ± 0.01	25.3 ± 3.19	1.63 ± 1.16	0.07 ± 0.00
		Mean	0.14 ± 0.01	29.3 ± 2.84	1.75 ± 0.33	0.10 ± 0.01
Mouth	50.2 ± 0.9	0-10	0.19 ± 0.01	42.7 ± 0.09	1.52 ± 0.00	0.21 ± 0.03
		10-20	0.14 ± 0.00	38.4 ± 1.86	1.83 ± 0.00	0.13 ± 0.01
		20-30	0.10 ± 0.01	24.5 ± 2.32	1.16 ± 0.21	0.08 ± 0.01
		> 30	0.13 ± 0.01	25.0 ± 0.01	0.95 ± 0.04	0.09 ± 0.00
		Mean	0.14 ± 0.02	32.9 ± 2.36	1.41 ± 0.19	0.13 ± 0.01

552 **Table 2.** Results of the ANOVA statistical tests for interstitial salinity (ppt), bulk density
 553 (g cm^{-3}), soil carbon (C) (g cm^{-3}), nitrogen (N) (g cm^{-3}) and total phosphorus (P) (g cm^{-3});
 554 n.s. = not significant ($p > 0.05$). DF_n = Degrees of freedom numerator; DF_d = Degrees
 555 of freedom denominator.

Variation source	<i>F</i> (DF _n , DF _d)	<i>p</i>
Salinity		
Site	(1.39, 65.5) = 295.7	< 0.0001
Bulk density		
Site	(2, 36) = 4.05	0.02
Depth	(3, 36) = 0.38	n.s.
Site x Depth	(6, 36) = 2.17	n.s.
C		
Site	(2, 36) = 2.31	n.s.
Depth	(3, 36) = 5.24	0.004
Site x Depth	(6, 36) = 1.58	n.s.
N		
Site	(2, 36) = 1.12	n.s.
Depth	(3, 36) = 0.32	n.s.
Site x Depth	(6, 36) = 0.20	n.s.
P		
Site	(2, 36) = 6.40	0.004
Depth	(3, 36) = 4.50	0.008
Site x Depth	(6, 36) = 2.81	0.023

556

557 **Table 3.** Results of the ANOVA statistical tests for root biomass (g m^{-2}), root production
 558 ($\text{g m}^{-2} \text{d}^{-1}$), turnover rates (yr^{-1}) and longevity (yr); n.s. = not significant ($p > 0.05$). DF_n =
 559 Degrees of freedom numerator; DF_d = Degrees of freedom denominator.

Variation source	<i>F</i> (DF _n , DF _d)	<i>p</i>
Root biomass		
Site	(2, 27) = 7.98	0.0019
Size class	(2, 27) = 11.3	0.003
Site x Size class	(4, 27) = 4.14	0.009
Root production		
Site	(2, 27) = 19.3	< 0.0001
Size class	(2, 27) = 23.2	< 0.0001
Site x Size class	(4, 27) = 3.65	0.016
Turnover rates		
Site	(2, 63) = 0.28	n.s.
Size class	(2, 63) = 1.57	n.s.
Site x Size class	(4, 63) = 1.31	n.s.
Longevity		
Site	(2, 63) = 0.68	n.s.
Size class	(2, 63) = 3.09	n.s.
Site x Size class	(4, 63) = 2.52	n.s.

560

561

562 **Table 4.** Fine root production after 6 months (T1) and one year (T2) in fringe mangroves
 563 from the inner, mid and mouth of Celestun Lagoon, Yucatan, Mexico. Root production
 564 corresponds to the first 0 - 35 cm from the surface soil. Mean root production refers to
 565 the production of root biomass of all size classes from two plots within each site.

Site	Size class (mm)	Production T1 (g m ⁻² d ⁻¹)	Production T2 (g m ⁻² d ⁻¹)
Inner	< 2	0.30 ± 0.10	0.11 ± 0.02
	2 – 5	0.35 ± 0.13	0.11 ± 0.04
	> 5	0.76 ± 0.35	0.24 ± 0.13
	Mean	0.47 ± 0.15	0.15 ± 0.04
Mid	< 2	0.17 ± 0.06	0.26 ± 0.11
	2 – 5	0.10 ± 0.03	0.11 ± 0.02
	> 5	0.42 ± 0.30	0.63 ± 0.20
	Mean	0.23 ± 0.10	0.34 ± 0.16
Mouth	< 2	0.45 ± 0.07	0.40 ± 0.07
	2 – 5	0.39 ± 0.10	0.35 ± 0.05
	> 5	0.65 ± 0.16	1.11 ± 0.40
	Mean	0.49 ± 0.08	0.62 ± 0.25

566

567

568 **Table 5.** Annual turnover rates of mangrove roots of fine (< 2 m), medium (2-5 mm) and
 569 large (> 5 mm) size classes for three zones (inner, mid and mouth) across Celestun
 570 Lagoon, Yucatan, Mexico.

Site	Size class (mm)	Turnover rates (yr ⁻¹)	Longevity (yr)
Inner	< 2	0.17 ± 0.03	7.64 ± 1.74
	2 – 5	0.18 ± 0.08	14.5 ± 5.18
	> 5	0.41 ± 0.27	4.61 ± 2.44
	Mean	0.39 ± 0.08	6.08 ± 1.17
Mid	< 2	0.50 ± 0.20	8.01 ± 2.91
	2 – 5	0.12 ± 0.04	13.9 ± 3.97
	> 5	0.36 ± 0.11	2.43 ± 0.39
	Mean	0.19 ± 0.04	11.01 ± 2.24
Mouth	< 2	0.46 ± 0.10	2.78 ± 0.47
	2 – 5	0.28 ± 0.06	5.32 ± 1.20
	> 5	0.21 ± 0.08	10.7 ± 3.52
	Mean	0.33 ± 0.10	6.71 ± 1.64

571

572

573 **Figure legends**

574 **Fig. 1** Sampling locations within Celestun Lagoon, Yucatan, Mexico. The shaded area
575 represents mangrove cover (CONABIO, 2009)

576

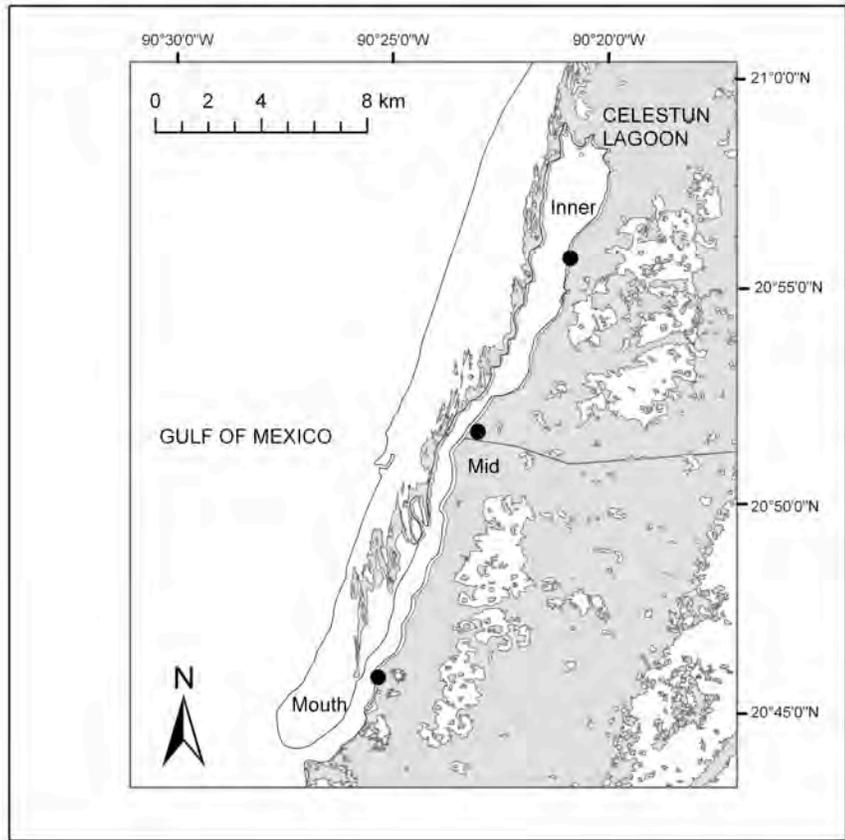
577 **Fig. 2** a) Root biomass (g m^{-2}) and b) root production ($\text{g m}^{-2} \text{d}^{-1}$) of mangroves from the
578 inner, mid and mouth of Celestun Lagoon. Means \pm SE with different letters indicate
579 significant differences among all site by size class designations ($p < 0.05$).

580

581 **Fig. 3** The relationship between mangrove root biomass (g m^{-2}) and a) soil phosphorus
582 (P) (mg cm^{-3}), b) interstitial salinity (ppt), c) forest density (trees ha^{-1}), and d) soil
583 nitrogen (N) (mg cm^{-3}). The lines represent significant linear regressions where: a) Root
584 biomass = $41023 P - 2671$; b) Root biomass = $88.35 \times \text{Interstitial salinity} - 1632$; and c)
585 Root biomass = $1.29 \times \text{Forest density} - 468.6$. Symbols represent location within the
586 Lagoon: Inner (filled circles), mid (filled triangles) and mouth of the lagoon (open
587 squares)

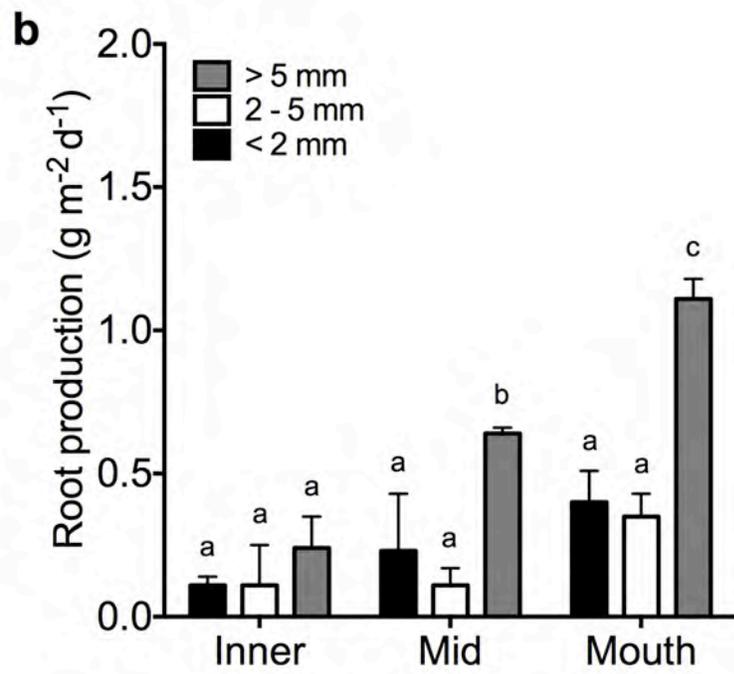
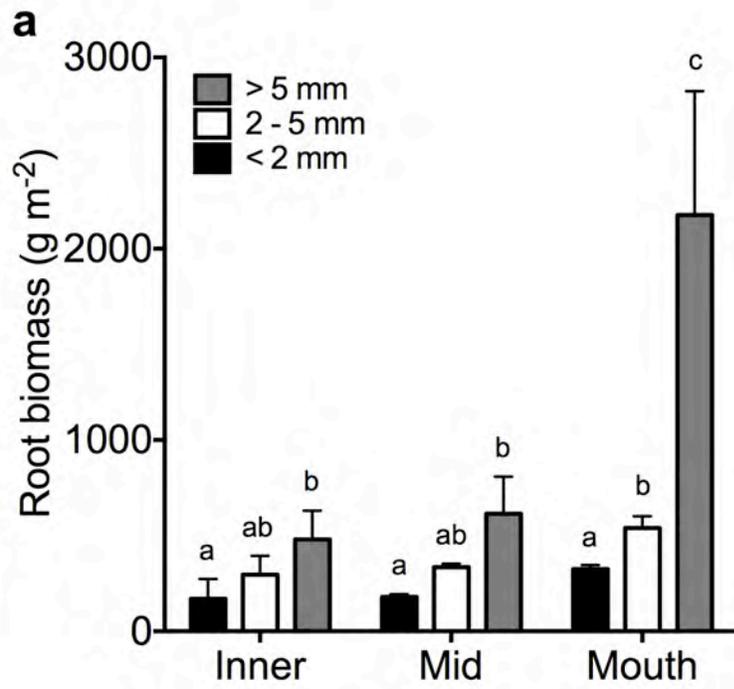
588

589 **Fig. 4** The relationship between mangrove root production ($\text{g m}^{-2} \text{d}^{-1}$) and a) soil
590 phosphorus (P) (mg cm^{-3}) and b) interstitial salinity (ppt). The lines represent significant
591 linear regressions where: a) Root production = $26.05 \times \text{Soil P} - 1.68$, and b) Root
592 production = $0.06 \times \text{Interstitial Salinity} - 1.19$. Symbols represent different mangrove
593 location within the Lagoon: inner (filled circles), mid (filled triangles) and mouth of the
594 lagoon (open squares)



595

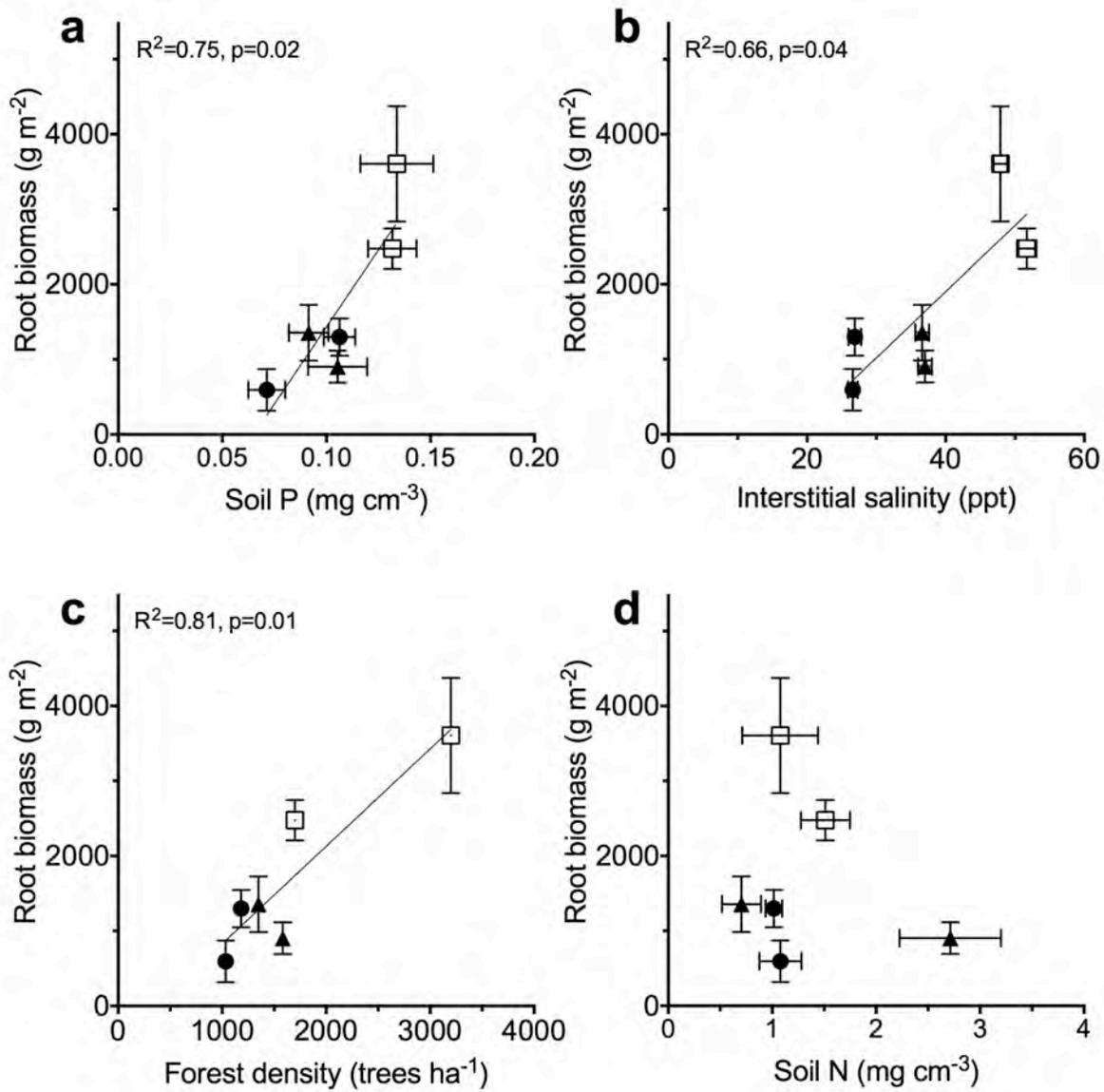
596 Figure 1



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598 Figure 2

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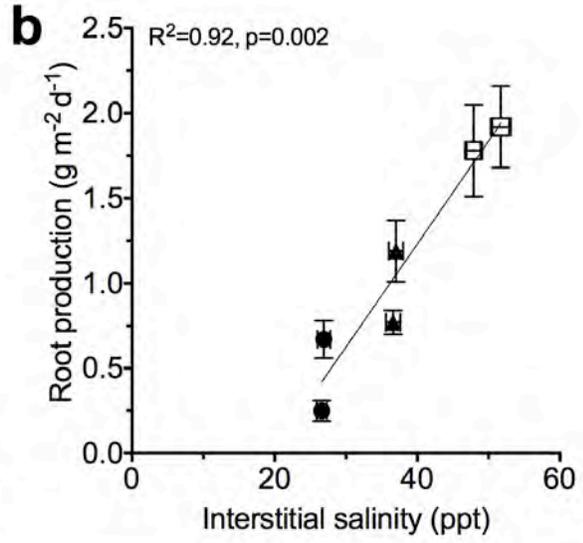
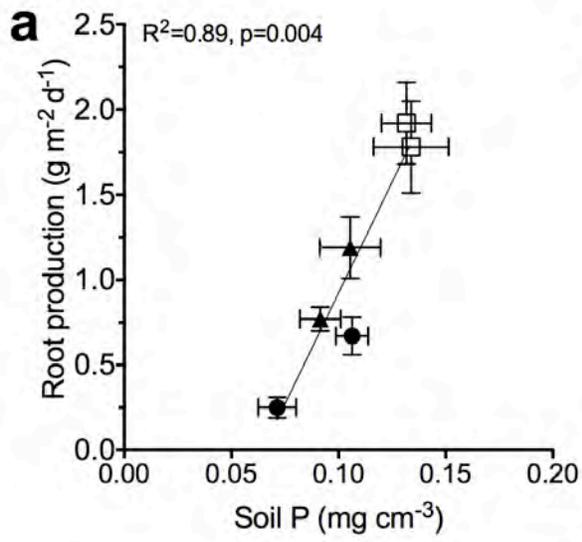


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602 Figure 3

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609 Figure 4

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612 **Material**

613 **Table S1.** Soil physicochemical characteristics of fringe mangroves from the inner, mid
614 and mouth of Celestun Lagoon, Yucatan, Mexico. C = carbon; N = nitrogen; P =total
615 phosphorus. Values are ranges (minimum, maximum).

Site	Salinity (ppt)	Depth (cm)	C (mg cm ⁻³)	N (mg cm ⁻³)	P (mg cm ⁻³)
Inner	(17, 41)	0-10	(17.2, 30.9)	(0.62, 1.44)	(0.05, 0.13)
		10-20	(26.0, 38.0)	(0.84, 1.77)	(0.05, 0.17)
		20-30	(16.0, 31.6)	(0.32, 1.53)	(0.02, 0.14)
		> 30	(22.0, 31.1)	(0.80, 1.30)	(0.08, 0.15)
Mid	(27, 53)	0-10	(29.0, 43.0)	(0.11, 6.20)	(0.10, 0.14)
		10-20	(20.2, 51.3)	(0.36, 3.97)	(0.08, 0.12)
		20-30	(20.2, 32.0)	(0.32, 4.21)	(0.07, 0.10)
		> 30	(16.0, 33.8)	(0.38, 3.86)	(0.06, 0.08)
Mouth	(27, 65)	0-10	(20.0, 39.1)	(0.34, 1.82)	(0.12, 0.26)
		10-20	(22.5, 50.3)	(0.52, 2.27)	(0.09, 0.17)
		20-30	(28.0, 52.8)	(1.03, 2.61)	(0.08, 0.16)
		> 30	(23.2, 32.2)	(0.76, 1.45)	(0.08, 0.15)

616