Biogeosciences Discuss., 12, 1015–1045, 2015
www.biogeosciences-discuss.net/12/1015/2015/
doi:10.5194/bgd-12-1015-2015

Biogeosciences Discussions
Open Access

Carbon stocks and soil sequestration rates of riverine mangroves and freshwater wetlands

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Received: 3 November 2014 – Accepted: 29 November 2014 – Published: 16 January 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Deforestation and degradation of wetlands are important causes of carbon dioxide emissions to the atmosphere. Accurate measurements of carbon (C) stocks and sequestration rates are needed for incorporating wetlands into conservation and restoration programs with the aim for preventing carbon emissions. Here, we assessed whole ecosystem C stocks (trees, soil and downed wood) and soil N stocks of riverine wetlands (mangroves, marshes and peat swamps) within La Encrucijada Biosphere Reserve in the Pacific coast of Mexico. We also estimated soil C sequestration rates of mangroves on the basis of soil accumulation. We hypothesized that riverine wetlands have large C stocks, and that upland mangroves have larger C and soil N stocks compared to lowland mangroves. Riverine wetlands had large C stocks with a mean of 784.5 ± 73.5 Mg C ha^{-1} for mangroves, 722.2 ± 83.4 Mg C ha^{-1} for peat swamps, and 336.5 ± 38.3 Mg C ha^{-1} for marshes. C stocks and soil N stocks were in general larger for upland (833.0 ± 7.2 Mg C ha^{-1}; 26.4 ± 0.5 Mg N ha^{-1}) compared to lowland mangroves (659.5 ± 18.6 Mg C ha^{-1}; 13.8 ± 2.0 Mg N ha^{-1}). Soil C sequestration values were 1.3 ± 0.2 Mg C ha^{-1} yr^{-1}. The Reserve stores 32.5 Mtons of C or 119.3 Mtons of CO_2, with mangroves sequestering (via soil accumulation) $27\,762 \pm 0.5$ Mg C ha^{-1} every year.

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).

Wetlands, such as mangroves and marshes, are within the most efficient ecosystems for C processing and sequestration, storing 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 $Mg\,ha^{-1}$ of organic C, while mangroves in the Indo-Pacific store up to 2203 $Mg\,ha^{-1}$ (including organic and inorganic C) (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 ($\sim 10\,g\,C\,m^{-2}\,yr^{-1}$) (Chmura et al., 2003; McLeod et al., 2011).

The C accumulated in wetlands originates from organic material such as leaves, twigs and roots produced in situ, but also from allochtonous C imported through tidal and river flushing. The organic material is either degraded and processed by bacteria and fungi, or buried within the soil (Holguin et al., 2001; Middleton and McKee, 2001; Kristensen et al., 2008). The amount of C produced and sequestered within a wetland depends on its geomorphological setting, which influences patterns of tidal and river flushing, and therefore the import and export of suspended sediment and organic matter (Eyre, 1993; Adame et al., 2010). Riverine wetlands are one of the most extensive, and are characterized by mature forests with large amounts of organic material and suspended sediment inputs (Woodrofe, 1992; Eyre, 1993). It has been suggested that riverine wetlands have one of the largest C stocks (Ewel et al., 1998).

Wetlands are efficient at accumulating nitrogen (N) in the soil when production exceeds N demand (e.g. Rivera Monroy et al., 1995). In the past century, increased anthropogenic derived N and inefficiencies in its use have resulted in a cascade of

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environmental problems (Galloway et al., 2004). Wetlands can decrease N inputs to aquatic systems, but the potential for N accumulation varies with anthropogenic activity, rainfall, runoff, geomorphological setting and production by organisms such as cyanobacteria and algae (Alongi, 2009; Reef et al., 2010; Adame et al., 2012a). N accumulation also increases with foliage cover and wood biomass (e.g. Hooker and Compton, 2003; Liao et al., 2007), and given that C and N cycles interact closely, N stocks can increase with increments in C (Yimer et al., 2006).

In this study, we assessed whole ecosystem C stocks (trees, soil and downed wood) and soil N stocks of riverine wetlands (mangroves, marshes and peat swamps) within La Encrucijada Biosphere Reserve (LEBR) in the Pacific coast of Mexico. We also estimated soil C sequestration rates of mangroves on the basis of soil accumulation and C content. We predict that the riverine wetlands within the LEBR have large ecosystem C stocks and high C sequestration rates. We also predict that upland mangroves with strong riverine influence have higher soil N, C stocks and soil C sequestration rates compared to lowland mangroves, which have a stronger marine influence.

2 Methodology

2.1 Study site

The LEBR is located in Chiapas, in the south Pacific coast of Mexico (14°43′ N, 92°26′ W). 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 freshwater and estuarine wetlands including mangroves, marsh and peatswamp forests. The LEBR has one of the most extense mangrove areas of the region; the forest is dominated by trees of *Rhizophora mangle* that range between 20 and 40 m in height, which are believed to be the tallest of the country (Tovilla et al., 2007). The

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mangroves of LEBRE support a high biodiversity, as well as fisheries and tourist activity (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 19.2 °C and a mean annual maximum of 36.5 °C; mean annual precipitation is 1567 mm (Sistema Meteorológico Nacional – Comisión Nacional del Agua, station No. 7320, 1951–2010).

2.2 Site stratification

To determine a criteria for stratification of the mangroves of the area, we used two SPOT 5 satellite images with geographical, geometric and radiometric correction, and the Universal Transverse Mercator projection system. From each image, the Normalized Difference Vegetation Index (NDVI) was obtained with ERDAS Imagine. The NDVI values ranged from −1 to 1, where negative values indicated areas without vegetation, values close to zero indicated senescent vegetation or in a stressed condition, and values close to 1, indicated green or healthy vegetation (Chuvieco, 2006). NDVI values were extracted from the mangrove coverage map (CONABIO, 2013) and classified according to Ruiz-Luna et al. (2010). The mangrove vegetation was divided in three classes: the most vigorous vegetation was Class I (9253 ha), which broadly corresponded to upland mangroves. The least vigorous vegetation was Class III (11 467 ha), which broadly corresponded to lowland or estuarine mangroves; Class II (6757 ha) had intermediate values of vegetation vigor (Fig. 1). Mangroves with low vegetation vigor were also found in forests close to human settlements (e.g. town and agricultural areas).

2.3 Field and laboratory analyses

Sampling was conducted during December 2012, where ecosystem C stocks, soil N stocks and soil C sequestration rates were measured. We sampled 9 sites: seven

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mangrove forests (3 for Class I, 2 for Class II and 2 for Class III mangroves), a peat swamp forest dominated by *Pachira aquatica* and a marsh dominated by the grass *Typha dominguensis* (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 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 cm × 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 ($t = 1.027$; df = 2284; $p = 0.30$). We chose the formula by Fromard et al. (1998) because it included trees with a DBH range similar to those found in LEBR (DBH_{Max} = 32 cm for *R. mangle*, 9.6 cm for *Laguncularia racemosa* and 42 cm for *Avicennia germinans*). Aboveground biomass of trees from the peat swamp (*P. aquatica*) were calculated with the formula of

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van Breugel et al. (2011), while belowground biomass of *P. aquatica* was determined with the equation of Cairns et al. (1997) for tropical forests. Belowground root biomass was calculated using the formula by Komiyama et al. (2005) and wood density values of Chave et al. (2009) (Table 2). Tree C was calculated from biomass by multiplying by a factor of 0.48 for aboveground and 0.39 for belowground biomass; C content of marshes was calculated using a factor of 0.45 of the total biomass (Kauffman et al., 2014a).

Standing dead trees were also included in the tree C stocks estimations. Each dead tree was assigned to one of three decay status (Kauffman et al., 2014a): Status 1 – dead trees without leaves, Status 2 – dead trees without secondary branches, and Status 3 – dead trees without primary or secondary branches. The biomass for each tree status was calculated as a percentage of the total biomass using the values provided by Fromard et al. (1998). For dead trees of Status 1, biomass was calculated as the total dry biomass minus the biomass of leaves, equivalent to 2.8 % of the total. The biomass of trees of Status 2 was calculated as the total biomass minus the biomass of leaves (2.8 % of the total) plus secondary branches (equivalent to 18.7 % of the total). 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.

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 center 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"

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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, 2011)

2.3.3 Soil C and N

Soil samples for bulk density and nutrient concentration were collected at each plot using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm-radius attached to a cross handle (Kauffman et al., 1995). The core was systematically divided into depth intervals of 0–15, 15–30, 30–50, 50–100 and > 100 cm. Soil depth was measured using a steel-2 m rod that was inserted in the ground at each plot. Samples of a known volume were collected in the field and then dried to constant mass to determine bulk density. Samples were sieved and homogenized and treated with Hydrochloric acid (HCl) to eliminate the inorganic carbon portion (carbonates) before analyses. Concentration of organic C and N were determined using a Costech Elemental Combustion System 4010 (CA, USA).

2.3.4 Soil C sequestration rates

We estimated C sequestration rates as the amount of C accumulated in the soil profile. To date the soil cores, we used a natural marker that consisted of a volcanic ash horizon that was clearly identified in all the cores. This ash horizon is the remaining of the volcano Santa Maria's eruption in 1902 that represented one of the four largest volcano eruptions of the 20th Century (Volcanic Explosivity Index of 6 out of 7, Williams and Self, 1983). As a result of the eruption, a recognizable plinian deposit of known date ashes can be established in the Mexican Pacific coast, northwest of the volcano.

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We estimated soil C sequestration within each plot of six of our mangrove sites by dividing the depth of the ash horizon by years since the volcano eruption occurred and multiplying it by bulk density of C content. Soil C sequestration rates are expressed in $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Chmura et al., 2003). We could not measure soil C sequestration rates of marsh and peat swamp forests, as these vegetation types frequently suffer from fires and thus, have confounding ash horizons.

2.3.5 Interstitial salinity

Salinity was measured with an YSI-30 multiprobe sensor (YSI, Xylem Inc. Ohio, USA) from water extracted from 30 cm deep. The water was obtained with a syringe and an acrylic tube (McKee et al., 1988).

2.4 Scaling up

We multiplied mean ecosystem C stocks and sequestration rates times the estimated area of each vegetation type to obtain the C budget for the LBRE. For mangroves, we used the area on the basis of our forest classification (Classes I, II and II; see above), which broadly represented a range from upland to downland mangroves. For marsh, we determined its area 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 slightly over or underestimated, as the marsh area includes waterholes and inundated vegetation ("popales") with unknown C stocks. The area of peat swamp forest is not available for the LEBR, and we could only identify from the satellite images the forest where our sampling was conducted (844 ha; Fig. 1). Therefore, the C stock of peat swamp forests was underestimated.

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2.5 Statistical analyses

Analysis of Variance (ANOVA) was performed to test differences of biomass and C stocks among mangrove classes (Classes I, II and III), where class was the fixed effect and plot (nested in site) was the random effect of the model. ANOVA models were also used to test differences of biomass and C stocks among sites, where plot (nested in site) was the random effect of the model. Differences in soil C and N concentrations by depth were also tested with ANOVA, with depth as the fixed effect and site 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 ver 6.0 (GraphPad Software, La Jolla, CA, USA) and SPSS Statistics (version 20, IBM, New York, USA). Throughout the manuscript, data are reported as mean ± standard error.

3 Results

3.1 Forest structure

Mangroves of the LEBR were dominated by trees of *R. mangle* with lesser contributions of *A. germinans, L. racemosa* and few trees of *R. harrisonii* (in sites Panzacola and Teculapa). Only one of our study sites – Las Palmas – was dominated by a different species, *A. germinans*. All the sampling sites were characterized by relatively low tree density forests (1213–5370 trees ha^{-1}) with tall trees (~ 20–40 m in height) of mean DBH of 8–11 cm (Table 1). The peat swamp forest was dominated by *P. aquatica* and had a similar structure than that of mangroves with a tree density of 2469 trees ha^{-1}, trees of up to 22 m in height and mean DBH of 14.5 cm. Finally, the marsh was dominated by tall grasses (2–3 m in height) of *T. dominguensis* (Table 1).

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3.2 Tree biomass and C

Mean tree aboveground and belowground biomass of mangroves was 421.1 ± 67.8 and $154.3 \pm 22.9\,\mathrm{Mg\,ha^{-1}}$, respectively. Lowest biomass (above and belowground) was measured at Santa Chila (198.8 ± 13.4 and $93.9 \pm 3.8\,\mathrm{Mg\,ha^{-1}}$) and largest at Las Palmas (706.6 ± 172.6 and $268.7 \pm 52.5\,\mathrm{Mg\,ha^{-1}}$) (Table 3).

Mean C stock in mangrove trees at LEBR was $215.0 \pm 44.4\,\mathrm{Mg\,C\,ha^{-1}}$ and was similar throughout upland and lowland forests. However, the site Las Palmas and Esterillo ($> 620\,\mathrm{Mg\,C\,ha^{-1}}$) had significantly higher C stocks in trees compared to Santa Chila and Zacapulco ($< 304\,\mathrm{Mg\,C\,ha^{-1}}$) ($F_{7,47} = 1.826$; $p < 0.05$). The swamp forest and marsh vegetation had lower vegetation C stocks ($95.1 \pm 15.7\,\mathrm{Mg\,C\,ha^{-1}}$and $38.2 \pm 5.8\,\mathrm{Mg\,C\,ha^{-1}}$, respectively, Table 3).

3.3 Downed wood C

Downed wood was insignificant in marsh and peat swamp forests, although it was considerable in some mangrove sites. The amount of downed wood in mangroves had a wide range within sites, from 11 to $205\,\mathrm{Mg\,ha^{-1}}$, with a mean biomass of $59.4 \pm 26.0\,\mathrm{Mg\,ha^{-1}}$ (Table 4). Down land mangroves (Class III) 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 ($102.4 \pm 27.0\,\mathrm{Mg\,C\,ha^{-1}}$) ($F_{7,47} = 8.147$; $p < 0.0001$). Small downed wood comprised 10.2 % of the total biomass ($6.0 \pm 0.8\,\mathrm{Mg\,ha^{-1}}$); large sound wood the 55.4 % ($33.0 \pm 13.9\,\mathrm{Mg\,ha^{-1}}$) and large rotten wood comprised 34.4 % of the total ($20.4 \pm 15.2\,\mathrm{Mg\,ha^{-1}}$). The mean C stock within downed wood was $29.4 \pm 3.7\,\mathrm{Mg\,C\,ha^{-1}}$.

3.4 Soil C

Soil C in mangroves accounted for 65 ± 7.8 % (between 18.4 % in Las Palmas to 87.2 % in Esterillo) of the total C stock. Most of the soil C was organic, with a contribution >

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86 % for all sites (Table 5). Mangrove soil C stock had a mean of 505.9±72.6 Mg C ha^{-1}. Upland mangroves had higher soil C (620.4 ± 6.8 Mg C ha^{-1}) than lowland mangroves (562.6 ± 169.6 Mg C ha^{-1} for Class II and 277.5 ± 102.7 Mg C ha^{-1} for Class III), but differences were not significant due to large soil C values at Esterillo (Class II). When Esterillo was not included in the analysis, upland mangroves exhibited significantly higher soil C than downland mangroves ($F_{2,5} = 9.42$; $p = 0.02$). The peat swamp had a similar soil C stock than upland mangroves (620.4 ± 6.8 Mg C ha^{-1}) while the marsh had the lowest soil C stock with 298.3 ± 39.0 Mg C ha^{-1}.

Surface soil C content (%) had a mean of 17.4 ± 2.8 %, with a minimum value at Las Palmas (6.2±1.2 %) and a maximum value at Santa Chila (29.1 ± 1.3 %). Surface soil N (%) was variable, with a mean of 2.70±0.52 % and a wide range between 0.32±0.07 % (Las Palmas) and 1.30 ± 0.06 % (Santa Chila). Soil C values increased with depth at Panzacola, remained similar in depth in Teculapa and Paistalon and decreased in depth at the rest of the lowland mangroves (Class II Esterillo, Santa Chila, and Class III Zacapulco and Las Palmas) (Table 5). Finally, soil N was higher in upland mangroves (Class I; 26.4±0.5 Mg ha^{-1}) compared to lowland mangroves (Class II and III with 15.3± 1.6 Mg ha^{-1} and 12.3 ± 3.2 Mg ha^{-1}, respectively) (Table 5). There was a decreasing gradient of C and N stocks from the most upland mangrove site (Panzacola) to lowland mangroves (Las Palmas, Santa Chila and Zacopulco, Table 5).

The peat swamp forest had soil surface C and N concentrations similar to those of mangroves (16.3 ± 15.3 % and 1.05 ± 0.77 %, respectively) and the highest N stock of all wetlands (40.4 ± 5.5 Mg ha^{-1}). The marsh had surface soil C and N concentrations (15.6 ± 4.0 % C and 1.10 ± 0.28 % de N) and N stocks (18.5 ± 1.7 Mg ha^{-1}) similar to those of mangroves and peat swamp forests (Table 5).

3.5 Ecosystem C stocks

Mean C stocks of mangroves in LEBR had a mean of 784.5 ± 73.5 Mg C ha^{-1}. Lowest C stocks were measured in the most lowland mangroves, i.e. those with

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highest marine influence (Class III; 659.5 ± 18.6 $\mathrm{Mg\,C\,ha^{-1}}$). Largest C stocks were measured at Esterillo (1114.9 ± 150.3 $\mathrm{Mg\,C\,ha^{-1}}$) and lowest at Las Palmas (640.9 ± 151.9 $\mathrm{Mg\,C\,ha^{-1}}$), the forest dominated by *A. germinans*. The peat swamp forest had similar C stocks than mangrove forests (722.2 ± 63.6 $\mathrm{Mg\,C\,ha^{-1}}$). Finally, marshes had the lowest ecosystem C stock with 336.5 ± 38.3 $\mathrm{Mg\,C\,ha^{-1}}$ (Fig. 2, Table 6).

3.6 C stocks of LEBR

By extrapolating the mangrove area by classes (Classes I, II and III) and excluding deteriorated forests, we estimated the C stock of mangrove forest of LEBR to be of 20.9 millions of Mg. The C stock of marshes was estimated to be close to 11.0 millions of Mg and that of peat swamps of at least 0.6 millions of Mg (Table 7). The total C stock for wetlands in LEBR was estimated to be around 32.5 millions of Mg.

3.7 Soil C sequestration rates

Mean soil C sequestration rates in mangroves was 1.3 ± 0.2 $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ and was similar among upland and lowland mangroves. Lowest values (0.4 ± 0.0 $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) were measured in the site dominated by *A. germinans* (Table 8).

4 Discussion

The riverine wetlands measured in this study had large C stocks, which were almost double than those measured in terrestrial forests (typically < 400 $\mathrm{Mg\,C\,ha^{-1}}$, IPCC, 2003). Mangroves had a mean ecosystem C stock of 784.5 ± 73.5 $\mathrm{Mg\,C\,ha^{-1}}$, with a maximum of 1115 $\mathrm{Mg\,C\,ha^{-1}}$, values similar to those measured in riverine mangroves in Vietnam (762.2 ± 57.2 $\mathrm{Mg\,C\,ha^{-1}}$, Nguyen et al., 2014) and the Dominican Republic (853 $\mathrm{Mg\,C\,ha^{-1}}$, Kauffman et al., 2014b). Our mangrove C stock estimations were higher than those in karstic settings in Yucatan, Mexico (mean of 663 ± 176 $\mathrm{Mg\,C\,ha^{-1}}$; Adame et al., 2013) and those in Northwest Madagascar (367–593 $\mathrm{Mg\,C\,ha^{-1}}$; Jones

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et al., 2014). Peat swamp forests had similar large C stocks with 722.2±83.4 Mg C ha^{-1}. Lowest C stocks were measured at the marshes with 336.5 ± 38.3 Mg C ha^{-1}.

In general, upland mangroves within LEBR had higher C stocks than lowland mangroves or those closer to the estuary mouth, however differences among sites were also notable. Differences in C stocks have been related to geomorphological and biological processes. For example, the location of a forest could influence the amount of sediment and its burial rate, as depositional landscapes have more soil C than eroding landscapes (Doetterl et al., 2012). Also, mangroves growing closer to the water edge have higher C stocks compared to those closer to the landward edge (Kauffman et al., 2011). Forest development and forest productivity also influence C stocks, with larger stocks in taller and more productive forests (Adame et al., 2012b).

We also found differences in soil C with depth according to geomorphological setting, with an increase in soil C with depth at the most upland mangroves and a decrease in C at the most lowland mangroves. We suggest that differences in the geomorphological and biological forces acting in riverine mangroves explain the variation in C stocks and the C distribution within the sediment column. Downland mangroves close to the mouth of the estuary are exposed to frequent changes in hydrology, sedimentology and are directly struck by tropical storms (Woodrooffe, 1992). As a result, these mangroves are likely to be young forests with low productivity, low soil C and thus, low C stocks. Comparatively, upland mangroves are likely to have higher C stocks as they are mature, productive and have high soil C as they grow in a relatively stable environment that allows C to be buried.

The N stocks within mangroves also differed according to geomorphology; higher N stocks were measured in upland compared to downland forests. 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 mangroves (Alongi, 1988). Higher nitrification and denitrification and lower

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N fixation rates could further explain low N stocks in lowland mangroves; however, this remains to be tested.

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 (0.67–0.99 $\mathrm{g\,cm^{-3}}$) than wood density of *R. mangle* (0.810–1.05 $\mathrm{g\,cm^{-3}}$), which dominated all other sites. Wood density is a major predictor of stored C in wood biomass and could explain the low values of C buried in the soil (Flores and Coomes, 2011), and thus, the low C stocks in the mangrove forest dominated by *A. germinans.*

Ecosystem C stocks were associated to soil C stocks, as this component contributes to most of the C in mangroves (Donato et al., 2011; Adame et al., 2013). The soil C sequestration rates measured in mangroves of LEBR (0.4–1.8 $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) are within the range of those reported in the review by Chmura et al. (2003), with lowest values in Rookery Bay, Florida (0.2 $\mathrm{Mg\,C\,ha^{-1}}$) and highest in Terminos Lagoon, Campeche, Mexico (6.5 $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$), and are similar to those measured in Moreton Bay, Australia (0.8 $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$; Lovelock et al., 2014). Long-term soil C sequestration rates are difficult to obtain, thus the values obtained in this study are valuable for estimations of C sequestration rates of mangrove forests. For example, we can estimate that the sequestration rate of the mangrove soil of LEBR is 27 762 $\mathrm{Mg\,C\,yr^{-1}}$, which is equivalent to the annual emissions of approximately 9143 Mexicans (using emissions by country from IEA, 2011).

Mangroves in riverine deltas are the most extensive and highly developed forests (Woodroofe, 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. Additionally, the LEBR is an important location for C studies as it is the base of C monitoring in Mexico, which includes a flux tower for monitoring daily C variations.

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The wetlands of LEBR store about 32.5 Mton C, which is equivalent to 119 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, personal communication, 2013). With the C stocks calculated in this study, we can estimate that every hectare of marsh or peat swamp forest that is burned emits 1237 ton CO_2 and 2650 ton CO_2, respectively. Every year between 500 and 4500 ha of marshes are burned within the reserve (L. Castro, personal communication, 2013), which results in an annual mean emission of $\sim$ 2.6 millions tons of C or 20.6 % of the emissions of the state of Chiapas (based on emissions reported by IEA, 2001). 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 USA, has signed an agreement to import C credits from forests 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 protecting biodiversity (Adame et al., 2014) and the various ecosystem services that mangroves provide.

Author contributions. M. F. Adame designed the project, leaded the field campaign, collected the data and wrote the manuscript. N. S. Santini designed the project, performed data analysis and participated in writing and preparation of the manuscript. C. Tovilla participated in field campaign, collected data and contributed to the manuscript. A. Vázquez-Lule prepared the geographical information system data and map, performed data analysis and contributed to the manuscript. L. Castro participated in field campaign, collected data and contributed to the manuscript.

Acknowledgements. We want to thank the Australian Rivers Institute at Griffith University and to 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 of data collection in the field. We are grateful for field support to the National Commission for Natural Protected Areas (CONANP) and to 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".

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Table 1. Characteristics of sampling sites within La Encrucijada Biosphere Reserve (LEBR). Values are shown as mean (standard error). Max = maximum; DBH = diameter at breast height. The mangrove classes represent a gradient from upland (Class I) to lowland mangroves (Class III) and were derived from a NDVI (normalized vegetation index). n.a. = not assessed.

Mangroves	Site	Max height (m)	DBH (cm)	Tree density (trees ha^{-1})	Salinity (ppt)	Dominant species
I	Panzacola	40	10.5 (1.1)	1213 (278)	n.a.	*R. mangle* (97.5 %)
	Teculapa	30	7.5 (1.0)	2761 (398)	19.3 (5.3)	*R. mangle* (94.5 %)
	Paistalon	25	9.9 (0.9)	2035 (134)	n.a.	*R. mangle* (100 %)
II	Esterillo	n.a.	8.8 (1.0)	3346 (148)	37.6 (5.3)	*R. mangle* (87.7 %) *A. germinans* (12.3 %)
	Sta Chila	22	9.9 (0.6)	2371 (157)	37.5 (0.6)	*R. mangle* (68.9 %) *A. germinans* (25.1 %)
III	Zacapulco	n.a.	8.8 (0.8)	1765 (274)	7.6 (0.4)	*R. mangle* (87.6 %) *L. racemosa* (10.6 %)
	Las Palmas	28	7.9 (0.4)	5370 (388)	28.9 (0.6)	*A. germinans* (83.2 %) *L. racemosa* (13.9 %)
Peat swamp		22	14.5 (0.9)	2469 (301)	0.0 (0.0)	*P. aquatica* (96.9 %)
Marsh		3	–	–	n.a.	*T. dominguensis* (100 %)

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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).

Aboveground biomass		
R. mangle	$AGB = 0.1282 \times D_R^{2.6}$	Fromard et al. (1998)
A. germinans	$AGB = 0.140 \times DBH^{2.4}$	
L. racemosa	$AGB = 0.1023 \times DBH^{2.5}$	
Pachira sp.	$\ln AGB = -2.514 + 2.295 \times \ln DBH$	Van Greugel et al. (2011)
Belowground biomass		
R. mangle	$BGB = 0.199 \times (0.84^{0.899}) \times (D_R^{2.22})$	Komiyama et al. (2005)
A. germinans	$BGB = 0.199 \times (0.67^{0.899}) \times (DBH^{2.22})$	
L. racemosa	$BGB = 0.199 \times (0.60^{0.899}) \times (DBH^{2.22})^{1.11}$	
P. aquatica	$BGB = \mathrm{Exp}(-1.0587 + 0.8836 \times \ln AGB)$	Cairns et al. (1997)

Table 3. Aboveground biomass, belowground biomass ($Mg\,ha^{-1}$) and total carbon (C) in vegetation ($Mg\,C\,ha^{-1}$) within La Encrucijada Biosphere Reserve. Values are shown as mean (standard error).

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

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Table 4. Biomass ($Mg\,ha^{-1}$) and C stocks ($Mg\,ha^{-1}$) of downed wood at 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 ($Mg\,C\,ha^{-1}$)
		Sound	Rotten	
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)
Sta 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)
Zapoton	9.2 (1.5)	3.0 (1.6)	20.4 (6.2)	12.5 (2.8)

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Table 5. Soil carbon (C) and nitrogen (N) concentrations (%), and soil C and N stocks ($\mathrm{Mg\,ha^{-1}}$) at different depths (0–150 cm) of wetlands from La Encrucijada Biosphere Reserve. Values are shown as mean (standard error).

Site	Depth (cm)	C (%)	N (%)	C stock ($\mathrm{Mg\,ha^{-1}}$)	N stock ($\mathrm{Mg\,ha^{1}}$)
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)	26.5 (1.1)
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)	27.2 (2.0)
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)	25.4 (1.5)
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)	13.6 (1.1)
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)	16.9 (5.7)
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)	15.5 (4.3)
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)	9.1 (1.7)
Zapotón	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. (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)	40.4 (5.5)
Tular	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)	18.5 (1.7)

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Table 6. Ecosystem C stocks for wetlands of La Encrucijada Biosphere Reserve. Values are shown as mean (standard error).

Vegetation		Site	C ($Mg\,C\,ha^{-1}$)
Mangrove	Class I	Panzacola	911.6 (74.5)
		Teculapa	743.6 (42.2)
		Paistalon	865.6 (55.1)
		mean	840.2 (50.1)
	Class II	Esterillo	1,114.9 (150.3)
		Santa Chila	536.6 (88.8)
		mean	825.8 (54.4)
	Class III	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)

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Table 7. C stocks (Millions of Mg) and their equivalent in CO_2 emissions (Millions of Mg) within wetlands of La Encrucijada Biosphere Reserve, Mexico. Mangroves were classified in Classes (I, II and III) which represented a gradient from upland (Class I) to lowland (Class III) mangroves.

Vegetation		Area (ha)	C stock (Millions of Mg)	CO_2 emisions (Millions of Mg)
Mangroves	Class I	9253	7.8	28.5
	Class II	6757	5.6	20.5
	Class III	11 467	7.6	27.8
Peat swamp		> 844	0.6	2.2
Marsh		~ 32 625	11.0	40.3
TOTAL		~ 45 543	32.5	119.3

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Table 8. Soil carbon (C) sequestration rates ($Mg\,C\,ha^{-1}\,yr^{-1}$) of mangroves within La Encrucijada Biosphere Reserve, Mexico.

Mangrove class	Site	Soil C sequestration rate ($Mg\,ha^{-1}\,yr^{-1}$)
Class I	Panzacola	1.0 (0.1)
	Teculapa	1.4 (0.1)
	Paistalon	1.7 (0.1)
Class II	Esterillo	1.8 (0.1)
	Santa Chila	1.3 (0.1)
Class III	Zacapulco	1.5 (0.0)
	Las Palmas	0.4 (0.0)
	MEAN	1.3 (0.2)

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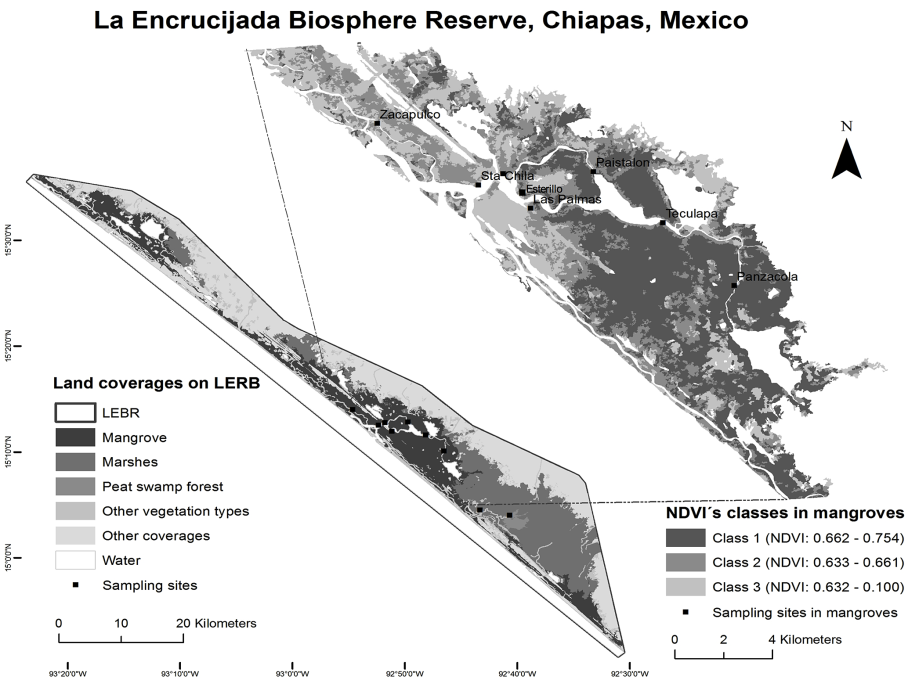

Figure 1. Sampling sites within La Encrucijada Biosphere Reserve, Chiapas, Mexico. Mangroves were classified according the NDVI (see Sect. 2) in three classes, which corresponded a range of sites from upland to lowland mangroves. A peat swamp forest and a marsh were also sampled.

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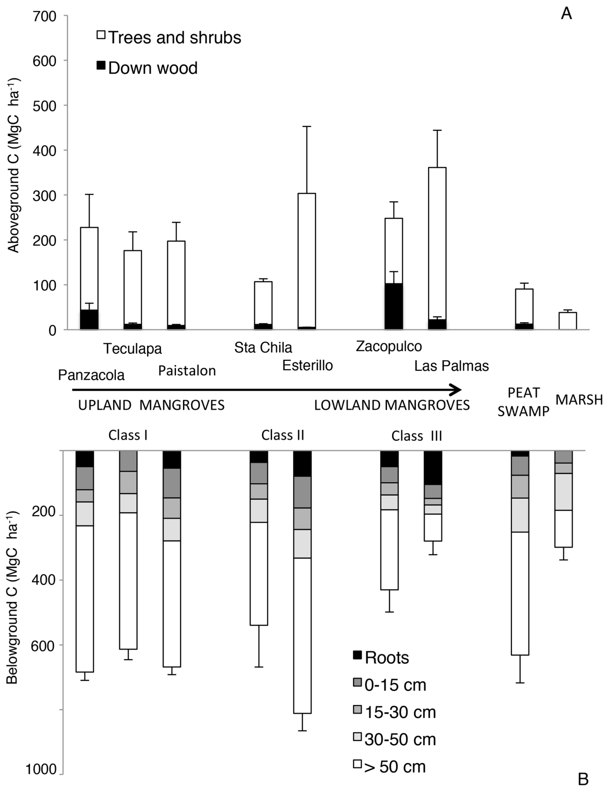

Figure 2. Aboveground **(a)** (trees and shrubs and down wood) and belowground **(b)** (soil at different depths and roots) carbon stocks ($\mathrm{Mg\,C\,ha^{-1}}$) of riverine wetlands (mangroves, peat swamp and marshes) within La Encrucijada Biosphere Reserve. Mangrove classes (I, II and III) represent a range from upland to lowland forests.

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