Carbon stocks and soil sequestration rates of tropical riverine wetlands

Adame, M.F.[a*], N.S. Santini[b], C. Tovilla[c], A. Vázquez-Lule[d], L. Castro[e], Guevara Santamaría, M.A.[f]

[a] Australian Rivers Institute, Griffith University, Nathan, 4111, QLD, Australia

[b] Coastal Plant Laboratory, The School of Biological Sciences, The University of Queensland, St Lucia, 4072, QLD, Australia

[c] Colegio de la Frontera Sur, Tuxtla Gutiérrez, Chiapas, Mexico

[d] Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico City, Mexico

[e] Comisión Nacional de Áreas Naturales Protegidas, Chiapas, Mexico.

[f] Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19716, U.S.A.

*Corresponding author

f.adame@griffith.edu.au

+617 3735 5359 ext. 57101

Fax: +617 3735 7615

Abstract

Riverine wetlands are created and transformed by geomorphological processes that determine their vegetation composition, primary production and soil accretion, all of which are likely to influence C stocks. Here, we compared ecosystem C stocks (trees, soil and downed wood) and soil N stocks of different types of riverine wetlands (marsh, peat swamp forest and mangroves) whose distribution spans from an environment dominated by river forces to an estuarine environment dominated by coastal processes. We also estimated soil C sequestration rates of mangroves on the basis of soil C accumulation. We predicted that C stocks in mangroves and peat swamps would be larger than marshes, and that C, N stocks and C sequestration rates would be larger in the upper compared to the lower estuary. Mean C stocks in mangroves and peat swamps (784.5 ± 73.5 MgC ha^{-1} and 722.2 ± 63.6 MgC ha^{-1}, respectively) were higher than those of marshes (336.5 ± 38.3 MgC ha^{-1}). Soil C and N stocks of mangroves were highest in the upper estuary and decreased towards the lower estuary. C stock variability within mangroves was much lower in the upper estuary (range 744-912 MgC ha^{-1}) compared to the intermediate and lower estuary (range 537-1,115 MgC ha^{-1}) probably as a result of a highly dynamic coastline. Soil C sequestration values were 1.3 ± 0.2 MgC $ha^{-1}yr^{-1}$ and were similar across sites. Estimations of C stocks within large areas need to include spatial variability related to vegetation composition and geomorphological setting to accurately reflect variability within riverine wetlands.

1. Introduction

Deforestation and ecosystem degradation is, after fossil fuel combustion, the largest cause of carbon dioxide (CO_2) emissions to the atmosphere (Van der Werf et al., 2009). Wetlands have one of the highest deforestation rates; one third of the world's mangrove forests have been lost in the past 50 years, while one third of saltmarshes has disappeared since the 1800s (Alongi, 2002; McLeod et al., 2011 and references therein). Because wetlands are rich in carbon (C), deforestation or disturbance of these ecosystems results in large emissions of CO_2 to the atmosphere (Lovelock et al., 2011). To prevent the large emissions that result from wetland loss, programs such as REDD+ (Reducing Emissions from Deforestation and forest Degradation) have been proposed. In order to target coastal wetlands within REDD+ and other financing programs, accurate estimates of C stocks and sequestration rates are needed (Alongi, 2011).

C stocks within wetlands can be associated with forest structure, with largest stocks in tall and vigorous forests (Adame et al. 2013). However, this is not always the case, as in some locations mangrove C stocks do not reflect the aboveground structure (Kauffman et al. 2014b). This could be partly because wetlands are highly dynamic and the existing vegetation might not reflect the wetland long-term condition (Thom 1967, 1975). For example, sparse mangroves growing in an accreting riverbank could become tall, productive forests in fifty years, but the soil C will take longer to accumulate. Thus, tall mangrove forests might not necessarily have larger C stocks than shorter ones. Geomorphic processes will constantly create, transform and

destroy landforms, resulting in changes in vegetation, production, sedimentation, and thus in C stocks (Adame et al. 2010, Alongi 2011).

Many forces contribute to the formation of riverine wetlands in deltaic-estuarine landscapes, including: river run-off, wave action, tidal inundation and the incidence of cyclones (Thom 1967, Woodroffe 1992). In the Southern Mexican Pacific (Fig. 1). In the Mexican southeast coast, wetlands are formed by a mosaic of marshes and peat swamps where freshwater input is constant, tidal inundation is negligible and wave and storm damage is relatively low. Lowland, mangroves dominate the vegetation from the upper to the lower estuary. Upper estuarine mangroves have periodic input of freshwater and lower tidal and wave influence compared to mangroves in the lower estuarine region (Thom 1975). In this study, we compared C stocks (trees, soil and downed wood) of riverine wetlands of La Encrucijada Biosphere Reserve (LEBR) in the Pacific south coast of Mexico. We compared C stocks of different vegetation types (mangroves, peat swamps and marsh) and throughout a geomorphological gradient (upper to lower estuary).

Wetlands are not only efficient at accumulating C, but also nitrogen (N) when production exceeds N demand (Rivera Monroy et al., 1995). C and N cycles interact closely, thus N stocks can increase with increments in C (Yimer et al., 2006). N accumulation increases with rainfall, runoff, and production by organisms such as cyanobacteria and algae (Alongi, 2009; Reef et al., 2010). Soil N accumulation is also associated with large foliage cover and wood biomass (e.g. Hooker and Compton, 2003; Liao et al., 2007). In this study we compare the capacity of different types of

wetlands (mangroves, marshes and peat swamps) and geomorphological settings (upper and lower estuary) to store N in the soil.

The high capacity of wetlands to store C and N is partly due to their high productivity and low soil decomposition rates. Mangroves and marshes can store up to three times more C than terrestrial ecosystems (Chmura et al., 2003; Donato et al., 2011; McLeod et al., 2011). For example, mangroves in the Caribbean can store up to 987 MgC ha^{-1}, while in the Indo-Pacific, mangroves store 1,023 MgC ha^{-1} (Donato et al., 2011; Adame et al., 2013). These values typically exceed those of tropical and temperate forests (< 400 Mg ha^{-1}, IPCC, 2003). Similarly, soil C sequestration rates of coastal wetlands (210 g C m^{-2} yr^{-1}) and freshwater wetlands (20 – 30 g C m^{-2} yr^{-1}) are higher than those of terrestrial forests (~ 10 g C m^{-2} yr^{-1}) (Chmura et al., 2003; McLeod et al., 2011). Long-term carbon sequestration rates of mangroves are very difficult to obtain, but are required to participate in carbon payments (Alongi 2011). In this study, we use a unique natural marker (ash horizon from a volcanic eruption in 1902, Supplementary Fig.1) to calculate soil carbon sequestration rates during the last century from a large number of locations (n = 36). We compared C sequestration rates of mangroves across a geomorphological gradient, from mangroves in the upper estuary to those in the lower estuary.

Riverine wetlands, particularly mangroves, are one of the most extensive types of wetlands and are predicted to have one of the largest C stocks on Earth (Ewel et al., 1998). We expect that C stocks within the riverine wetlands of the south Mexican Pacific coast have large C stocks compared to any other terrestrial forest. We also

predict that mangroves and peat swamps have higher C stocks compared to marshes. Finally, we expect that geomorphological setting will affect C and N stocks and C sequestration rates with higher values for mangroves in the upper estuary compared to those in the lower estuary.

2. Methodology

2.1 Study site

The Encrucijada Biosphere Reserve (LEBR) is located in Chiapas, in the south Pacific coast of Mexico (14° 43' N, 92° 26' W) (Fig. 1). The LEBR comprises an area of 144,868 ha. The Reserve has five coastal lagoons connected to seven river systems. The LEBR is characterized by large areas of wetlands including mangroves, marsh and peat swamp forests. The LEBR has one of the most extensive mangrove areas of the region, with forests dominated by trees of *Rhizophora mangle* that range between 20 - 40 m in height, and are believed to be the tallest in the country (Tovilla et al., 2007). The mangroves of LEBR support a high biodiversity, as well as fisheries and tourist activities (UNESCO, 2013).

The climate of the LEBR is warm, sub humid with most precipitation occurring in the summer months (June - October). The mean annual temperature of the region is 28.2°C, with a mean annual minimum of 19.2ºC and a mean annual maximum of 36.5ºC; mean annual precipitation is 1567 mm (Sistema Meteorológico Nacional - Comisión Nacional del Agua, station No. 7320, 1951-2010).

2.2 Site stratification

144 In this study, we sampled three types of wetlands: peat swamp forest, marsh
145 and mangroves. To determine a criteria for stratification of mangroves, we used two
146 SPOT 5 satellite images with geographical, geometric and radiometric correction, and
147 the Universal Transverse Mercator projection system. From each image, the
148 Normalized Difference Vegetation Index (NDVI) was obtained with ERDAS Imagine.
149 The NDVI values ranged from -1 to 1, where negative values indicated areas without
150 vegetation, values close to zero indicated senescent or stressed vegetation, and
151 values close to 1, indicated green or healthy vegetation (Chuvieco, 2006). NDVI values
152 were extracted from the mangrove coverage map (CONABIO, 2013) and classified
153 according to Ruiz-Luna et al. (2010). The mangrove vegetation was divided in three
154 classes: the most vigorous vegetation was Class I (9,253 ha), the least vigorous
155 vegetation was Class III (11,467 ha), Class II (6,757 ha) had intermediate values of
156 vegetation vigour. The mangrove Classes along with the distance to the mouth of the
157 estuary were used to classify our sites into three categories: upper estuary mangroves
158 with the most vigorous vegetation, lower estuary mangroves with the least vigorous
159 vegetation and intermediate mangroves in terms of vigour and distance to the mouth of
160 the estuary (Fig. 1). Hereinafter, we will refer to our mangrove locations as “upper
161 estuary”, “intermediate” and “lower estuary”.
162
163 ***2.3 Field and laboratory analyses***
164 Sampling was conducted during December 2012, where ecosystem C stocks,
165 soil N stocks and soil C sequestration rates were measured. We sampled 9 sites: a
166 peat swamp forest dominated by *Pachira aquatica*, a marsh dominated by the grass
167 *Typha dominguensis* and seven mangrove forests (three sites in the upper estuary,

two in the intermediate estuary and two in the lower estuary) (Fig. 1; Table 1). We measured whole-ecosystem C stocks in six plots (radius of 7 m; 154 m^2) per site using methodologies described in Kauffman et al. (2014a). The plots were established 25 m apart along a 125 m transect set in a perpendicular direction from the water edge. At each plot, we sampled C stocks within trees and shrubs, downed wood and the soil profile. We also sampled soil N stocks and interstitial salinity. To estimate C sequestration rates in mangroves, we used a natural ash horizon marker to calculate soil C accumulation. The detailed methodology is explained below.

2.3.1. Biomass and C stock within trees and shrubs

Forest structure was measured at each plot through measurements of the species and the diameter at 1.3 m height (DBH) of all trees. The diameter of trees of *R. mangle* and *R. harrisonii* was measured at the main branch, above the highest prop root (D_R). Aboveground biomass in the marsh communities was determined through plant harvest within two 20 x 20 cm quadrants within each of the 6 plots. The wet mass was determined in the field and then a subsample was collected from each quadrant and oven-dried to determine its dry weight.

Tree biomass was calculated using allometric equations (Table 2). We used the formula by Fromard et al. (1998), which was obtained for mangroves of French Guiana, which is a location with similar characteristics than those found in LEBR (riverine mangroves with a tropical hot humid climate). We compared the formulas of Fromard et al. (1998) and Day et al. (1987), the latter obtained from mangroves in Campeche, Mexico. The results using both formulas were not significantly different (t =

192 1.027; df = 2284; p = 0.30). We chose the formula by Fromard et al. (1998) because it
193 included trees with a DBH range similar to those found in LEBR (DBH $_{Max}$= 32 cm for
194 *R. mangle*, 9.6 cm for *Laguncularia racemosa* and 42 cm for *Avicennia germinans*).
195 Aboveground biomass of trees from the peat swamp (*P. aquatica*) was calculated with
196 the formula of van Breugel et al. (2011), while belowground biomass of *P. aquatica*
197 was determined with the equation of Cairns et al. (1997) for trees of tropical forests.
198 Belowground root biomass for mangroves was calculated using the formula by
199 Komiyama et al. (2005) and wood density values (Chave et al. 2009, Zanne et al.
200 2009) of comparable climatic regions as the LEBR (Table 2). Tree C was calculated
201 from biomass by multiplying by a factor of 0.48 for aboveground and 0.39 for
202 belowground biomass; C content of marshes was calculated using a factor of 0.45 of
203 the total biomass (Kauffman et al. 2014a).
204
205 Standing dead trees were also included in the tree C stocks estimations. Each
206 dead tree was assigned to one of three decay status (Kauffman et al. 2014a): Status
207 1- dead trees without leaves, Status 2- dead trees without secondary branches, and
208 Status 3- dead trees without primary or secondary branches. The biomass for each
209 tree status was calculated as a percentage of the total biomass using the values
210 provided by Fromard et al. (1998). For dead trees of Status 1, biomass was calculated
211 as the total dry biomass minus the biomass of leaves, equivalent to 2.8 % of the total
212 biomass. The biomass of trees of Status 2 was calculated as the total biomass minus
213 the biomass of leaves (2.8% of the total) and minus secondary branches (equivalent to
214 18.7 % of the total biomass). Finally, the biomass of trees of Status 3 was calculated

as the biomass of the main stem, which is equivalent to 76.6% of the total biomass (Table 2).

2.3.2. Downed wood

The mass of dead and downed wood was calculated with the planar intersect technique (Van Wagner, 1968) adapted for mangroves (Kauffman et al. 2014a). Four 14 m transects were established at the centre of each plot: the first one established at 45° off the direction of the main transect, the other three were established 90° off from the previous transect. The diameter of any downed, dead woody material (fallen/detached twigs, branches, prop roots or stems of trees and shrubs) intersecting each transect was measured. Along the last 5 m of the transect, wood debris > 2.5 cm but < 7.5 cm in diameter (hereafter "small" debris) was counted. From the second meter to the end of the transect (12 m in total), wood debris > 7.5 cm in diameter (hereafter "large" debris) was measured. Large downed wood was separated in two categories: sound and rotten. Wood debris was considered rotten if it visually appeared decomposed and broke apart when kicked. To determine specific gravity of downed wood we collected ~ 60 pieces of down wood of different sizes (small, large-sound, and large-rotten) and calculated their specific gravity as the oven-dried weight divided by its volume. Using the specific gravity for each group of wood debris, biomass was calculated and converted to C using a conversion factor of 0.50 (Kauffman et al. 1995)

2.3.3. Soil C and N

238 Soil samples for bulk density and nutrient concentration were collected at each
239 plot using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm-radius
240 attached to a cross handle (Kauffman et al., 1995). The core was systematically
241 divided into depth intervals of 0 - 15 cm, 15 - 30 cm, 30 - 50 cm, 50 -100 cm and > 100
242 cm. Soil depth was measured using a steel-2 m rod that was inserted in the ground at
243 each plot. Samples of a known volume were collected in the field and then dried to
244 constant mass to determine bulk density. Samples were sieved and homogenized and
245 treated with hydrochloric acid to eliminate the inorganic carbon portion before
246 analyses. Concentration of organic C and N were determined using a Costech
247 Elemental Combustion System 4010 (CA, USA, Michigan Technological University,
248 Forest Ecology Stable Isotope Laboratory).
249
250 *2.3.4 Soil C sequestration rates*
251 We estimated C sequestration rates in mangroves as the amount of C
252 accumulated in the soil profile. To date the soil cores, we used a natural marker that
253 consisted of a volcanic ash horizon that was clearly identified in all the cores
254 (Supplementary Fig. 1). This ash horizon is the remaining of the volcano Santa Maria's
255 eruption in 1902 that represented one of the four largest volcano eruptions of the 20th
256 Century (Volcanic Explosivity Index of 6 out of 7, Williams and Self, 1983). As a result
257 of the eruption, a recognizable plinian deposit of known date ashes can be established
258 in the Mexican Pacific coast, northwest of the volcano. We estimated soil C
259 sequestration within each plot of six of our mangrove sites by dividing the depth of the
260 ash horizon by years since the volcano eruption occurred and multiplying it by bulk
261 density and C content. Soil C sequestration rates are expressed in g C m^{-2} yr^{-1}. We

262 couldn't measure soil C sequestration rates of marsh and peats swamp forest, as
263 these vegetation types frequently suffer from fires and thus have confounding ash
264 horizons.
265
266 *2.3.5 Interstitial salinity*
267 Salinity was measured with an YSI-30 multiprobe sensor (YSI, Xylem Inc. Ohio,
268 USA) from water extracted from 30 cm deep. The water was obtained with a syringe
269 and an acrylic tube (McKee et al., 1988).
270
271 ***2.4 Scaling up***
272 To scale up our field measurements to the LEBR ,we conducted different
273 approaches for each vegetation type. We relied on modelling approaches to predict
274 values of variables of interest in places where no information was available.
275
276 For mangroves, we first estimated aboveground C (trees) throughout the LEBR.
277 Data was spatially harmonized with vegetation-related remote sensing products and
278 the first three principal components of the SAGA GIS standard terrain parameters
279 derived from a digital elevation model (Supplementary Table 1). A pixel size of 25 m
280 was selected to resample remote sensing and topographic layers given the coarser
281 spatial resolution of ALOS Palsar products. Upscaling of aboveground C was
282 performed in R (Core Team 2015) by the means of a machine learning random forest
283 tree ensemble (Breiman, 2001). The number of covariates to fit each tree (mtyr
284 parameter) was tuned by ten-fold cross validation. The number of trees to grow was
285 1000, which was enough to stabilize the error. For external validation purposes, 20%

of available data was randomly leaved out of the model. Selection of external validation and modelling was repeated 400 times to analyse the effects of the random split on error metrics by the correlation between observed and modelled and the root mean squared error (RMSE). Additionally, we implemented the quantile regression forest method proposed by Meinhausen (2006), which allows the inference of the full conditional distribution of the response variable as a function of its covariates. Having this information, prediction intervals (at 95%) were identified and their range was used to provide a spatially explicit measure of uncertainty, considering the number of data, the correlation among predictive variables, as well as the complexity and geographical dimensions of the study area. The aboveground C was extrapolated to total C stocks based on the field-collected data. As a comparison exercise, we also estimated mean ecosystem C stocks times the estimated area for each vegetation type on the basis of the NDVI classification, which broadly represented mangroves from the upper, intermediate and lower estuary (Fig. 1).

For the extrapolation of marsh dominated by *T. dominguensis* to the whole LEBR, we included a number of sites where aboveground and belowground biomass and organic matter content have been measured (C. Tovilla, unpublished data, Fig. 1), which together with our field measurements, was used to roughly estimate C stocks within the LEBR. The total area of marsh was calculated on the basis of the "other wetlands" category obtained from the coastal vegetation map of the Pacific south region (CONABIO, 2013), as well as from auxiliary cartographic (SERIE IV; INEGI, 2012) and our field experience. It is likely that the area of the marsh –and thus its C

stock– was over or underestimated, as the marsh area included waterholes and inundated vegetation ("popales") with unknown C stocks.

For peat swamps, we extrapolated our six sampling plots to the forest surrounding our sampling area, which had an area of 844 ha (Fig. 1). The rest of the area of peat swamp forest is not available for the LEBR. Therefore, the C stock estimated for peat swamp forests was underestimated.

2.5 Statistical analyses

One-Way Analysis of Variance (ANOVA) was performed to test differences of above and belowground biomass and C stocks among wetland types (mangroves, marsh and peat swamp forest), sites, and geomorphological setting (upper estuary, intermediate and lower estuary mangroves). To avoid uncertainties associated to imbalance designs, when comparing vegetation types (mangroves vs. peat swamps vs. marsh), we used the mean for all mangrove sites for each of the five plots which represented a range a vegetation from the water edge to the landward side of the forest. The mean of the plots was compared against the plots laid in a similar way for peat swamp forest and marsh (n= 5 plots per site). Differences in soil C and N concentrations by depth were tested with a Two-Way ANOVA, with site as the fixed effect and depth as the random effect of the model. Normality was assessed using Shapiro-Wilk tests. When significant differences were found, pair-wise comparisons were explored using Scheffé post-hoc tests. Analyses were performed using Prism v6.0 (GraphPad Software, La Jolla, CA, USA) and SPSS Statistics v20 (IBM, New York, USA). Throughout the manuscript, data are reported as mean ± standard error.

333

334 **3. Results**

335 *3.1 Forest structure*

336 Mangroves of the LEBR were dominated by trees of *R. mangle* with lesser
337 contributions of *A. germinans, L. racemosa* and few trees of *R. harrisonii* (in sites
338 Panzacola and Teculapa). Only one of our study sites –Las Palmas– was dominated
339 by a different species, *A. germinans*. All the sampling sites were characterized by
340 relatively low tree density forests (1,213 - 5,370 trees ha^{-1}) with tall trees (~ 20 - 40 m
341 in height) of mean DBH of 8 - 11 cm (Table 1). The peat swamp forest was dominated
342 by *P. aquatica* and had a similar structure than that of mangroves with a tree density of
343 2,469 trees ha^{-1}, trees of up to 22 m in height and mean DBH of 14.5 cm. Finally, the
344 marsh was dominated by tall grasses (2 - 3 m in height) of *T. dominguensis* (Table 1).

345

346 *3.2 Tree biomass and C*

347 Mean tree aboveground biomass of mangroves was 421.1 ± 67.8 Mg ha^{-1} and
348 was higher than the biomass for the peat swamp and marsh, which was 162.2 ± 27.3
349 Mg ha^{-1} and 76.5 ± 11.6 Mg ha^{-1}, respectively. Thus, mean C stock in mangrove trees
350 was significantly higher in mangroves (215.0 ± 44.4 MgC ha^{-1}) compared to swamp
351 forests and marsh (95.1 ± 15.7 MgC $ha^{-1}$and 38.2 ± 5.8 MgC ha^{-1}, respectively) ($F_{2,12}$ =
352 167.4; $p < 0.0001$) (Table 3, Fig. 2).

353

354 Tree biomass and vegetation C stocks were not significantly different among
355 upper, intermediate and lower estuary mangroves ($F_{7,40}$= 1.826; p = 0.109). However,
356 there were significant differences among sites with lowest C stocks measured in the

vegetation of Santa Chila (132.1 MgC ha^{-1}) (t= 2.54; $p = 0.015$) and highest at Las Palmas (440.0 MgC ha^{-1}) (t= 2.03; $p = 0.049$), the only site dominated by *A. germinans* and not *R. mangle*. The vegetation biomass and C stocks were quite similar among sites within the upper estuary (range 211 - 243 MgC ha^{-1}), but highly variable among sites within the intermediate and lower estuary (132 - 440C Mg ha^{-1}) (Table 3, Fig. 3).

3.3 Downed wood C

Downed wood C was low in peat swamp wetlands (12.5 ± 2.8 MgC ha^{-1}), but considerable in some mangrove sites (mean of 29.4 ± 3.7 MgC ha^{-1}). The amount of downed wood in mangroves had a wide range within sites, from 11 Mg ha^{-1} to 205 Mg ha^{-1}, with a mean biomass of 59.4 ± 26.0 Mg ha^{-1} (Table 4, Fig. 3). Mangroves in the lower estuary had the highest biomass and C stocks of downed wood ($F_{2,39} = 6.86$; p = 0.0028), mainly due to large amounts of downed wood at Zacapulco (102.4 ± 27.0 MgC ha^{-1}) ($F_{7,47} = 8.147$; $p < 0.0001$). Small downed wood comprised 10.2 % of the total biomass (6.0 ± 0.8 Mg ha^{-1}); large sound wood the 55.4% (33.0 ± 13.9 Mg ha^{-1}) and large rotten wood comprised 34.4 % of the total (20.4 ± 15.2 Mg ha^{-1}).

3.4 Soil C and N

Soil C content (%) was higher in peat swamps (19.9 ± 3.4%) compared to marsh (10.1 ± 2.5%); mangroves had intermediate values (14.6 ± 2.5%) ($F_{2,12} = 3.616$; p = 0.04). Soil N (%) was higher in peat swamps (1.2 ± 0.2%) compared to mangroves and marsh (0.6 ± 0.1% and 0.6 ± 0.2%, respectively) ($F_{2,12} = 5.558$; p = 0.019). Soil C stock (MgC ha^{-1}) was significantly higher in mangroves (505.9 ± 72.6 MgC ha^{-1}) and the peat swamp forest (620.4 ± 6.8 MgC ha^{-1}) compared to the marsh (298.3 ± 39.0

381 MgC ha^{-1}) (Fig. 2) ($F_{2,12}$ = 5.42; p = 0.02). Finally, soil N stocks were higher for peat
382 swamps (40.4 ± 5.5 Mg ha^{-1}) compared to mangroves (19.2 ± 2.7 Mg ha^{-1}) and
383 marshes (18.5 ± 1.7 Mg ha^{-1}) ($F_{2,12}$ = 11.51; p = 0.0016) (Table 5).
384
385 When comparing mangroves from the upper to the lower estuary we found that
386 the soil C stocks from the upper and intermediate estuary were significantly higher
387 than those from the lower estuary ($F_{2,12}$ = 25.43; p < 0.0001). Soil C stocks were also
388 significantly different among sites and depths (Site $F_{7,64}$ = 16.03, p < 0.0001; Depth
389 $F_{3,64}$ = 8.83; p < 0.001) (Table 5), with highest C density in the soil horizon > 50 cm.
390 Soil N stocks were higher in mangroves of the upper estuary (26.4 ± 0.5 Mg ha^{-1})
391 compared to mangroves in the intermediate and lower estuary (15.3 ± 1.6 Mg ha^{-1} and
392 12.3 ± 3.2 Mg ha^{-1}, respectively) ($F_{2,4}$ = 20.35; p = 0.008) (Table 5). We also found a
393 trend of the distribution of soil C with depth among mangroves from the upper to the
394 lower estuary. Soil C values increased with depth at Panzacola (upper estuary),
395 remained similar in depth in Teculapa and Paistalon (upper estuary) and decreased in
396 depth at the rest of the mangroves within the intermediate and lower estuary (Table 5).
397
398 Overall, C stocks were highest in mangroves and peat swamp forests, while N
399 stocks were highest in peat swamp forests. Soil C and N stocks were highest in the
400 upper estuary and decreased towards the lower estuary. Finally, the variation of site
401 replicates was different within the upper and lower estuary: inter-site variability was
402 much lower in mangroves from the upper estuary compared to the mangroves from the
403 intermediate and lower estuary (Fig. 3).
404

405 *3.5 Ecosystem C stocks*

406 Mean C stocks of wetlands in the LEBR were significantly different, with highest
407 stocks for mangroves (784.5 ± 73.5 MgC ha^{-1}) and peat swamps (722.2 ± 63.6 MgC
408 ha^{-1}) and lowest for marsh (336.5 ± 38.3 MgC ha^{-1}) ($F_{2,12}$ = 16.9; p = 0.0004) (Fig. 2,
409 Table 6).

410

411 There was a significant difference among mangroves along the estuary, with
412 mangroves from the upper (871.0 ± 22.0 MgC ha^{-1}) and intermediate estuary (825.8 ±
413 289.2 MgC ha^{-1}) having higher C stocks compared to those in the lower estuary (659.5
414 ± 18.6 MgC ha^{-1}) ($F_{2,12}$ = 25.43; p < 0.0001). Largest C stocks were measured at
415 Esterillo (1,114.9 ± 150.3 MgC ha^{-1}) and lowest at Santa Chila (536.6 ± 88.8 MgC ha^{-}
416 ^{1}). The C stocks of mangroves within the upper estuary were quite similar among sites
417 (CV= 4.4%), while the stocks from mangroves within the intermediate and lower
418 estuary had large variability (CV= 34.4%).

419

420 *3.6 C stocks of LEBR*

421 With the use of the cross-validated correlation from 400 realizations, we
422 selected a model that was able to explain 34% of aboveground C variance, with a
423 RMSE of 111.29 MgC ha^{-1}. External validation had a higher correlation value (R^2=
424 0.73, RMSE = 60.28 MgC ha^{-1}), but was less reliable since there were only 12 points
425 (20% of available data). Predicted aboveground C for the LEBR ranged between 18 -
426 567 MgC ha^{-1}, with a mean of 118 ± 54 MgC ha^{-1}, with an estimated total of 3.5
427 millions MgC for aboveground mangrove C for the LEBR (Fig. 4). However, the results
428 had a large degree of uncertainty, mostly in mangroves at the water edge, at the

429 landward side, and mangroves close to the estuary mouth (Fig. 4B), some of these
430 sites identified as monospecific forests of *A. germinans*.
431
432 Although the prediction of the aboveground C was low, we were able to identify
433 that most forests within the LEBR have less than 300 MgC ha^{-1} (Fig. 4C). Based on
434 our field data, we identified that fringe forest dominated by *R. mangle* had between
435 300 - 400 MgC ha^{-1}, while forest of *A. germinans* had aboveground biomass > 400
436 MgC ha^{-1}, most forests with aboveground values below 300 MgC ha^{-1} were basin
437 forests dominated by *R. mangle*. According to the model, and agreeing with our field
438 experience, this kind of forests comprises more than 90% of the mangroves of the
439 LEBR. On the basis of this result, we calculated the mean C stock for plots of
440 mangroves with these characteristics and obtained a value of 848.0 ± 31.6 MgC ha^{-1},
441 which extrapolated to the whole LEBR provides a rough estimate of 23.3 millions of
442 MgC. The uncertainty of this estimation is highest in mangroves from the lower estuary
443 and mangroves close to water or the landward edge. As a comparison, if we
444 extrapolated the C stocks of the mangroves using the classes obtained from the NDVI
445 classification (upper, intermediate and lower estuary) the estimation is similar with 20.9
446 millions of MgC for the LEBR.
447
448 The C stock of marshes was estimated to vary between 37.1 - 720.4 MgC ha^{-1}
449 across the LEBR. Using the mean value of 432.2 MgC ha^{-1} obtained from data from
450 this study and from Tovilla et al. (unpublished data, Fig. 1), we estimated that the C
451 stock of marshes within the LEBRE is close to 14.0 millions of MgC. Finally, peat
452 swamps only cover a very small area of the LEBR and their C stocks were estimated

to be of at least 0.6 millions of MgC. Summed up, the approximate C stock value for the LEBR is 38 millions of MgC.

3.7 Soil C sequestration rates

Mean soil C sequestration rates in mangroves was 1.3 ± 0.2 Mg ha^{-1} yr^{-1}; soil C sequestration was similar among all sites (upper, intermediate and lower estuary) ($F_{2,4}$ = 0.78; p = 0.516). Lowest values (0.4 ± 0.0 MgC ha^{-1} yr^{-1}) were measured in the site Las Palmas, which was dominated by *A. germinans* (Table 7). Considering than less than 10% of the mangroves in LEBR are dominated by *A. germinans*, we can estimate that the C sequestration of mangroves in LEBR through soil accretion is close to 39,842 MgC every year.

4. Discussion

The riverine wetlands measured in this study had large C stocks, with values for mangroves and peat swamps almost twice as high as those measured in terrestrial forests (typically < 400 MgC ha^{-1}, IPCC, 2003). C stocks of mangroves within LEBR (mean of 784.5 ± 73.5 MgC ha^{-1}; maximum of 1,115 MgC ha^{-1}) were similar to other mangroves around the world, such as in Vietnam (762.2 ± 57.2 MgC ha^{-1}, Nguyen et al 2014), the Dominican Republic (853 MgC ha^{-1}, Kauffman et al., 2014b), Yucatan, Mexico (663 ± 176 MgC ha^{-1}; Adame et al., 2013) and Northwest Madagascar (367-593 MgC ha^{-1}; Jones et al., 2014). As hypothesised, C stocks of mangroves and peat swamps were higher than those of marshes (336.5 ± 38.3 MgC ha^{-1}).

In general, mangroves within the upper estuary had higher C stocks compared to mangroves in the lower estuary. However, the most striking difference was not related to C content, but to site variability. Mangroves from the upper estuary were quite similar in structure and C stocks within sites. On the contrary, mangroves from the intermediate and lower estuary were much more variable. We also found differences in soil C with depth: soil C increased or was similar with depth at mangroves in the upper estuary, while soil C decreased with depth in mangroves from the lower estuary (similar to Donato et al. 2011). We suggest that differences in geomorphological forces explain the variation in C stocks and soil C distribution within the sediment column. Mangroves in the upper estuary have grown in a relatively stable environment that allowed C to be buried and forests to develop into a mature state. Comparatively, mangroves in the lower estuary are exposed to frequent changes in hydrology, sedimentology and are directly struck by tropical storms (Woodroffe, 1992).

As a result, mangroves in the lower estuary are a mosaic of old and young forests, some of them with productivities and soil C similar to those in the upper estuary, but others with low productivity, statures and soil C, and thus, C stocks.

The N stocks within mangroves also differed between mangroves, with highest stocks in mangroves from the upper estuary. Upland mangroves receive high N inputs due to agricultural activity in the catchment (UNESCO, 2014); lowland mangroves probably receive lower N loads as oceanic water has usually lower nutrients than riverine water. Differences in N content have also been associated to microbial activity such as bacteria and protozoans, which are in turn linked to tidal flushing in the mangrove soil (Alongi, 1988). Higher nitrification and denitrification and lower N fixation rates could further explain low N stocks in lowland mangroves; however, this remains to be tested. The higher N inputs in mangroves in the upper estuary, coupled with lower salinity values throughout the year probably contribute to higher productivity of mangroves in the upper estuary compared to those in the lower estuary (Tovilla et al. unpublished data).

Besides the differences in C and N stocks between upland and downland mangroves, it stands out that the mangrove forest dominated by *A. germinans* (Las Palmas) was notably different. This forest had the highest tree biomass, lowest soil C and lowest C sequestration rates measured in this study. Lowest C stocks in soils *of A. germinans* can be due to the lower C wood content that is buried in the soil. Wood density of *A. germinans* is lower (0.67 g cm^{-3}– 0.90 g cm^{-3}) than wood density of *R. mangle* (0.810 g cm^{-3}– 1.05 g cm^{-3}) (Chave et al. 2009, Zanne et al. 2009), which

513 dominated all other sites. Wood density is a major predictor of stored C in wood
514 biomass and could explain the low values of C buried in the soil (Flores and Coomes,
515 2011), and thus, the low C stocks in the mangrove forest dominated by *A. germinans.*
516
517 Most of the C stocks in mangroves is stored in the soil (Donato et al., 2011;
518 Adame et al., 2013), thus the potential of mangroves to sequester C is closely related to
519 their soil C sequestration rates. The soil C sequestration rates measured in mangroves
520 of LEBR (0.4 - 1.8 MgC ha^{-1} yr^{-1}) were similar throughout upper and lower estuary
521 mangroves, which suggests that over the long term, variability among sites in C
522 sequestration was not high enough to be detected with our method. However, the C
523 sequestration rate of the site dominated by *A. germinans* was two to three times lower
524 compared to forests dominated by *R. mangle*. The soil C sequestration estimates in this
525 study are within the range of those reported in the review by Chmura et al. (2003), with
526 lowest values in Rookery Bay, Florida (0.2 MgC ha^{-1}) and highest in Terminos Lagoon,
527 Campeche, Mexico (6.5 MgC ha^{-1} yr^{-1}), and are similar to those measured in Moreton
528 Bay, Australia (0.8 MgC ha^{-1} yr^{-1}; Lovelock et al. 2014). Long-term soil C sequestration
529 rates are difficult to obtain, thus the values obtained in this study are valuable
530 estimations of C sequestration rates of mangrove forests. For example, we can roughly
531 estimate that the sequestration rate of the mangrove soil of LEBR is 39,842 MgC yr^{-1},
532 which is equivalent to the annual emissions of approximately 10,348 Mexicans (using
533 emissions by country from IEA, 2014).
534
535 To include wetlands in REED+ and other financial incentives for climate change
536 mitigation, it is usually necessary to estimate C stocks and sequestration data for large

areas of wetlands. Extrapolation of field data was challenging, with models showing poor agreement between external and cross validation, and high uncertainty in some areas of mangroves. Other studies have faced similar problems, with previous reports at a national level only being able to explain 2% of spatial variability (Cartus et al, 2014). Water level dynamics and the complexity of structural diversity of mangroves are important sources of uncertainty when using remote sensing sources. It is important to distribute sampling efforts wisely as to include as much spatial variability as possible. Additionally, sampling variables such as pH and salinity, that could further explain vegetation variability could be helpful (Vaiphasa, et al, 2006). In this study, we identified that species composition is an important variable as well as geomorphic location (upper and lower estuary) to explain spatial variability within C stocks. Our results also show, that the most variable, and thus, were field sampling should be concentrated, are mangroves close to the mouth of the estuary and in the landward and water edges.

Mangroves in riverine deltas are the most extensive and developed forests (Woodroffe, 1992). Thus, the results in this study contribute to the C budgets of riverine wetlands, which are likely to be one of the most C rich ecosystems in the world. The wetlands of LEBR store about 38.0 M ton C, which is equivalent to 139.5 Mton CO_2. Degradation of wetlands in the region due to increased sediment loads derived from upriver dredging, fires, hydrological modifications, and illegal harvesting threaten the potential C storage of these wetlands.

The C stocks and sequestration values shown in this study can help provide incentives into the reforestation and conservation projects of this reserve and throughout similar wetland ecosystems. For example, marsh and swamp forests are very susceptible to fire damage during the dry season (L. Castro, pers. comm). With the C stocks calculated in this study, we estimated that if fire consumes all the vegetation and the top 15 cm of soil (Schmalzer and Hinkle 1992), every hectare of burned marsh or peat swamp could emit 287 ton CO_2 and 567.4 ton CO_2, respectively. Every year between 500 and 4,500 ha of marshes are burned within the reserve (L. Castro pers. comm.), which results in an annual mean emission of ~0.6 millions tons of C or 4.6% of the emissions of the state of Chiapas (based on emissions reported by IEA, 2014). This information can be used to emphasize the importance of managing fires in the LEBR in order to maintain its large C stocks and avoid CO_2 emissions to the atmosphere. Another example is to use the C stocks provided in this study to negotiate for offsetting emissions within the country or abroad. For instance, California U.S.A. has signed an agreement to import C credits from forests in Chiapas, the state where this study takes place (Morris et al. 2011). To include mangroves and other wetlands in similar agreements could be a cost-effective way to reduce C emissions (Siikamäki et al. 2012), while at the same time protecting the biodiversity and the ecosystem services they provide (Adame et al. 2014). Finally, our results have also showed that extrapolation of C stocks to larger areas require to include not only aboveground biomass, but also field measurements of soil C stocks and to consider differences among vegetation types, species composition and geomorphological setting.

References

Adame, M.F., Hermoso, V., Perhans, K., Lovelock, C.E., Herrera, J.A.: Selecting cost-effective areas for restoration of ecosystem services, Conservation Biology, 29, 493–502, 2014

Adame, M.F., Kauffman, J.B., Medina, I., Gamboa, J.N., Torres, O., Caamal, J.P., Reza, M., and Herrera-Silveira J.A.: Carbon stocks of tropical coastal wetlands within the karstic landscape of the Mexican Caribbean, PLoS ONE, 8, 2, e56569. doi:10.1371/journal.pone.0056569., 2013.

Adame, M.F., Neil, D., Wright, S.F., and Lovelock, C.E.: Sedimentation within and among mangrove forests along a gradient of geomorphological settings, Estuar. Coast. Shelf. S., 86, 21–30, 2010.

Alongi, D.M.: Bacterial productivity and microbial biomass in tropical mangrove sediments, Microb. Ecol., 15, 59–79, 1988.

Alongi, D.M.: Present state and future of the world's mangrove forests, Environ. Conserv., 29: 331–349, 2002.

Alongi, D.M.: The Energetics of Mangrove Forests, Springer, Dordrecht, 2009.

Alongi, D.M.: Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential, Environ. Sci. Policy, 14, 462–470, 2011.

Böhner, J., McCloy, K.R., Strobl, J. [Eds.]: SAGA – Analysis and Modelling Applications. Göttinger Geographische Abhandlungen, Vol.115, 130pp, 2006.

Breiman, L.: Random Forest, Machine Learning, 45, 5-32, 2001.

Cairns, M.A., Brown, S., Helmer, E.H., and Baumgardner, G.A.: Root biomass allocation in the world's upland forests, Oecologia., 111, 1–11, 1997.

Cairns, M.A., Brown, S., Helmer, E.H., and Baumgardner, G.A.: Root biomass allocation in the world's upland forests, Oecologia, 111, 1–11, 1997.

Cartus, O., Kellndorfer, J., Walker, W., Franco, C., Bishop, J., Santos, L., Michel-Fuentes, J. M.: A national, detailed map of forest aboveground carbon stock in Mexico, Remote sensing, 6, 5559-5588, 2014.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., and Zanne, A.E.: Towards a worldwide wood economics spectrum, Ecol. Lett., 12, 351–366, 2009.

Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., and Lynch, J.C.: Global carbon sequestration in tidal, saline wetland soils, Glob. Biogeochem. Cycles, 17, 1111, doi:10.1029/2002GB001917, 2003

Chuvieco, S.E.:Teledetección ambiental, España, Ariel, 2006.

CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversdiad). Mapa de uso de suelo y vegetación de la zona costera asociada a los manglares, Región Pacífico Sur (2005), escala 1:50,000. CONABIO, Mexico, 2013.

Core Team R: A language and environment for statistical computing. R . Foundation for Statistical Computing, Vienna, Austria. URL http://www.Rproject.org/., 2015.

Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., and Kanninen, M.: Mangroves among the most carbon-rich forests in the tropics, Nat. Geosci., 4, 293–297, 2011.

Ewel, K.C., Twilley, R.R., and Ong, J.E.: Different kinds of mangroves forests provide different goods and services, Glob. Ecol. Biogeogr. Lett., 7, 83–94, 1998.

Flores, O., and Comes, D.A.: Estimating the wood density of species for carbon stock assessments, Methods Ecol. Evol., 2, 214–220, 2011.

Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.L., and Cadamuro, L.: Structure, above-ground biomass and dynamics of mangrove ecosystems: New data from French Guiana, Oecologia., 115: 38–53, 1998.

Hooker, T.D., Compton, J.E.: Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment, Ecol. Appl., 13, 299–313, 2003.

IPCC, Intergovernmental Panel on Climate Change: Good practice guidance for land use, land-use change, and Forestry, Penman J. et al. (eds) Kanagawa, Japan: Institute for Global Environmental Strategies, 2003.

IEA, International Energy Agency, CO_2 emissions from fuel combustion- highlights. Paris, France, OECD Publishing, 134pp, 2014

INEGI (Instituto Nacional de Estadística y Geografía) Conjunto de datos vectoriales de uso del suelo y vegetación serie IV, escala 1:250,000. INEGI, Mexico, 2012.

Jones, T.G., Ratsimba, H.R., Ravaoarinorotsihoarana, L., Cripps, G., and Bey, A.: Ecological variability and carbon stock estimates of mangrove ecosystems in Northwestern Madagascar, Forests, 5, 177–205, 2014.

Kauffman, J.B., Cummings, D.L., Ward, D.E., and Babbitt, R.: Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests, Oecologia, 104, 397–408, 1995.

Kauffman, B.J., Donato, D.C., and Adame, M.F.: Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests (Protocolo para la medición, monitoreo y reporte de la estructura,

biomasa y reservas de carbono de los manglares,), Working paper 117, Center for International Forestry Research, Bogor, Indonesia, 2014a.

Kauffman, J.B., Heider, C., Norfolk, J., Payton, F.: Carbon stocks of intact mangroves and carbon emissions arising from their conversion in the Dominican Republic, Ecol. Appl., 24, 518–527, 2014b

Komiyama, A., Poungparn, S. and Kato, S.: Common allometric equations for estimate the tree weight of mangroves, J. Trop. Ecol., 21, 471–477, 2005.

Liao, C., Luo, Y., Jiang, L., Zhou, X., Wu, X., Fang, C., Chen, J., and Li, B.: Invasion of *Spartina alternifolia* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China, Ecosystems, 10, 1351–1361, 2007.

Lovelock, C.E., Bennion, V., Grinham, A., and Cahoon, D.R.: The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. Ecosystems, 14, 745–757, 2011.

Lovelock, C.E., Adame, M.F., Bennion, V., Hayes, M., O'Mara, J., Reef R., Santini, N.S.: Contemporary rates of carbon sequestration and vertical accretion of sediments in mangroves and saltmarshes of South East Queensland, Australia, Estuaries and Coasts, 37,763–771, 2014.

McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Bjork, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., and Silliman, B.R.: A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2, Front. Ecol. Environ., 9, 552–560, 2011.

McKee, K.L., Mendelssohn, I.A., and Hester, M.W.: Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*, Am. J. Bot., 75, 1352–1359, 1988.

Meinhausen, N.: Quantile regression forest., Journal of machine learning, 7, 983-990, 2006.

Morris, D.F., Richardson, N., Riddle, A.: Importing climate mitigation: The potential and challenges of international forests offsets in California climate policy. Resources for the Future Issue Brief, 2011-12

Nguyen, T.T., Dung, L.V., Nhuan, M.T., and Omori, K.: Carbon storage of a tropical mangrove forest in Mui Ca Mau National Park, Vietnam, Catena, 119–126, 2014.

Ruiz-Luna, A., Cervantes-Escobar, A., and Berlanga-Robles, C.: Assessing distribution patterns, extent and current condition of Northwest Mexico mangroves, Wetlands, 30, 717–723, 2010.

Reef, R., Feller, I.C., and Lovelock, C.E.: Nutrition of mangroves, Tree Physiol., 30: 1148–1160, 2010.

Rivera-Monroy, V.H., Day, J.W., Twilley, R.R., Vera-Herrera, and Coronado-Molina, F.: Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico, Est. Coast Shelf Sci., 40, 139-160, 1995.

SAGA GIS. System for Automatic Geoscientific Analyses, Hamburg, Germany http://www.saga-gis.org/

Schmalzer, P.A., Hinkle, C.R.: Soil dynamics following fire in *Juncus* and *Spartina* marshes, Wetlands, 1, 8-21, 1992.

Sistema Meteorológico Nacional Comisión Nacional del Agua, SMN, http://www.conagua.gob.mx/ocgc/, Accessed September 2014.

Thom, B.G.: Mangrove ecology and deltaic geomorphology: Tabasco, Mexico, J. Ecol., 55: 301-343, 1967

Thom, B.G., Wright, L.D., Coleman, J.M.: Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord River, Western Australia, J. Ecol., 63: 203-232, 1975

Tovilla, H.C., R.L.R. Salas, P.J.C. De la Presa, E.I.B. Romero, E.F. Ovalle and O.R. Gómez.: Informe final: Inventario forestal de los bosques de manglar del Soconusco, Gobierno del Estado de Chiapas, Consejo Nacional de Ciencia y Tecnología, Consejo de Ciencia y Tecnología de Chiapas, Laboratorio de Ecología de Manglares y Zona Costera, El Colegio de La Frontera Sur, Tapachula, Chiapas, México, 2007.

United Nations Educational, Scientific and Cultural Organization, http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?mode=all&code=MEX+23, 2013.

Woodroffe, C.: Mangrove sediments and geomorphology, In Tropical Mangrove Ecosystems, John Wiley & Sons, American Geophysical Union, 1992.

Williams, S., and Self, S.: The October 1902 plinian eruption of Santa Maria Volcano, Guatemala, J. Volc. Geot. Res., 16, 33–56,1983

Yimer, F., Ledin, S., and Abdelkair, A.: Soil organic carbon and total nitrogen stocks affected by topographic aspect and vegetation in the Bale Mountains, Ethiopia, Geoderma, 135, 335-344, 2006.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F., and Hall, J.S.: Estimating carbon stock in secondary forests: Decisions and uncertainties associated with allometric biomass models, For. Ecol. Manag., 262, 1648–1657, 2011.

van der Werf, G.R., Morton, D.C., DeFries, R.S., Olivier, J.G.J., Kasibhatla, P.S., Jackson, R.B., Collatz, G.J., and Randerson, J.T.: CO_2 emissions from forest loss, Nat. Geosci., 2, 737–738, 2009.

van Wagner, C.E.: The line intersect method in forest fuel sampling. Forest Sci., 24, 469–483, 1968.

Zanne, A.E., G.,Lopez-Gonzalez, D.A., Coomec, J., Ilic, S., Jansen, S.L., Lewis, R.B., Miller, N.G., Swenson, M.C., Wiemann, J. Chave. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository, 2009. http://dx.doi.org/10.5061/dryad.234

Acknowledgements

We want to thank the Australian Rivers Institute at Griffith University, the Mexican Fund for the Conservation of Nature (Fondo Mexicano para la Conservación de la Naturaleza (FMCN), A.C.) and the USDA Forest Service. Funding for the study was provided by the US Agency for International Development (USAID Mexico) as part of a workshop on quantification of wetland carbon stocks. We wish to thank the participants of this workshop for their contributions on data collection in the field. We are grateful for field support to the National Commission for Natural Protected Areas (CONANP) and to Dr. Vanessa Valdez, Juan Manuel Frausto Leyva and Richard Birdsey for logistic support. Finally, we thank the Secretariat of the Navy, Mexico and the National Comission for Knowledge and Use of Biodiversity (CONABIO) which contributed with their data from the project "Mexican mangroves, current state and long term monitoring".

Author contribution

MFA designed the project, led the field campaign, collected the data and wrote the manuscript. NSS designed the project, performed data analysis and participated in writing and preparation of the manuscript. CT participated in field campaign, collected data and contributed to the manuscript. AV prepared the geographical information system data and map, and AV and MAGS performed data analysis and contributed to the manuscript. LC participated in the field campaign, collected data and contributed to the manuscript.

Table 1. Characteristics of sampling sites within La Encrucijada Biosphere Reserve. Values are shown as mean (standard error). Max = maximum; DBH = diameter at breast height; n.a. = not assessed; *Rm* = *Rhizophora mangle; Ag* = *Avicennia germinans; Lr* = *Laguncularia racemosa*

	Max height (m)	DBH (cm)	Tree density (trees ha^{-1})	Salinity (ppt)	Dominant species
MANGROVES					
Upper estuary					
Panzacola	40	10.5 (1.1)	1,213 (278)	n.a.	*Rm* (97.5%)
Teculapa	30	7.5 (1.0)	2,761 (398)	19.3 (5.3)	*Rm* (94.5%)
Paistalon	25	9.9 (0.9)	2,035 (134)	n.a.	*Rm* (100%)
Intermediate					
Esterillo	n.a.	8.8 (1.0)	3,346 (148)	37.6 (5.3)	*Rm* (87.7%), *Ag* (12.3%)
Sta Chila	22	9.9 (0.6)	2,371 (157)	37.5 (0.6)	*Rm* (68.9%), *Ag* (25.1%)
Lower estuary					
Zacapulco	n.a.	8.8 (0.8)	1,765 (274)	7.6 (0.4)	*Rm* (87.6%), *Lr* (10.6%)
Las Palmas	28	7.9 (0.4)	5,370 (388)	28.9 (0.6)	*Ag* (83.2%), *Lr* (13.9%)
PEAT SWAMP	22	14.5 (0.9)	2,469 (301)	0.0 (0.0)	*P.aquatica* (96.9%)
MARSH	3	-	-	n.a.	*T. dominguensis* (100%)

Table 2. Allometric equations used to calculate aboveground and belowground biomass (kg) of mangrove and peat swamp trees. AGB= Aboveground biomass; BGB= Belowground biomass; D_R = diameter above highest prop root (cm); DBH = diameter at breast height. Wood density (g cm^{-3}) values used for calculating belowground biomass were obtained from Chave et al. (2009) and Zanne et al. (2009)

Aboveground biomass		
R. mangle	$AGB = 0.1282*D_R^{2.6}$	Fromard et al. 1998
A. germinans	$AGB = 0.140*DBH^{2.4}$	
L. racemosa	$AGB = 0.1023*DBH^{2.5}$	
Pachira sp.	$lnAGB = -2.514 + 2.295*lnDBH$	Van Greugel et al. 2011
Belowground biomass		
R. mangle	$BGB = 0.199*(0.84^{0.899})*(D_R^{2.22})$	Komiyama et al. 2005
A. germinans	$BGB = 0.199*(0.67^{0.899})*(DBH^{2.22})$	
L. racemosa	$BGB = 0.199*(0.60^{0.899})*(DBH^{2.22})$	
P. aquatica	$BGB = Exp(-1.0587 + 0.8836*lnAGB)$	Cairns et al. 1997

774 Table 3. Aboveground biomass, belowground biomass (Mg ha^{-1}) and total carbon (C)
775 in vegetation (MgC ha^{-1}) within wetlands of La Encrucijada Biosphere Reserve. Values
776 are shown as mean (standard error). Different letters indicate significant differences
777 among sites ($p < 0.05$). The marsh was not included in analysis due to missing
778 belowground biomass.

	Biomass (Mg ha^{-1})		C (MgC ha^{-1})
Site	Aboveground	Belowground	
Mangroves			
Panzacola	383.6(153.6)^{ab}	127.9 (47.6)^{ab}	234.0 (92.3)^{ab}
Teculapa	342.4 (87.0)^{ab}	118.3 (20.4)^{ab}	210.5 (49.4)^{ab}
Paistalon	391.6 (87.0)^{ab}	140.0 (25.4)^{ab}	242.6 (51.6)^{ab}
Esterillo	621.3 (310.9)^{b}	203.1 (85.1)^{b}	377.4 (182.4)^{bc}
Santa Chila	198.8 (13.4)^{a}	93.9 (3.8)^{ab}	132.1 (7.8)^{a}
Zacopulco	303.5 (76.5)^{a}	127.8 (29.9)^{a}	195.5 (48.3)^{ab}
Las Palmas	706.6 (172.6)^{b}	268.7 (52.5)^{c}	440.0 (103.1)^{c}
Peat swamp	162.2 (27.3)^{a}	43.5 (6.8)^{a}	95.1 (15.7)^{a}
Marsh	76.5 (11.6)^{a}	n.a.	38.2 (5.8)

779

780

Table 4. Biomass (Mg ha^{-1}) and C stocks (MgC ha^{-1}) of downed wood in La Encrucijada Biosphere Reserve. Wood debris was calculated separately for small wood (diameter > 2.5 and < 7.5 cm), and large sound and large rotten wood (diameter > 7.5 cm). Values are shown as mean (standard error).

	Site	Small wood (< 7.5 cm) (Mg ha^{-1})	Large wood (> 7.5 cm) (Mg ha^{-1})		C stock (MgC ha^{-1})
			Sound	Rotten	
Mangroves	Panzacola	5.8 (1.0)	79.8 (24.0)	1.4 (0.6)	43.5 (15.5)
	Teculapa	10.3 (2.8)	14.0 (4.4)	3.4 (1.3)	11.9 (3.0)
	Paistalon	5.3 (1.1)	7.7 (2.7)	5.8 (3.0)	9.4 (2.2)
	Esterillo	5.5 (0.9)	0.5 (0.4)	4.5 (1.4)	5.3 (0.4)
	Santa Chila	6.6 (1.9)	5.7 (1.7)	10.8 (3.5)	11.5 (1.9)
	Zacapulco	4.4 (1.3)	88.9 (26.7)	111.5 (45.2)	102.4 (27.0)
	Las Palmas	4.4 (0.9)	34.1 (11.1)	5.7 (2.1)	22.1 (6.6)
Peat swamp		9.2 (1.5)	3.0 (1.6)	20.4 (6.2)	12.5 (2.8)

787
788 Table 5. Soil carbon (C) and nitrogen (N) concentrations (%), and soil C and N stock
789 (Mg ha^{-1}) at different depths (0- 150 cm) of wetlands from La Encrucijada Biosphere
790 Reserve. Values are shown as mean (standard error). Different letters indicate
791 significant differences between sites ($p < 0.05$).

Site	Depth (cm)	C (%)	N (%)	C stock (Mg ha^{-1})	N stock (Mg ha^{1})
Panzacola	0- 15	16.6 (1.5)	0.88 (0.08)	71.0 (4.2)	3.6 (0.2)
	15-30	14.6 (3.7)	0.76 (0.19)	37.9 (7.1)	1.9 (0.3)
	30-50	21.0 (2.8)	0.92 (0.13)	73.6 (7.8)	3.5 (0.5)
	> 50	26.8 (1.4)	1.04 (0.07)	451.6 (30.0)	17.5 (1.3)
	Total			634.0 (25.7)[a]	26.5 (1.1)[ac]
Teculapa	0- 15	14.8 (4.0)	0.78 (0.20)	64.3 (9.1)	3.7 (0.4)
	15-30	20.1 (3.9)	0.76 (0.21)	68.6 (6.7)	2.6 (0.5)
	30-50	8.8 (3.7)	0.37 (0.16)	59.4 (11.8)	2.4 (0.5)
	> 50	15.9 (3.1)	0.67 (0.12)	421.2 (29.5)	18.4 (1.4)
	Total			613.6 (32.2)[a]	27.2 (2.0)[ac]
Paistalon	0- 15	22.3 (4.4)	0.82 (0.15)	91.6 (7.5)	3.6 (0.4)
	15-30	19.4 (4.0)	0.82 (0.16)	63.0 (6.5)	2.6 (0.2)
	30-50	13.0 (4.0)	0.50 (0.13)	69.6 (9.0)	2.9 (0.1)
	> 50	17.1 (3.9)	0.71 (0.17)	389.4 (21.1)	16.4 (1.3)
	Total			613.6 (23.6)[a]	25.4 (1.5)[ac]
Esterillo	0- 15	20.4 (3.7)	0.95 (0.18)	98.1 (6.6)	4.8 (0.4)
	15-30	21.7 (4.2)	0.91 (0.17)	66.7 (8.2)	3.1 (0.4)
	30-50	16.5 (4.1)	0.65 (0.15)	88.1 (14.3)	3.1 (0.6)
	> 50	16.1 (3.4)	0.56 (0.11)	479.3 (44.6)	2.6 (0.2)
	Total			732.2 (53.8)[b]	13.6 (1.1)[ab]
Santa Chila	0- 15	29.1 (1.3)	1.30 (0.06)	66.1 (6.2)	3.1 (0.4)

	15-30	23.2 (2.4)	1.08 (0.12)	47.2 (5.6)	2.8 (0.3)
	30-50	12.0 (2.6)	0.45 (0.09)	71.9 (8.8)	3.4 (0.4)
	> 50	14.8 (1.7)	0.49 (0.07)	317.7 (83.8)	11.7 (3.3)
	Total			393.0 (128.8)[ac]	16.9 (5.7)[ab]
Zacapulco	0- 15	12.4 (2.9)	0.58 (0.15)	49.6 (8.1)	2.9 (0.6)
	15-30	11.8 (3.7)	0.58 (0.20)	37.9 (5.6)	3.8 (1.5)
	30-50	3.9 (1.6)	0.18 (0.06)	45.5 (10.9)	1.3 (0.5)
	> 50	8.5 (1.5)	0.34 (0.06)	247.2 (61.2)	12.7 (2.1)
	Total			380.1 (68.6)[ac]	15.5 (4.3)[ab]
Las Palmas	0- 15	6.2 (1.2)	0.32 (0.07)	43.1 (5.5)	2.8 (0.3)
	15-30	1.7 (0.4)	0.09 (0.03)	20.3 (3.1)	1.3 (0.2)
	30-50	1.2 (0.2)	0.07 (0.01)	28.0 (5.5)	1.5 (0.2)
	> 50	0.8 (0.3)	0.04 (0.01)	83.4 (34.7)	3.5 (1.3)
	Total			174.8 (41.9)[c]	9.1 (1.7)[b]
Peat swamp	0- 15	16.3 (5.5)	1.05 (0.32)	59.5 (15.13)	3.6 (0.1)
	15-30	19.2 (5.9)	1.18 (0.41)	70.3 (26.1)	3.6 (1.2)
	30-50	30.0 (7.2)	1.69 (0.35)	105.0 (21.8)	6.8 (1.4)
	> 50	16.7 (5.2)	1.02 (0.39)	379.8 (68.8)	26.4 (5.6)
	Total			614.6 (85.7)[a]	40.4 (5.5)[c]
Marsh	0- 15	15.6 (4.0)	1.10 (0.28)	38.3 (7.9)	3.0 (0.5)
	15-30	6.9 (1.8)	0.42 (0.08)	32.0 (6.0)	2.8 (0.3)
	30-50	13.0 (3.0)	0.65 (0.17)	113.8 (19.2)	5.8 (0.8)
	> 50	4.7 (0.9)	0.24 (0.03)	114.1 (21.1)	6.8 (0.7)
	Total			298.3 (39.0)[c]	18.5 (1.7)[ab]

794
795 Table 6. Ecosystem C stocks (MgC ha^{-1}) for wetlands of La Encrucijada Biosphere

796 Reserve. Values are shown as mean (standard error).

Vegetation		Site	C (MgC ha^{-1})
Mangrove	Upper estuary	Panzacola	911.6 (74.5)
		Teculapa	835.8 (42.2)
		Paistalon	865.6 (55.1)
		mean	871.0 (22.0)
	Intermediate	Esterillo	1,114.9 (150.3)
		Santa Chila	536.6 (88.8)
		mean	825.8 (289.2)
	Lower estuary	Zacapulco	678.1 (115.7)
		Las Palmas	640.9 (114.8)
		mean	659.5 (18.6)
	Mangrove mean		784.5 (73.5)
Peat swamp			722.2 (63.6)
Marsh			336.5 (38.3)

797
798

799
800 Table 7. Soil carbon (C) sequestration rates (MgC ha^{-1} yr^{-1}) of mangroves within La
801 Encrucijada Biosphere Reserve, Mexico.
802

	Site	Soil C sequestration rate (Mg ha^{-1} yr^{-1})
Upper estuary	Panzacola	1.0 (0.1)
	Teculapa	1.4 (0.1)
	Paistalon	1.7 (0.1)
Intermediate	Esterillo	1.8 (0.1)
	Santa Chila	1.3 (0.1)
Lower estuary	Zacapulco	1.5 (0.0)
	Las Palmas	0.4 (0.0)
	MEAN	1.3 (0.2)

803
804

Figure legends

Fig. 1. Mangrove, peat swamp and marsh sampling sites within La Encrucijada Biosphere Reserve, Mexico. Mangroves were classified according the NDVI (see methods) in three classes, which broadly corresponded to a range of mangroves from the upper to the lower estuary.

Fig. 2. Aboveground (A) (trees and shrubs and down wood) and belowground (B) (soil at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves, peat swamp forests and marsh wetlands within La Encrucijada Biosphere Reserve.

Fig. 3. Aboveground (A) (trees and shrubs and down wood) and belowground (B) (soil at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves along a gradient from the upper to the lower estuary within La Encrucijada Biosphere Reserve.

Fig. 4. Aboveground C stocks (trees) (Mg ha^{-1}) (A) estimated for the sampling locations within La Encrucijada Biosphere Reserve; (B) uncertainty associated to estimations; and (C) frequency of occurrence of estimated C stock values within mangroves within La Encrucijada Biosphere Reserve

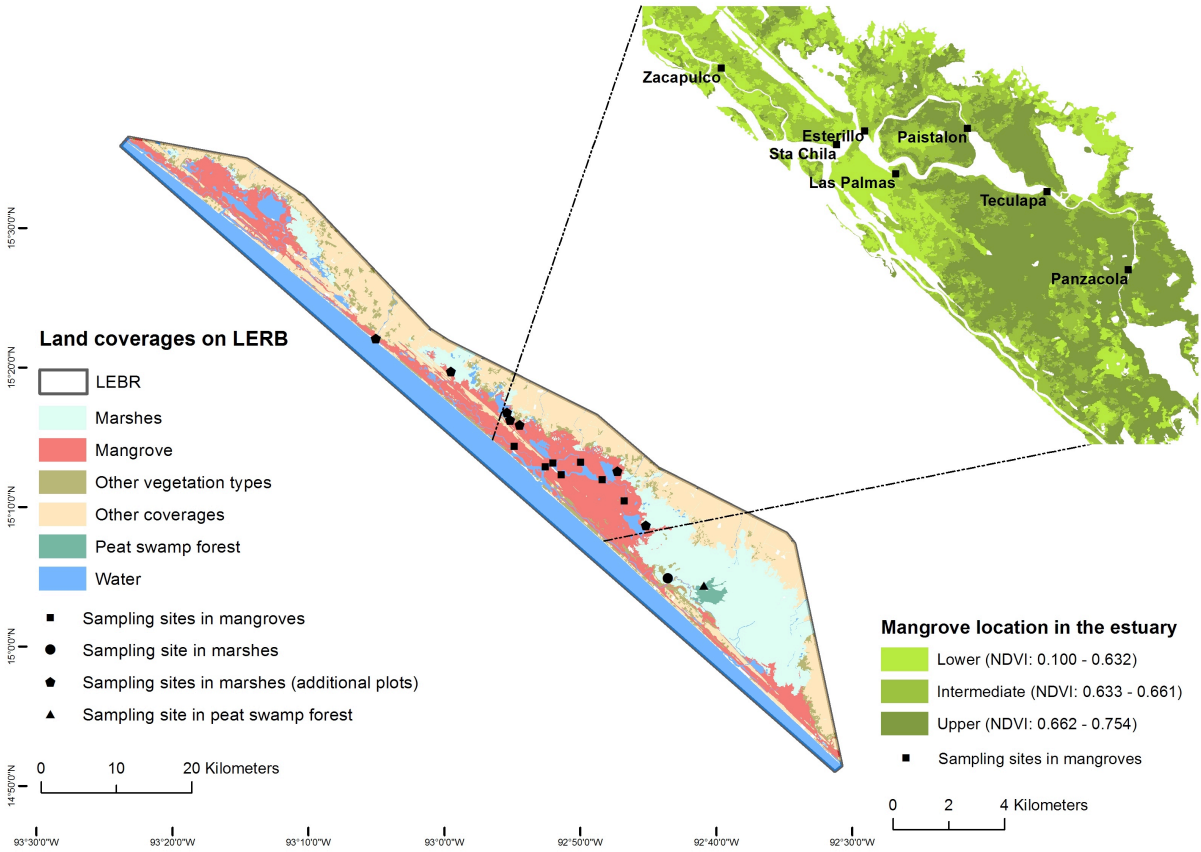
Zacapulco
Esterillo
Sta Chila
Paistalon
Las Palmas
Teculapa
Panzacola
Land coverages on LERB
LEBR
Marshes
Mangrove
Other vegetation types
Other coverages
Peat swamp forest
Water
Sampling sites in mangroves
Sampling site in marshes
Sampling sites in marshes (additional plots)
Sampling site in peat swamp forest
0 10 20 Kilometers
Mangrove location in the estuary
Lower (NDVI: 0.100 - 0.632)
Intermediate (NDVI: 0.633 - 0.661)
Upper (NDVI: 0.662 - 0.754)
Sampling sites in mangroves
0 2 4 Kilometers
15°30'0"N
15°20'0"N
15°10'0"N
15°0'0"N
14°50'0"N
93°30'0"W
93°20'0"W
93°10'0"W
93°0'0"W
92°50'0"W
92°40'0"W
92°30'0"W

Figure 1

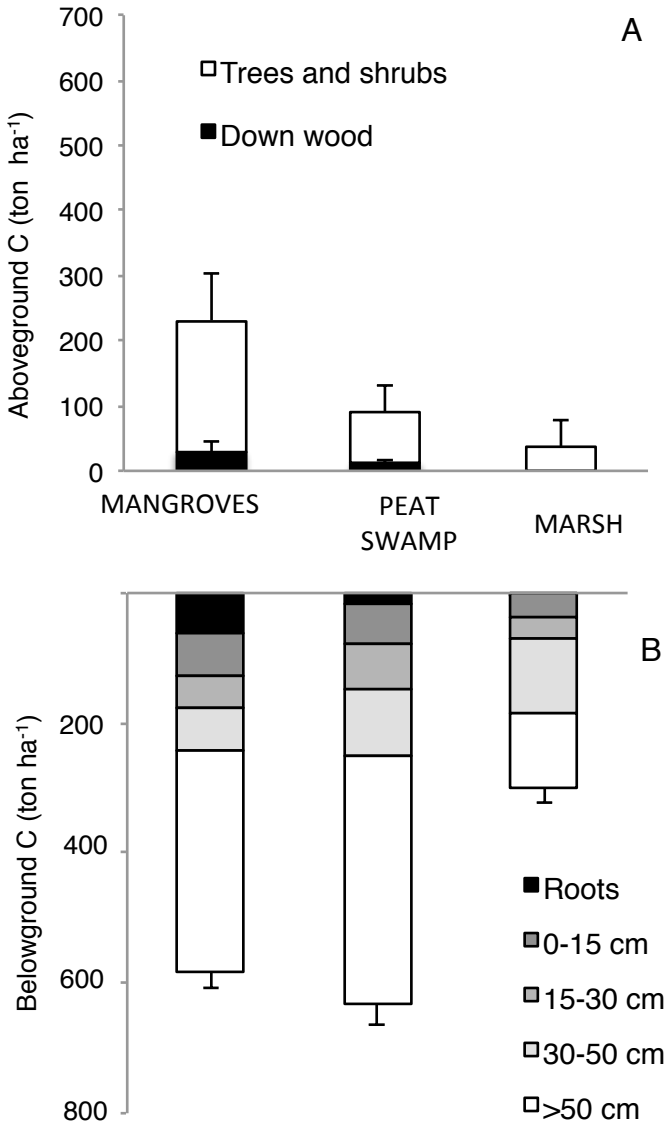
A
Trees and shrubs
Down wood
Aboveground C (ton ha-1)
700
600
500
400
300
200
100
0
MANGROVES
PEAT SWAMP
MARSH
B
Belowground C (ton ha-1)
200
400
600
800
Roots
0-15 cm
15-30 cm
30-50 cm
>50 cm

Figure 2

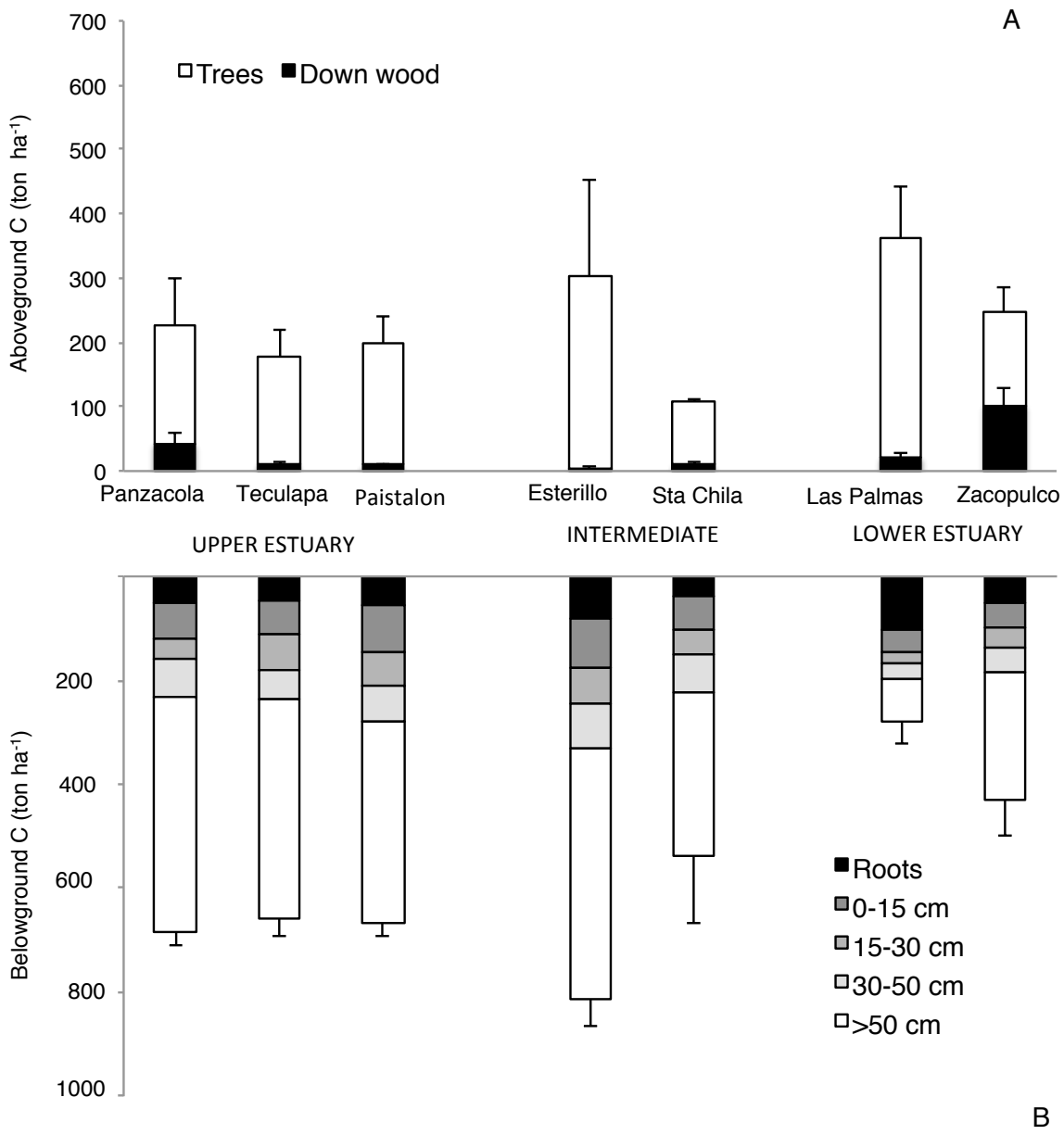
A
Trees
Down wood
Aboveground C (ton ha-1)
700
600
500
400
300
200
100
0
Panzacola
Teculapa
Paistalon
Esterillo
Sta Chila
Las Palmas
Zacopulco
UPPER ESTUARY
INTERMEDIATE
LOWER ESTUARY
Belowground C (ton ha-1)
200
400
600
800
1000
Roots
0-15 cm
15-30 cm
30-50 cm
>50 cm
B

Figure 3

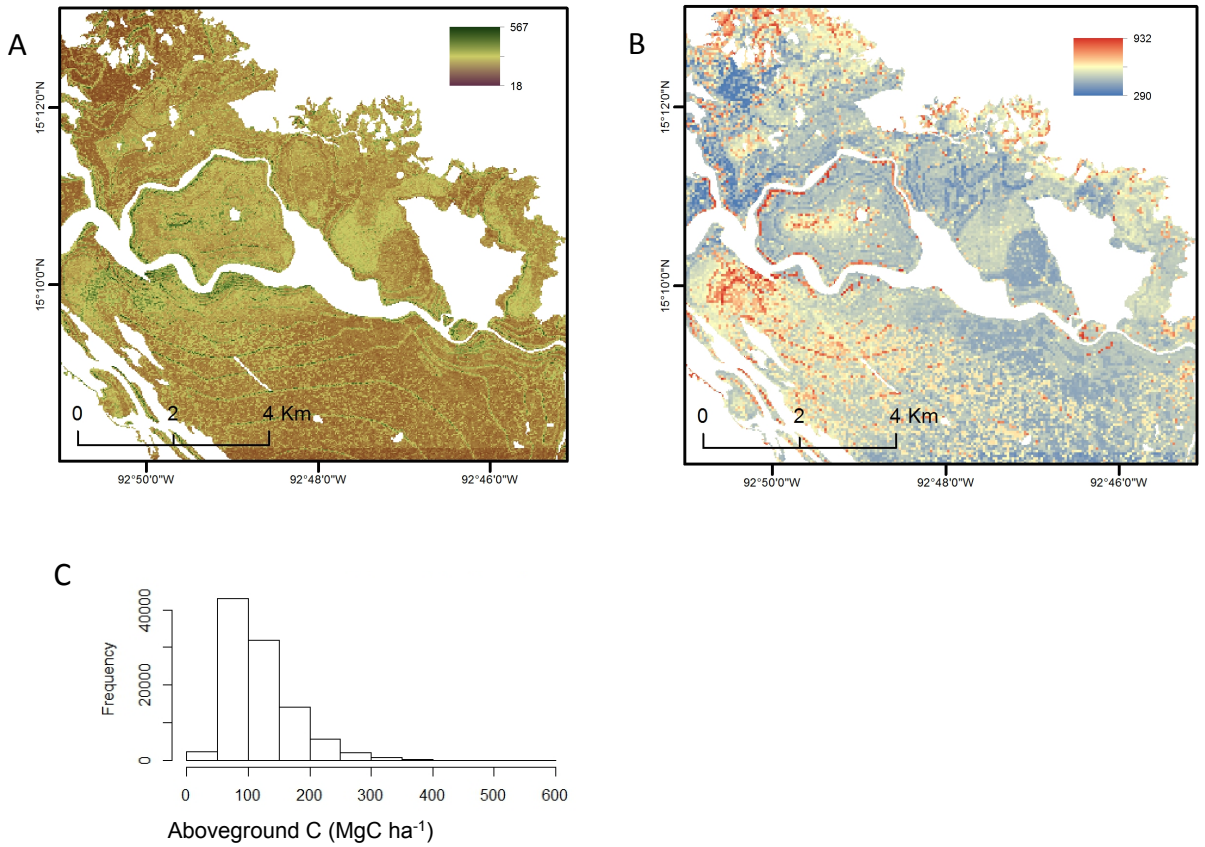
A
567
18
15°12'0"N
15°10'0"N
0
2
4 Km
92°50'0"W
92°48'0"W
92°46'0"W
B
932
290
15°12'0"N
15°10'0"N
0
2
4 Km
92°50'0"W
92°48'0"W
92°46'0"W
C
Frequency
0
20000
40000
0
100
200
300
400
500
600
Aboveground C (MgC ha-1)

Figure 4