# Leaf litter production and soil carbon storage in forested freshwater wetlands and mangrove swamps in Veracruz, Gulf of Mexico

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## SUMMARY

Stored carbon varies among wetlands, yet they rank among the highest carbon accumulating ecosystems. Leaf litter production and aboveground carbon storage are frequently used as proxies for estimating primary productivity, which can be affected by flooding, salinity and other environmental factors. The objective of this study was to quantify leaf litter production and soil carbon density in two coastal tropical wetland types, namely mangrove swamps and forested freshwater wetlands. Water and soil physicochemical properties, together with leaf litter production, were measured bimonthly between 2007 and 2009 in wetlands of both types, located on the coast of the Gulf of Mexico. The soils ranged from entirely mineral to entirely organic in the top metre. Mangrove sites had relatively uniform hydroperiods and moderately reductive soils, whereas forested freshwater wetlands had reducing conditions. Electrical conductivity was lower and pH less acidic in forested freshwater wetland soils. Litterfall was around 1000 g m$^{-2}$ yr$^{-1}$ and annual production did not differ significantly between wetlands, despite the presence of acidic soils with prolonged flooding and high salinity in the mangrove swamps. Also, there were no consistent differences in soil carbon density between the two wetland types. Some forested freshwater wetlands had low litter production and high soil carbon density, whereas some mangrove swamps had high litter production and low soil carbon density. We present information regarding aboveground biomass turnover and belowground carbon storage in coastal tropical forested wetlands which is greatly needed to support us in understanding, valuing and conserving these neglected ecosystems.

**KEY WORDS:** coastal wetlands, flooding, litterfall, organic soils, salinity, tropical wetlands

## INTRODUCTION

Wetlands are intrinsically linked to water and carbon cycling through their interactions with surrounding terrestrial and other aquatic (river, lake, lagoon) systems, and through internal hydrological processes such as groundwater recharge and flood regulation (Bullock & Acreman 2003). The interactions are complex and vary with latitude as well as between landscapes.

On coastal floodplains in many tropical areas, mangroves are found in estuaries where there is a saline influence, while forested freshwater wetlands are found on floodplains just upslope, creating a coastal–inland gradient in space driven by superficial and underground freshwater from the catchment in combination with tidal flooding and salinity differences (Moreno-Casasola *et al*. 2017, Martínez-Camilo *et al.* 2020). In a case study on the island of Kosrae (Micronesia), Ewel (2010) demonstrated the hydrological interdependence of these two wetland types, as well as their importance to the local economy, and pointed out that similar contiguous mangrove and freshwater forests are extensively used by local populations elsewhere in the world. While the importance of mangroves is well recognised, goods and services provided by the freshwater wetlands that are located nearby and part of the same wetland system are not nearly so well documented (Ewel 2010).

Carbon storage varies among landscapes based on soil and vegetation types, but there is consensus about the high potential of wetlands (whether natural or engineered) to store and sequester carbon. Wetlands store around 34 % of the estimated global soil carbon (489 × 10$^{15}$ g), although their carbon concentration varies with location (Chen & Twilley 1999). Schlesinger (1986) estimated that soil organic matter in wetlands contains as much as three times the carbon found in the soils of non-flooded terrestrial vegetation. However, wetlands can also become sources of carbon and other greenhouse gases through the decomposition of stored organic matter, depending on land use, temperature and the hydrological regime (Raich & Schlesinger 1992, Kayranli *et al*. 2010, Atwood *et al.* 2017). The decomposition of organic matter in wetlands proceeds both aerobically and anaerobically, and often at different rates (Kayranli *et al.* 2010 and references therein). Globally, soil carbon can be divided into labile and refractory pools. Labile soil carbon decomposes at high rates and represents most of the carbon moving across the soil-atmosphere interface over the short term (Trumbore *et al.* 1996). Refractory soil carbon is not readily available for most biotic processes, and thus remains in the soil for the long term (Kiem *et al.* 2000, Félix-Faure *et al.* 2019).

Net aerial (aboveground) primary productivity (NPP) is the energy stored as biomass in the aerial parts of the plant community (leaves, stems, seeds and associated organs) after respiration, and is an important driver of ecosystem energy and carbon flows (Richardson & Vymazal 2001, Bortolotti *et al.* 2016). In forests, leaf litter production is a dominant component of primary productivity that is frequently used as a proxy for net primary production (NPP) of components with a high turnover rate (Day *et al.* 1996, Pierfelice *et al.* 2015). In this research we focus on aboveground biomass as the fraction of biomass that is most easily quantified; yet we acknowledge that belowground biomass (i.e., root material) is also an important biomass component that responds to several stimuli (Graham & Mendelssohn 2016) which, if not accounted for, can lead to incomplete conclusions about the carbon stored in an ecosystem (Day & Megonigal 1993).

In wetlands, the frequency and duration of flooding may enhance or reduce primary productivity, depending on whether it induces a physiological benefit or stress in the plants (Venterink *et al.* 2002, Torres *et al.* 2018). There is evidence showing that the longer the flooding period, the lower the productivity in forested wetlands (Mitsch *et al.* 1991) and herbaceous wetlands (Casanova & Brock 2000, Snedden *et al.* 2015); and that, in modulating aboveground biomass and productivity, flooding sometimes acts synergistically with other factors such as salinity (Janousek & Mayo 2013) and DBH (diameter at breast height) categories (Lucas *et al.* 2014). For example, in southern Florida, Ross *et al.* (2001) observed a decrease in productivity closer to the sea as a result of the saline influence. In another example, a seven-year-long study of depression swamps in Campeche (Mexico) showed that mangroves had higher NPP at the fringes of the flooded area (with shorter flooded periods) than on lower-lying land (with longer flooded periods) (Day *et al.* 1996). Infante-Mata *et al.* (2011) found that there was a tidal influence on the establishment of mangroves and that diversity was not affected by flood duration but was influenced by salinity. In addition to hydroperiod, physicochemical properties such as soil redox potential, pH and the distribution and availability of nutrients are important drivers of plant diversity, vegetation structure and wetland dynamics (Seybold *et al.* 2002, Boomer & Bedford 2008, Thomas *et al.* 2009, Foster *et al.* 2011, Torres *et al.* 2018). Wetlands on large floodplains and in deltaic areas are highly productive due to the availability of nutrient-rich sediments brought down from the entire watershed (Fennessy *et al.* 2019), and soil exchangeable cations point towards an effect from the main water source (Infante-Mata *et al.* 2011). Thus, in order to characterise and understand these systems, it is necessary to know the chemical properties of the soil as well as to monitor the flooding regime.

Infante-Mata *et al.* (2014) described forested freshwater wetlands located just inland from mangrove forests on the coast of the Gulf of Mexico, forming gradients bordering floodplains, depressions and coastal lagoons. These ecosystems are nowadays substantially affected by coastal development and many have been reduced to isolated fire-vulnerable relicts surrounded by crops, cattle ranches and herbaceous wetland (e.g., the Ciénaga del Fuerte site in this study). The aim of the research reported here was to quantify leaf litter production and soil carbon density as surrogate metrics of the capacity for organic carbon accumulation in these two naturally contiguous wetland types. We investigated the differences in leaf litter production and carbon density between mangrove swamps and forested freshwater wetlands with different geomorphological settings, hydroperiods, salinities and soil physicochemical properties. We also investigated the relationship between physical factors (salinity and flooding regime) and biological response variables (productivity and soil carbon), expecting that high salinity and longer periods of flooding would reduce productivity, consequently yielding smaller carbon stocks.

## METHODS

### Study sites

The study area is located on the coastal floodplain in the state of Veracruz (Mexico). It encompasses eleven sampling locations (Figure 1) in seven coastal municipalities (from north to south: Tuxpan, Tecolutla, Vega de Alatorre, Alto Lucero, Actopan, Jamapa, Alvarado). Four of these municipalities (Tuxpan, Tecolutla, Vega de Alatorre and Alvarado) have locations with mangrove and forested


Figure 1. Locations of the study sites on the central Gulf of Mexico coastline (Veracruz, Mexico) and the watersheds (hydrological catchments) with which they are associated.

freshwater wetlands forming a salinity gradient from the coast to areas farther inland, where we established paired sampling sites in neighbouring wetlands of the two types. In the municipalities of Alto Lucero, Actopan and Jamapa we sampled only freshwater forested wetlands.

Field studies were conducted from 2007 until 2009 at six sites dominated by mangroves and nine sites in forested freshwater wetlands (Table 1). Photographs of selected sites are provided in Appendix 1, and full species lists in Appendix 2. The study sites were distinguished and named according to their dominant plant species The mangrove sites were dominated by one or more of the four mangrove species present in this area (*Rhizophora mangle*, *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). The forested freshwater wetlands were more variable in species composition but were dominated by tree species such as *Pachira aquatica*, *Annona glabra* or *Ficus* spp. and did not contain the mangrove species mentioned above.

### Field measurements and sample collection

*Water*

At each study site, between five and ten sampling plots (10 × 10 m) were established. The number of plots per site was determined on the basis of size and

Table 1. Characteristics of the mangrove and forested freshwater wetland study sites, ordered from north to south (see Figure 1). Location name refers to the closest settlement. Floodplain* indicates an inland wetland, disconnected from the river. Climate type according to Köppen's Classification System (*Cfa* = humid subtropical, *Am* = tropical wet and *Aw* = tropical wet and dry); P is the total annual precipitation (mm) and MAT is the mean annual air temperature (°C) (ten-year average values) recorded at the closest meteorological station (CONAGUA, Mexico; https://smn.conagua.gob.mx/es/). Dominant plant species include trees, herbaceous plants and climbers; n is the number of plots per site and wetland type.

| Location and geomorphological setting | Municipality and coordinates | *climate type* P (mm $yr^{-1}$) MAT (°C) | wetland type | | | |
|---|---|---|---|---|---|---|
| | | | mangrove | | forested freshwater | |
| | | | n | dominant plant species | n | dominant plant species |
| Galindo Floodplain | Tuxpan 21º 03' 39' 'N 97º 21' 33" W | *Cfa* 1343 22.8 | 10 | *Conocarpus erectus Dalbergia brownei Rhabdadenia biflora Microgramma nitida* | 5 | *Ficus maxima Ficus pertusa Stemmadenia obovata Bursera simaruba* |
| Ciénaga del Fuerte Floodplain | Tecolutla 20º18'49" N 96º55'22"W | *Cfa* 1395 22.4 | 0 | | 8 | *Pachira aquatica Pithecellobium latifolium Hippocratea celastroides Ardisia revoluta* |
| Estero Dulce Floodplain | Tecolutla 20º 17' 38' 'N 96º 52' 24" W | *Cfa* 1317 21.0 | 10 | *Laguncularia racemosa Rhizophora mangle Pachira aquatica Rhabdadenia biflora* | 5 | *Pachira aquatica Inga vera Ficus insipida Rhabdadenia biflora* |
| Laguna Grande-Chica Coastal lagoon | Vega de Alatorre 20º 05' 46" N 96º 41' 23" W | *Am* 1397 22.8 | 10 | *Laguncularia racemosa Rhizophora mangle Rhabdadenia biflora Hymenocallis littoralis* | 9 | *Pachira aquatica Hippocratea celastroides Dalbergia brownei Rhabdadenia biflora* |
| Boquilla Depression | Alto Lucero 19º 49' 47" N 96º 26' 59" W | *Aw* 1460 23.9 | 0 | | 8 | *Ficus insipida Ficus pertusa Brosimum alicastrum Tabebuia rosea* |
| La Mancha Dune depression | Actopan 19º 35' 48" N 96º 22' 54" W | *Aw* 1156 24.5 | 0 | | 5 | *Annona glabra Pachira aquatica Ficus aurea Tabebuia rosea* |
| Apompal Floodplain* | Jamapa 19º 01' 23" N 96º 17' 03" W | *Aw* 1360 21.8 | 0 | | 9 | *Pachira aquatica Attalea butyracea Roystonea dunlapiana Dalbergia brownei* |
| Mandinga Coastal lagoon | Alvarado 19º 00' 35" N 96º 05' 33" W | *Aw* 1645 29.8 | 10 | *Rhizophora mangle Avicennia germinans Laguncularia racemosa Batis maritima* | 5 | *Diospyros digyna Stemmadenia ovobata Sabal Mexicana Dalbergia brownei* |
| Rincón Floodplain | Alvarado 18° 48' 07" N 95° 52' 11" W | *Aw* 1910 23.8 | 8 | *Avicennia germinans Laguncularia racemosa Dalbergia brownei* | 0 | |
| Rio Blanco Floodplain | Alvarado 18º 44' 47" N 95º 52' 42" W | *Aw* 1434 23.8 | 0 | | 10 | *Pachira aquatica Hippocratea volubilis Annona glabra Dalbergia brownei* |
| Acula Floodplain | Alvarado 18° 42' 23" N 95° 46' 18" W | *Aw* 1910 24.3 | 8 | *Avicennia germinans Laguncularia racemosa Rhabdadenia biflora* | 0 | |

accessibility of the wetland, and the total number of plots was 120. A mini-piezometer was installed at the centre of each plot and provided a reference point for measuring relative flood level. The mini-piezometers were made from PVC pipe (diameter 25 mm, length 3 m). The buried end of each pipe was sealed while the adjacent 20 cm of its wall was slotted at 2 cm intervals and wrapped with Nytex™ microfilament mesh held in place with stainless steel wire. The mini-piezometers were buried to a depth of 1.5 m (depth to screen) and relative depth to phreatic level was measured during site visits with a water-level dip meter (Solinst Mini 101). The mini-piezometers were not referenced to a common datum; therefore, depth of the water table was measured relative to the soil surface.

The sites were visited at approximately bimonthly intervals (every 60 days or on the closest workdays), forested freshwater wetland sites from August 2007 to December 2008 and mangrove sites from February 2008 to December 2009. To represent the portion of the year that each site had standing water above the soil surface and relate this to aboveground primary production, we calculated hydroperiod based on the number of days flooded (water table above the soil surface) divided by 365.

In each plot, pH and salinity were measured bimonthly in surface water, interstitial water (0.15 m depth, sensu McKee 1993) and groundwater (1.5 m depth) with a multiparametric probe YSI 556 MPS (Xylem Inc., USA). Surface water was measured directly (under flooded conditions). Interstitial water was collected using a copper tube (diameter 25 mm, length 1 m) with perforated tip, and a peristaltic pump. The perforated end of the tube was buried 15 cm into the saturated soil close to plant roots (to minimise clogging) before extracting a 100 mL water sample. Groundwater was pumped out from the mini-piezometer through a 3.1 mm HDPE tube using a peristaltic pump. When pumping was employed, the water samples were pumped out slowly to avoid bubbling and breaking of the water column.

*Soil*

Soil redox potential (in mV) was measured bimonthly in all plots (at a soil depth of 15 cm) using three platinum electrodes, one calomel reference electrode (Corning 476340) and an ORP Barnant digital pH meter. The platinum electrodes were calibrated in the laboratory with quinhydrone (Sigma Q-1001) in a pH 4.0 buffer solution following Bohn (1971). Field measurements were estimated by adding 244 mV to the average mV reading in the field (n=3 per plot).

Pits (1 $m^2$) ranging from 95 to 190 cm deep (according to the water table level at the time) were dug to investigate the morphological and physicochemical characteristics of the soils. Soils were sampled only once, in locations where both wetland types (mangrove and freshwater forested) were contiguous or in proximity, in order to compare their soils in similar geomorphological settings (Table 1). At these locations (Galindo, Estero Dulce, Laguna Grande-Chica, Mandinga), one pit was dug in the most accessible plot with mangrove and another in the most accessible plot with forested freshwater wetland. A fifth pair of pits (Alvarado) was dug at Rincón (mangrove) and the adjacent Rio Blanco (forested freshwater wetland) site (n=10). Soil samples were collected from each soil horizon for chemical characterisation. Undisturbed cores (diameter 5.5 cm, length 5 cm) were collected in triplicate from each horizon to measure bulk density, determined by oven drying the cores (at 105 °C) then dividing the dry weight by the (known) wet volume (Grossman & Reinsch 2002). Soil samples were also collected from each horizon for chemical analysis. Before analysis, the soil was air-dried and then sieved through a 2 mm screen to achieve a uniform particle size for the analyses.

*Leaf litter*

Circular traps suspended one metre above ground level were used to collect litterfall. Each trap consisted of a 52 cm diameter flexible ring made from 25 mm PVC tubing (A=0.2123 $m^2$) and a cone-shaped collector made of mosquito netting (nine holes per centimetre). In total, 120 traps were installed, 56 traps in mangrove sites and 64 traps in forested freshwater wetland sites. Leaf litter was collected every two months, over total periods of 22 months (February 2008 to December 2009) for mangrove and 16 months (August 2007 to December 2008) for forested freshwater wetland sites. The litter samples (leaves and reproductive structures) were stored in paper bags, then dried in an electric oven (70 ºC, 48 h), and weighed with an OHAUS balance (model CT200). Leaf litter dry weight per trap was converted to g $m^{-2}$ for each collection date, then summed to obtain the annual leaf litter production (g $m^{-2}$ $yr^{-1}$). These data were used for comparisons between sites and wetland types. We did not assess any effects of inter-annual variations in climatic conditions on litter production; however, we consider that large variations in annual litterfall were unlikely because we did not observe any hydrometeorological events that could have affected the hydroperiod during any of the years when litterfall was measured.

**Analytical methods**

*Soil physicochemical properties*

Electrical conductivity (EC) was measured in a saturated paste (Rhoades 1982). Soil aqueous pH was determined following McLean (1982). Exchangeable cations ($Ca^{2+}$, $Mg^{2+}$, $K^+$, $Na^+$) were extracted with $NH_4OAc$ buffered at pH 7 (Thomas 1982) and analysed using atomic absorption spectrometry ($Ca^{2+}$, $Mg^{2+}$) and flame photometry ($K^+$, $Na^+$).

*Soil carbon concentration*

Total carbon concentration (*TC*; g kg$^{-1}$) in the soil samples was determined by dry combustion in a CN analyser (LECO CN2000). Inorganic carbon was quantified as $CaCO_3$ using the acid neutralisation method (Van Reeuwijk 2006). Soil organic carbon (SOC) concentration (*SOC*; g kg$^{-1}$) was then calculated using the following formula:

$$SOC = TC - 0.12 \times CaCO_3 \quad [1]$$

For each soil horizon, *SOC* (g kg$^{-1}$) was adjusted according to the bulk density of the soil in order to transform units of concentration into units of areal density (kg m$^{-2}$), and SOC density (g cm$^{-2}$) to a depth of 1 m calculated, using the following equation:

$$\text{SOC density} = \sum_{i=1}^{k} \left(\frac{SOC \times D_b \times Z}{10}\right)_i \quad [2]$$

where *SOC*/10 is SOC concentration (%), $D_b$ is soil bulk density (g cm$^{-3}$), $Z$ is the thickness of the $i^{th}$ soil layer (cm), and $k$ is the number of soil layers. The results were then converted to kg m$^{-2}$.

**Statistical analysis**

Statistical analyses were conducted and Figures prepared using SSPS 13 software. Student's *t*-test was used to compare the differences in leaf litter production and carbon density for the two types of forested wetlands. One-way ANOVAs and Tukey-Kramer HSD post-hoc tests ($\alpha = 0.05$) were performed to evaluate differences in leaf litter among wetlands. We used the Pearson correlation coefficient (r) to explore the relationship between soil pH and EC (for assessment of cation leachability) and the possible relationship of litterfall production with hydroperiod and salinity. Finally, we did one-way ANCOVA tests with wetlands as the categorical variable, covariate productivity with (i) hydroperiod and (ii) salinity. The same test was performed for C stocks (covariate C stock with hydroperiod and salinity).

**RESULTS**

**Hydroperiod and water chemistry**

The hydroperiod (Figure 2) varied notably among forested freshwater wetlands (individual sites were flooded for 8–100 % of total time) but was more uniform (33–75 %) among the mangrove sites (see hydroperiod (%) in Table 4 later). The duration of flooding in *Pachira* and *Annona* forested freshwater wetland was generally greater than in *Ficus* and *Diospyros* forested freshwater wetland.

Water pH in mangrove swamps was slightly more alkaline in the surface water than in the interstitial water or groundwater (Table 2). Forested freshwater wetlands did not follow the same trend and had less variation in the values. Salinity was the most important environmental factor in determining the differential establishment and zonation between mangrove and forested freshwater wetland in locations with both wetland types. The range of mean salinity measured at mangrove sites was 3.7–58.7 g L$^{-1}$, while the range in forested freshwater wetland sites was 0.3–8.6 g L$^{-1}$ (see Table 4). In the forested freshwater wetland sites there appeared to be saline influence in the groundwater at Estero Dulce and Laguna Grande-Chica, but not elsewhere (Table 2).

**Soil physicochemical properties**

All mangrove locations had soil with moderately reducing conditions (redox potential 91.3–221.7 mV) while six of the nine forested freshwater wetlands had reducing conditions (< 90 mV); the exceptions were Galindo, Ciénaga del Fuerte and Boquilla (Table 2). The uppermost metre of mangrove soils was mainly mineral (< 20 % organic matter); only Estero Dulce had mostly organic soil (93 cm thick) and there were surface organic layers at Galindo (20 cm) and Laguna Grande-Chica (10 cm) (Table 3). Soils in the forested freshwater wetlands were also mostly mineral although there were thin surface organic layers at Mandinga (5 cm) and Laguna Grande-Chica (10 cm), and the whole top metre of soil at Rio Blanco (Alvarado) was organic (Table 3). Electrical conductivity (EC) in mangrove soils varied from 7.4 dS m$^{-1}$ to 92.5 dS m$^{-1}$, whereas in forested freshwater wetland soils the range was 0.1–12.9 dS m$^{-1}$. Soils in mangrove sites had pH values ranging from 2.0 to 6.7, whereas the range of soil pH in forested freshwater wetlands was 3.6–7.4. There was a weak correlation between soil pH and electrical conductivity in mangroves (r = -0.30), and a stronger (more negative) correlation in the forested freshwater wetlands (r = -0.78). $Ca^{2+}$ concentrations varied more in forested freshwater than in mangrove wetlands, being particularly high in Estero Dulce and Alvarado (44.9 and 59.0 cmol$_c$ kg$^{-1}$, respectively). In contrast, $Mg^{2+}$ concentrations had a greater range in mangrove soils (6.8–33.8 cmol$_c$ kg$^{-1}$) than in forested freshwater wetland soils (0.1–25.3 cmol$_c$ kg$^{-1}$). The lowest $Mg^{2+}$ concentration (0.1 cmol$_c$ kg$^{-1}$) was recorded in the Galindo forested freshwater wetland. $K^+$ concentrations were almost always lower in forested freshwater wetland soils than in mangrove soils. $Na^+$ concentrations were generally higher in mangrove than in forested freshwater wetland soils because of the brackish water influence. High concentrations of soluble salts (particularly $Na^+$) were observed at Mandinga relative to other mangrove sites.

**Leaf litter production**

The annual litterfall measured at the different sites varied greatly (Table 4), but annual litterfall production did not differ significantly ($t = 0.13$, $p = 0.901$) between mangrove sites (992 ± 167 g m$^{-2}$ yr$^{-1}$) and forested freshwater wetlands (1017 ± 65 g m$^{-2}$ yr$^{-1}$). No differences were observed between the total leaf litter production of mangroves ($F = 1.66$, $p = 0.178$) and forested wetlands ($F = 1.07$, $p = 0.040$) (Table 4). Comparing annual leaf litter production in the five sites where mangroves and forested freshwater wetlands coexist (Figure 3), a difference was apparent only at Galindo, where the forested freshwater wetland (876 g m$^{-2}$ yr$^{-1}$) was more productive than the mangrove swamp (379 g m$^{-2}$ yr$^{-1}$) ($F = 10.18$, $p = 0.011$). Our results showed a weak correlation between litterfall production and hydroperiod (mangroves: $r = -0.17$; forested freshwater wetlands: $r = 0.39$) and with salinity (mangroves $r = -0.05$; forested freshwater wetlands $r = 0.02$). The one-way ANCOVA tests did not reveal any covariation of leaf litter production with either hydroperiod ($p = 0.843$) or salinity ($p = 0.998$).

**Soil organic carbon**

Soil organic carbon density in mangrove sites ranged from 17 to 41 kg m$^{-2}$ (Table 4). As might be expected, the mangrove sites with organic soil layers (Estero Dulce, Galindo, Laguna Grande-Chica) had the highest values, while Mandinga, had the lowest. In forested freshwater wetlands, soil carbon density to 1 m depth ranged from 22 to 70 kg m$^{-2}$; the value for Boquilla was even higher than that for the completely organic 1 m soil layer observed at Rio Blanco (60 kg m$^{-2}$). Comparing soil carbon density between mangrove and forested freshwater wetland soils

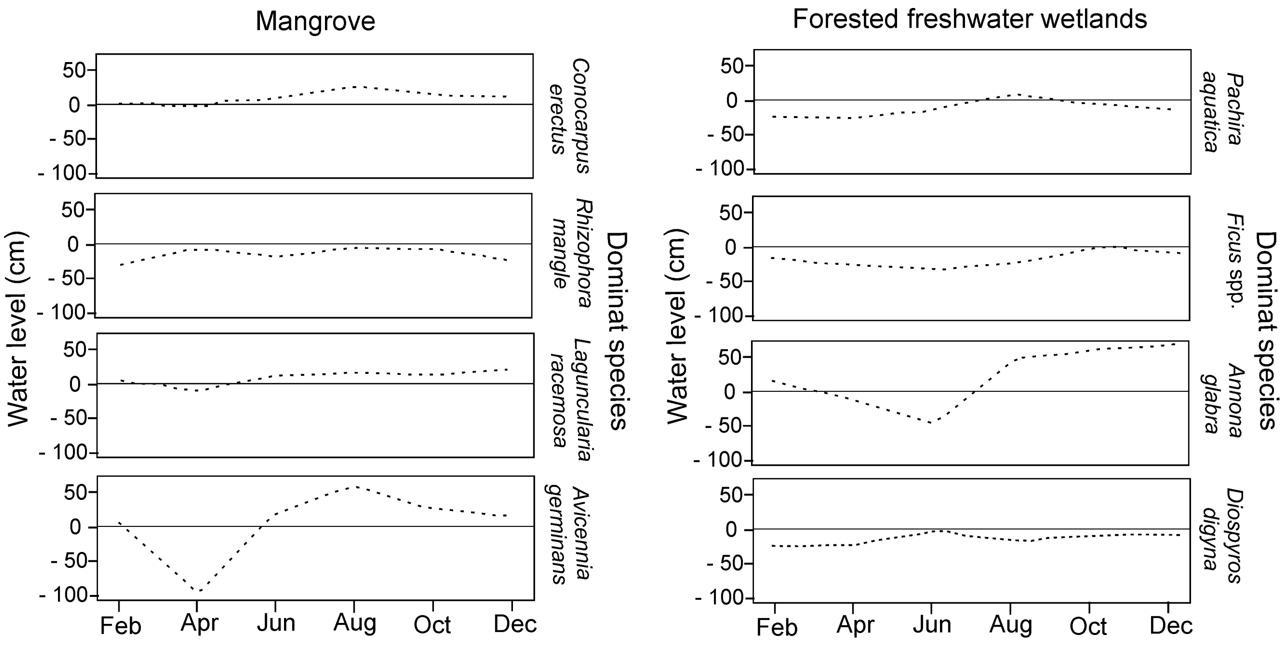


Figure 2. Bimonthly data (2008–2009) showing water level fluctuations at mangrove and forested freshwater wetland sites with different dominant plant species. For categories represented by more than one sampling plot (see Table 1), mean values are shown. Mangrove sites include one dominated by *Conocarpus erectus*, one by *Rhizophora mangle*, two by *Laguncularia racemosa* and two by *Avicennia germinans*. Forested freshwater wetlands include five sites dominated by *Pachira aquatica*, two by *Ficus* spp., one by *Annona glabra* and one by *Diospyros digyna*. The horizontal lines at [water level = 0 cm] indicate ground level.

within the same locations, we observed that the Mandinga forested freshwater wetland had a higher carbon density than the mangrove soil at the same location. The opposite was observed in Galindo, Estero Dulce, Laguna Grande-Chica and Alvarado (mangrove in Alvarado represented by Acula and Rincón). Comparing the carbon stocks in soils across all of our study sites, we found that forested freshwater wetlands had slightly higher carbon stocks but the difference was not statistically significant ($t=1.75$, $p=0.11$). Similar to leaf litter production, the one-way ANCOVA tests did not show any covariation between soil C stocks and hydroperiod ($p= 0.156$) or salinity ($p=0.932$).

Table 2. Physicochemical properties measured in water at mangrove and forested freshwater wetland study sites. The values for pH, salinity and soil oxidation-reduction (redox) potential are annual means ± 1 s.d. SW: surface water; IW: interstitial water (0.15 m deep in saturated sediments); GW: groundwater, collected in mini-piezometers at a depth of 1.5 m.

| Site | mangrove | | | forested freshwater wetland | | |
|---|---|---|---|---|---|---|
| | pH. | salinity (ppm) | soil redox potential (mV) | pH. | salinity (g $L^{-1}$) | soil redox potential (mV) |
| Galindo | SW: 8.6 ± 1.4<br>IW: 6.8 ± 0.4<br>GW: 7.0 ± 0.1 | SW: 11.8 ± 0.9<br>IW: 22.4 ± 1.6<br>GW: 20.9 ± 0.6 | 156.6 ± 13.1 | SW: 7.9 ± 0.2<br>IW: 7.9 ± 0.2<br>GW: 7.6 ± 0.1 | SW: 0.7 ± 0.3<br>IW: 0.7 ± 0.3<br>GW: 0.5 ± 0.1 | 158.4 ± 24.4 |
| Ciénaga del Fuerte | no data | | | SW: 7.3 ± 0.1<br>IW: 7.2 ± 0.1<br>GW: 7.3 ± 0.1 | SW: 0.3 ± 0.1<br>IW: 0.3 ± 0.1<br>GW: 0.8 ± 0.1 | 107.4 ± 15.3 |
| Estero Dulce | SW: 7.4 ± 0.05<br>IW: 7.1 ± 0.1<br>GW: 7.2 ± 0.05 | SW: 4.1 ±1.1<br>IW: 3.7 ± 0.4<br>GW: 5.8 ± 0.3 | 206.9 ± 7.9 | SW: 7.3 ± 0.1<br>IW: 7.1 ± 0.1<br>GW: 7.2 ± 0.1 | SW: 0.8 ± 0.1<br>IW: 1.7 ± 0.2<br>GW: 8.6 ± 1.0 | 50.2 ± 12.6 |
| Laguna Grande-Chica | SW: 7.3 ± 0.1<br>IW: 6.9 ± 0.1<br>GW: 7.2 ± 0.05 | SW: 8.1 ± 1.1<br>IW: 10.6 ± 0.1<br>GW: 22.0 ± 2.5 | 221.7 ± 9.7 | SW: 7.2 ± 0.1<br>IW: 6.7 ± 0.1<br>GW: 7.4 ± 0.1 | SW: 2.3 ± 0.3<br>IW: 3.3 ± 0.3<br>GW: 7.7 ± 0.6 | 13.1 ± 32.2 |
| Boquilla | no data | | | SW: 6.9 ± 0.1<br>IW: 6.8 ± 0.1<br>GW: 7.2 ± 0.1 | SW: 1.0 ± 0.2<br>IW: 0.8 ± 0.2<br>GW: 0.9 ± 0.2 | 99.4 ± 15.6 |
| La Mancha | no data | | | SW: 7.3 ± 0.05<br>IW: 7.0 ± 0.05<br>GW: 7.2 ± 0.1 | SW: 0.5 ± 0.1<br>IW: 0.8 ± 0.1<br>GW: 0.5 ± 0.1 | -33.9 ± 14.9 |
| Apompal | no data | | | SW: 7.0 ± 0.05<br>IW: 6.7 ± 0.1<br>GW: 7.0 ± 0.1 | SW: 0.3 ± 0.05<br>IW: 0.3 ± 0.05<br>GW: 0.3 ± 0.05 | 65.1 ± 10.9 |
| Mandinga | SW: 7.3 ± 0.1<br>IW: 6.8 ± 0.1<br>GW: 7.1 ± 0.05 | SW: 17.2 ± 3.0<br>IW: 35.7 ± 5.2<br>GW: 58.7 ± 6.2 | 199.6 ± 8.4 | SW: 7.6 ± 0.1<br>IW: 7.3 ± 0.1<br>GW: 7.7 ± 0.1 | SW: 1.1 ± 0.1<br>IW: 1.1 ± 0.2<br>GW: 1.4 ± 0.6 | 55.5 ± 42 |
| Rincón | SW: 6.9 ± 0.1<br>IW: 6.5 ± 0.1<br>GW: 6.4 ± 0.1 | SW: 7.2 ± 1.3<br>IW: 32.6 ± 0.9<br>GW: 11.1 ± 1.7 | 106.5 ± 26.3 | no data | | |
| Rio Blanco | no data | | | SW: 7.3 ± 0.1<br>IW: 7.3 ± 0.05<br>GW: 7.0 ± 0.1 | SW: 1.4 ± 0.2<br>IW: 4.1 ± 0.5<br>GW: 1.2 ± 0.1 | 86.3 ± 18.6 |
| Acula | SW: 7.2 ± 0.1<br>IW: 6.9 ± 0.1<br>GW: 6.8 ± 0.1 | SW: 8.6 ±1.8<br>IW: 25.1 ± 1.3<br>GW: 12.1 ± 1.9 | 91.3 ± 22.2 | no data | | |

Table 3. Soil horizons, types (O=organic, M=mineral), bulk density (BD) and chemical properties: pH, electrical conductivity (EC) and exchangeable cations in mangrove and forested freshwater wetlands. For the pairing labelled 'Alvarado' (bottom row), the soil pits were dug at the Rincón (mangrove) and Rio Blanco (forested freshwater wetland) sites.

| | mangrove | | | | | | | | | forested freshwater wetland | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | depth (cm) | soil type | BD ($g\ cm^{-3}$) | pH | EC ($dS\ m^{-1}$) | exchangeable cations ($cmol_c\ kg^{-1}$) | | | | depth (cm) | soil type | BD ($g\ cm^{-3}$) | pH | EC ($dS\ m^{-1}$) | exchangeable cations ($cmol_c\ kg^{-1}$) | | | |
| Site(s) | | | | | | $Ca^{2+}$ | $Mg^{2+}$ | $K^+$ | Na+ | | | | | | $Ca^{2+}$ | $Mg^{2+}$ | $K^+$ | Na+ |
| Galindo | 0–10 | O | 0.30 | 5.3 | 26.8 | 35.1 | 26.6 | 1.3 | 33.9 | 0–15 | M | 0.78 | 7.2 | 0.9 | 18.6 | 0.4 | 0.0 | 0.2 |
| | 10–20 | O | 0.28 | 5.7 | 22.8 | 25.5 | 17.7 | 1.0 | 20.5 | 15–30 | M | 1.09 | 7.1 | 0.5 | 8.1 | 0.2 | 0.0 | 0.0 |
| | 20–65 | M | 1.27 | 6.6 | 12.7 | 9.6 | 7.0 | 0.7 | 2.4 | 30–55 | M | 1.65 | 6.4 | 0.5 | 3.7 | 0.1 | 0.0 | 0.0 |
| | 65–110 | M | 1.48 | 6.7 | 9.9 | 8.5 | 7.1 | 0.5 | 1.7 | 55–95 | M | 1.68 | 7.4 | 0.5 | 3.0 | 0.1 | 0.0 | 0.0 |
| Estero Dulce | 0–15 | O | 0.24 | 5.2 | 7.4 | 37.0 | 18.8 | 1.2 | 6.4 | 0–8 | M | 0.50 | 6.2 | 1.2 | 44.9 | 5.6 | 1.0 | 2.0 |
| | 15–30 | O | 0.16 | 4.7 | 8.5 | 34.8 | 23.1 | 1.2 | 4.1 | 8–23 | M | 0.82 | 6.3 | 0.6 | 35.6 | 5.2 | 0.9 | 1.4 |
| | 30–50 | O | 0.37 | 4.2 | 9.7 | 24.4 | 19.9 | 1.3 | 4.9 | 23–45 | M | 0.92 | 6.9 | 0.6 | 34.5 | 5.3 | 0.8 | 1.3 |
| | 50–75 | O | 0.52 | 3.6 | 12.1 | 22.7 | 20.8 | 1.4 | 7.4 | 45–72 | M | 0.92 | 6.9 | 0.3 | 32.3 | 5.2 | 0.8 | 1.3 |
| | 75–93 | O | 0.54 | 4.7 | 12.7 | 22.9 | 18.6 | 1.8 | 10.6 | 72–100 | M | 1.14 | 7.2 | 0.1 | 29.6 | 4.9 | 0.8 | 1.5 |
| | 93–120 | M | 0.79 | 6.7 | 9.2 | 29.1 | 9.8 | 1.4 | 1.6 | | | | | | | | | |
| Laguna Grande-Chica | 0–10 | O | 0.29 | 4.3 | 44.9 | 21.2 | 27.8 | 2.4 | 47.6 | 0–10 | O | 0.15 | 5.2 | 7.9 | 34.9 | 16.1 | 0.6 | 17.1 |
| | 10–30 | M | 0.91 | 6.3 | 27.9 | 11.5 | 22.9 | 2.6 | 31.2 | 10–25 | M | 0.50 | 5.1 | 7.9 | 20.1 | 15.8 | 0.9 | 8.6 |
| | 30–70 | M | 0.69 | 5.1 | 30.1 | 9.7 | 21.4 | 1.8 | 31.9 | 25–55 | M | 1.10 | 6.5 | 3.7 | 9.1 | 10.0 | 0.6 | 5.1 |
| | 70–110 | M | 0.88 | 2.9 | 45.0 | 11.9 | 17.1 | 0.8 | 29.1 | 55–120 | M | 0.87 | 3.6 | 10.7 | 11.9 | 13.0 | 0.8 | 7.9 |
| Mandinga | 0–10 | M | 0.70 | 5.2 | 80.2 | 13.0 | 30.3 | 3.2 | 108.4 | 0–5 | O | 0.13 | 6.3 | 3.0 | 33.7 | 16.5 | 1.0 | 8.6 |
| | 10–27 | M | 0.82 | 6.1 | 71.8 | 9.3 | 24.1 | 2.8 | 83.8 | 5–15 | M | 0.35 | 5.3 | 1.0 | 20.8 | 9.7 | 0.1 | 2.2 |
| | 27–42 | M | 0.70 | 5.2 | 82.5 | 11.9 | 29.3 | 3.6 | 97.9 | 15–38 | M | 0.43 | 6.1 | 0.3 | 16.9 | 8.0 | 0.0 | 1.5 |
| | 42–64 | M | 0.54 | 2.6 | 86.9 | 15.7 | 33.8 | 2.8 | 106.7 | 38–77 | M | 0.43 | 6.3 | 0.2 | 16.3 | 9.2 | 0.0 | 1.5 |
| | 64–120 | M | 0.51 | 3.4 | 92.5 | 22.4 | 26.1 | 2.6 | 97.9 | 77–150 | M | 0.46 | 7.0 | 0.3 | 10.7 | 5.4 | 0.3 | 1.2 |
| Alvarado (Rincón/ Rio Blanco) | 0–7 | M | 0.90 | 4.4 | 23.2 | 11.0 | 19.3 | 1.7 | 18.8 | 0–8 | O | 0.10 | 6.1 | 7.5 | 52.9 | 21.7 | 1.8 | 19.6 |
| | 7–35 | M | 1.00 | 5.2 | 11.9 | 7.8 | 14.9 | 1.7 | 9.8 | 8–18 | O | 0.13 | 5.6 | 6.1 | 56.4 | 24.6 | 0.9 | 17.0 |
| | 35–70 | M | 1.00 | 5.7 | 9.7 | 5.9 | 12.3 | 1.1 | 14.5 | 18–50 | O | 0.13 | 5.7 | 5.9 | 59.0 | 25.3 | 0.8 | 16.2 |
| | 70–105 | M | 1.10 | 2.0 | 29.6 | 14.6 | 7.9 | 0.0 | 6.8 | 50–75 | O | 0.17 | 5.8 | 9.3 | 46.9 | 23.1 | 1.0 | 10.2 |
| | 105–135 | M | 1.50 | 2.5 | 30.7 | 3.6 | 6.8 | 0.0 | 6.0 | 75–100 | O | 0.27 | 5.0 | 12.9 | 48.5 | 20.4 | 1.2 | 11.1 |

Table 4. Summary of annual leaf litter production (LLP), salinity (annual means of all measurements on surface water, interstitial water and groundwater), hydroperiod and carbon density across all sites in mangrove and forested freshwater wetlands. n = number of leaf litter traps per site (one per sampling plot).

| | mangrove | | | | | | forested freshwater wetland | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | n | dominant species | LLP (g $m^{-2}$ $y^{-1}$) | salinity (g $L^{-1}$) | hydro-period (%) | carbon density (kg $m^{-2}$) | n | dominant species | LLP (g $m^{-2}$ $y^{-1}$) | salinity (g $L^{-1}$) | hydro-period (%) | carbon density (kg $m^{-2}$) |
| Galindo | 10 | *Conocarpus erectus* | 379.37 | 23.3 | 75 | 27.5 | 5 | *Ficus* spp. | 876.37 | 0.70 | 25.0 | 22 |
| Ciénaga del Fuerte | 0 | | | | | | 8 | *Pachira aquatica* | 1244.78 | 0.30 | 58.3 | 52 |
| Estero Dulce | 10 | *Laguncularia racemosa* | 856.94 | 3.7 | 41.7 | 41 | 5 | *Pachira aquatica* | 836.40 | 1.70 | 50.0 | 24 |
| Laguna Grande-Chica | 10 | *Laguncularia racemosa* | 1306.95 | 10.7 | 66.7 | 28 | 9 | *Pachira aquatica* | 1130.88 | 3.23 | 66.7 | 26 |
| Boquilla | 0 | | | | | | 8 | *Ficus* spp. | 1302.90 | 0.80 | 50.0 | 70 |
| La Mancha | 0 | | | | | | 5 | *Annona glabra* | 1118.36 | 0.90 | 66.7 | no data |
| Apompal | 0 | | | | | | 9 | *Pachira aquatica* | 904.23 | 0.40 | 100.0 | 33 |
| Mandinga | 10 | *Rhizophora mangle* | 1043.1 | 35.7 | 33.3 | 17 | 5 | *Diospyros digyna* | 708.32 | 1.10 | 8.3 | 26 |
| Rincón | 8 | *Avicennia germinans* | 819.41 | 32.6 | 66.7 | 22 | 0 | | | | | |
| Rio Blanco | 0 | | | | | | 10 | *Pachira aquatica* | 1035.76 | 4.1 | 50 | 60 |
| Acula | 8 | *Rhizophora mangle* | 1546.38 | 25.1 | 62.5 | 21 | 0 | | | | | |
| Means | | | 992.03 | 21.85 | 57.65 | 26.08 | | | 1017.55 | 1.76 | 56.95 | 39.13 |

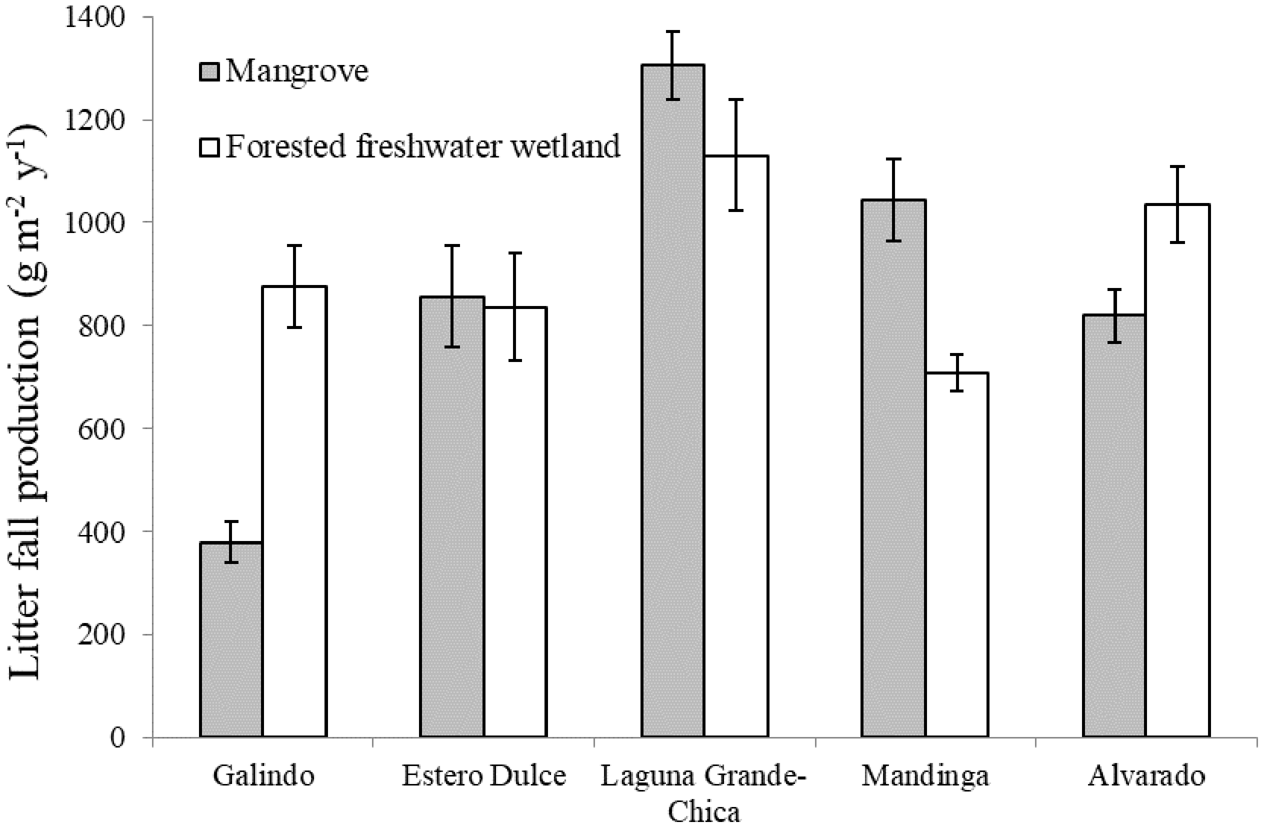


Figure 3. Litterfall production (g $m^{-2}$ $y^{-1}$) in locations with both types of vegetation: mangroves (grey) and freshwater forested wetlands (white). ANOVA (a=0.05) detected differences in litterfall production between the two vegetation types only at Galindo (F=10.18, p=0.011). For the pairing labelled 'Alvarado' (far right), litterfall data for the Acula (mangrove) and Rio Blanco (forested freshwater wetland) sites are compared.

## DISCUSSION

Abiotic factors such as flood regime and average water depth can explain primary production in wetlands (Byun *et al.* 2017, Allen *et al.* 2019). We expected that high salinity and longer periods of flooding would reduce productivity. However, litterfall was not always greater in forested freshwater wetlands than in mangrove swamps (Table 4). We did notice a trend in forested freshwater wetlands where litterfall increased as the hydroperiod decreased. The weak correlation of litterfall with hydroperiod holds for forested freshwater wetlands but not for mangroves. This same pattern with respect to the hydroperiod was also reported by Mitsch *et al.* (1991) and Miller & Fujii (2010); whereas Pezeshki *et al.* (1990) and Day *et al.* (1996) found that litterfall decreased as soil salinity increased. It is likely that locations with an extended hydroperiod (or even the same location during wet years) exhibit reduced biomass production because of differential nutrient allocation (Megonigal & Day 1992, Wang *et al.* 2015) or decreased carbon assimilation due to changes in photosynthetic sensitivity (Pezeshki *et al.* 1990). Combined flooding and salinity induced physiological stress and reduced productivity across several wetland species (Conner & Day 1992, Janousek & Mayo 2013). Overall, our prediction was not proven. Both mangrove and forested freshwater wetlands in different sites differ in species dominance, which might account for the variability encountered, and this is related to the site's position in the landscape (floodplain, coastal lagoon or depression), which affects hydroperiod and salinity. A greater number of sites is probably needed in order to reduce this variability and obtain stronger correlations.

Day *et al.* (1996) reported annual and aboveground NPP (measured as litterfall) in mangroves dominated by *Avicennia germinans* ranging from 319 to 759 g $m^{-2}$ $yr^{-1}$ for the east side of the southern Gulf of Mexico. Litterfall in our mangrove sites dominated by *A. germinans* fell within the same range, but in some *Rhizophora mangle* and *Laguncularia racemosa* - dominated mangrove sites it was higher. Day *et al*. (1996) also reported annual variation in litterfall as great as 16 %. According to their analyses, 74 % of the total litter variability was explained by soil salinity, minimum temperature and minimum rainfall, suggesting a strong climate component.

In addition to flood duration and salinity, pH seems to be an additional factor affecting aerial biomass production. Our study found that mangrove sites where pH was very low (Rincón and Acula) were not the least productive. However, acidic soil was associated with prolonged flood periods (> 60 %) and high salinity (> 25 g $L^{-1}$). Therefore, the occurrence of these three conditions together might possibly result in low biomass production. Acidic soil in wetlands is a key factor controlling nutrient availability (Mitsch *et al.* 2013), denitrification (Peralta *et al.* 2013), methane ($CH_4$) production (Inubushi *et al.* 2005) and the precipitation and dissolution of elements such as iron, sulfate and manganese (Reddy & DeLaune 2008). In the forested freshwater wetlands studied, low soil pH values (3–5) coincided with electrical conductivity values above 5 dS $m^{-1}$, suggesting that cations were more prone to leach under acidic conditions. We do not have enough evidence to judge whether micronutrients, rather than factors such as salinity, hydroperiod and soil acidity, might be limiting aboveground production.

At our study sites the organic soils had low pH values, probably as a result of the decomposition of organic matter releasing organic acids because of anaerobic decomposition. Low soil pH (as low as 3 in our study area) has not been reported previously in these wetlands (Infante-Mata *et al.* 2011) and could be caused by the oxidation of sulfidic materials (Vithana *et al.* 2013). It has been proposed that the decomposition of organic matter in freshwater wetlands concludes with methanogenesis, whereas sulfate reduction is more important in salt marshes and marine ecosystems (Reddy & DeLaune 2008). Thus, it is probable that the more acidic conditions observed in our mangrove sites were due to sulfate reduction that generated $H_2S$. Low pH has been associated with reduced decomposition rates in freshwater swamps (Benner *et al.* 1985, Gorham 1991). Thus, a complex and mutually influenced combination of physicochemical conditions is likely to be controlling decomposition, pH and redox potential in these tropical wetlands. A controlled biogeochemical study is necessary to shed light on the intensity and correlation of these processes.

Redox potential is closely associated with flooding, and decreases or becomes negative as the water table rises. Faulkner & Patrick (1992) defined wetland soils as having weak reducing potential (> 300 mV) due to the saturated conditions in the rooting zone. Those wetlands were flooded for 46–100 % of the time, similar to most of our sites. Reducing conditions result in reduced oxygen diffusion (Pezeshki *et al.* 1990) and nutrient availability (Niedermeier & Robinson 2007), both of which have a negative influence on aerial biomass production. According to Seybold *et al.* (2002), permanently reductive areas that support biological activity year-round owing to relatively high temperatures and large organic matter supply are characteristic features of some freshwater wetlands such as the sites monitored in this study.

Appendix 3 provides a comparison of litterfall in temperate and tropical freshwater wetlands and mangrove swamps in different regions of the world. This shows litterfall ranging from 300 to 2700 g $m^{-2}$ $yr^{-1}$ and slightly greater in tropical than in temperate zones. As we have discussed, it is very likely that a combination of stressors, namely hydroperiod and salinity, explain the variable aerial biomass production observed in mangrove and forested freshwater wetlands on the central coastal plain of the Gulf of Mexico. Micronutrients and pH can also contribute to regulating aerial primary productivity and carbon storage. For example, higher exchangeable cations ($Ca^{2+}$ and $Mg^{2+}$) and phosphorus in flooded forests with a riverine or lacustrine influence might have the effect of boosting productivity (Infante-Mata *et al.* 2011). Working in the Lower Amazon, Lucas *et al*. (2014) observed that flood duration was the most important predictor of aboveground biomass, but this variable was also explained by forest age, with more biomass in mature forests. Short, frequent flood events promote increased productivity and species richness; however, the depth of the water column has a crucial effect on the biomass produced by different species, and varies between flood-tolerant and flood-responder species (Casanova & Brock 2000). Infante-Mata *et al.* (2012) found that forested freshwater wetlands with lianas had greater litter production. Currently, the knowledge of tolerant and responder species in tropical wetlands is limited. We did not evaluate species diversity, though it is known that flooding can also regulate diversity in certain types of wetlands (Sjöberg & Danell 1983, Bailey-Serres & Voesenek 2008, Infante-Mata *et al.* 2012).

Our measurements in the forested freshwater wetland of Boquilla suggest that its high litterfall production (1302 g $m^{-2}$ $yr^{-1}$) corresponds to the greatest soil carbon density (70 kg $m^{-2}$). However, this observation was not consistent across study sites; we also had forested freshwater wetlands with low leaf litter production and high soil carbon density (Rio Blanco) and mangroves with high litter productivity and a low soil carbon density

(Mandinga). Carbon pool size varies widely amongst different wetlands. In the tropics, wetlands with sparse vegetation may have limited carbon turnover, whereas those with high primary productivity are expected to accumulate C in their soils. The opposite may be true for high latitude wetlands or peatlands, in which low aboveground biomass can yield high belowground carbon stocks (Ma *et al.* 2017). However, the global importance of wetlands as carbon sinks is widely recognised (Bouillon *et al.* 2008, Mitsch *et al.* 2013), given that wetlands store around 15 Gt of carbon in vegetation and 225 Gt in the uppermost metre of soil, accounting for 3.2 % and 11.2 % of the global carbon storage in vegetation and soil, respectively (IPCC 2000). Some estimates suggest that the net carbon retention in tropical and subtropical wetlands is around 100 g $m^{-2}$ $yr^{-1}$ (Mitsch *et al.* 2013). This is very important in the context of global warming and climate change and, for tropical peatlands, an emergent topic in great need of research considering the amount of C that could return to the atmosphere should tropical wetlands with large C stocks be lost.

Coastal wetlands are among the most productive ecosystems (Jespersen & Osher 2007). Research that mentions wetlands as net carbon sinks (Brix *et al.* 2001, Whiting & Chanton 2001, Mitsch *et al.* 2013) states that carbon storage might be sufficient to have a noticeable influence on peat deposition and accumulation (Yavitt *et al.* 1987, Ezcurra *et al.* 2016). A substantial part of the atmospheric $CO_2$ fixed by photosynthesis is later deposited and effectively stored in wetland soils due to the low decomposition rates under anaerobic conditions (Mitra *et al.* 2005). In our study area, we found that tropical freshwater wetland soils accumulate carbon at a slightly higher rate than mangrove soils but the difference was not statistically significant. This is congruent with previous reports of high carbon stocks in freshwater wetlands on the central plain of the Gulf of Mexico (Campos-Cascaredo *et al.* 2011, Marín-Muñiz *et al.* 2014, Hernandez *et al.* 2015). Carbon stock in the mangrove soils investigated in this study was between 17 and 41 kg $m^{-2}$, though it reached values as high as 70 kg $m^{-2}$ in forested freshwater wetlands nearby. To our knowledge, the greatest carbon stock reported for Mexico is 82 kg $m^{-2}$ in mangroves in Tabasco (Moreno *et al.* 2002). Carbon accumulation in temperate wetland soils has received a great deal of attention (Craft & Casey 2000, Pant *et al.* 2003, Adhikari *et al.* 2009, Loomis & Craft 2010, Bernal & Mitsch 2012, 2013). However, there is less information about carbon storage in tropical wetland soils (Chmura *et al.* 2003, Campos-Cascaredo *et al.* 2011, Adame *et al.* 2013, Marín-Muñíz *et al.* 2014, Hernandez *et al.* 2015). Comparing carbon data for forested freshwater wetlands in other tropical regions with our results, Bernal & Mitsch (2013) found 15–45 kg $m^{-2}$, which is at the lower extreme of the values found in our study. Another study combining several published results reported carbon stocks of over 100 kg $m^{-2}$ in Indo-Pacific mangrove swamps (Donato *et al.* 2011). Such variability could be due to different sampling depths (ranging from 0.5 to 3 m). Wetland soils are very dynamic because of the continuous supply of organic matter, the thickness of the organic horizon, the nature of the mineral horizon, the flooding frequency, and changes in vegetation, all of which affect carbon distribution (Jobbágy & Jackson 2000), cycling (Cao & Woodward 1998) and storage (Kayranli *et al.* 2010). Research in tropical coastal marshes shows that their soils accumulate 20–100 kg $m^{-2}$ of carbon (SOC; Coultas 1996, Köchy *et al.* 2015). For mangrove soils, lower carbon densities (15 kg $m^{-2}$) were reported for Africa (Henry *et al.* 2009). In Japan, mangrove soils dominated by *Kandelia obovata* had carbon densities of 5.73 to 15 kg $m^{-2}$ (Khan *et al.* 2007).

In general, our research showed that litter production in forested freshwater wetlands is as high as that reported for mangrove swamp, which is recognised worldwide as one of the most productive ecosystems. High salinity and extended flooding were not always associated with low leaf litter production, and several combinations were observed. The carbon content of leaf litter produced by mangroves ranged from 0.38 to 1.5 tonnes $m^{-2}$ $yr^{-1}$, compared to a range of 0.7 to 1.3 tonnes $m^{-2}$ $yr^{-1}$ in forested freshwater wetlands. Carbon density, as a measure of carbon storage in the soil, was also variable, with values as high as 70 kg $m^{-2}$ in forested freshwater wetlands. In other words, forested freshwater wetlands are as important as mangroves in terms of carbon storage and peat deposition.

It is important to highlight our findings since forested freshwater wetlands are ecosystems that have received much less attention than mangroves. Usually, in considerations of tropical wetlands, mangroves are included but forested freshwater wetlands are not. Mexican federal law (SEMARNAT 2010) protects mangroves whereas forested freshwater wetlands are not protected, and this has led to rapid loss of these ecosystems. Ewel (2010) has highlighted the importance of conserving these ecosystems because of their key locations in coastal landscapes and their relevance to carbon sequestration (Craft *et al.* 2018). The preservation and restoration of these ecosystems and the coastal gradient should be implemented as a strategy for mitigating the effects of global climate change. Of overriding importance is whether the current climate conditions - as well as those of the near future - are sufficient, in combination with local factors such as topography, substrate conditions, vegetation, soil and rainwater acidity, nutrient status and biogeochemical cycling, to enable new soil formation and carbon storage. This topic needs more research.

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## AUTHOR CONTRIBUTIONS

PM-C: research design, data collection, generating manuscript and discussion; EC: data collection, data analysis, generating manuscript and discussion; MEH: carbon stock data analysis, generating manuscript and discussion; AC: soil analysis and discussion (RIP October 2021); DI-M: statistical analysis, generating manuscript and discussion.

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**Appendix 1:** Photographs of the study sites.

**MANGROVE SITES**

Estero Dulce

Laguna Grande-Chica

Rincón and Acula

**MANGROVE SITES (continued)**

Mandinga

Galindo

**FORESTED FRESHWATER WETLAND SITES**

Estero Dulce

**FORESTED FRESHWATER WETLAND SITES (continued)**

Ciénaga del Fuerte

Laguna Grande-Chica

Apompal

Boquilla

La Mancha

**Appendix 2:** Plant species lists.

**A: Mangrove sites**

| | Species | Estero Dulce | Galindo | Laguna Grande-Chica | Mandinga | Rincón | Acula |
|---|---|---|---|---|---|---|---|
| 1 | *Acrostichum aureum* L. | x | | | | | |
| 2 | *Avicennia germinans* (L.) L. | x | | x | x | x | x |
| 3 | *Bacopa monnieri* (L.) Wettst. | | | | | x | |
| 4 | *Batis maritima* L. | | | | x | x | x |
| 5 | *Borrichia frutescens* (L.) DC. | | | | | x | |
| 6 | *Bromelia* sp. | | x | | | | |
| 7 | *Cabomba aquatica* Aubl. | | | | | x | x |
| 8 | Cabomba caroliniana A. Gray | | | | | | x |
| 9 | *Conocarpus erectus* L. | | x | | | x | |
| 10 | *Dalbergia brownei* (Jacq.) Schinz | | x | | | x | |
| 11 | *Gardenia aculeata* (L.) Aiton | x | | | | | |
| 12 | *Hymenocallis littoralis* (Jacq.) Salisb. | | | x | | | |
| 13 | *Laguncularia racemosa* (L.) C.F. Gaertn. | x | | x | x | x | x |
| 14 | *Microgramma nitida* (J. Sm.) A.R. Sm. | | x | | | | |
| 15 | *Pachira aquatica* Aubl. | x | | | | | |
| 16 | *Psychotria macrophylla* Ruiz & Pav. | | | | | x | |
| 17 | *Rhabdadenia biflora* (Jacq.) Müll. Arg. | x | x | x | | x | x |
| 18 | *Rhizophora mangle* L. | x | | x | x | x | x |
| 19 | *Sesuvium portulacastrum* L. | | | | | | x |
| 20 | *Solanum tampicense* Dunal | | | | | x | |
| 21 | *Spartina spartinae* (Trin.) Merr. ex Hitchc | | | | | x | x |

**B: Forested freshwater wetland sites**

| | Species | Apompal | Laguna Grande-Chica | La Mancha | Ciénaga del Fuérte | Galindo | Boquilla | Mandinga | Estero Dulce | Río Blanco |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Acacia cornigera* (L.) Willd | | | | | | | | x | |
| 2 | *Acrocomia mexicana* Karw. ex Mart. | | | | | | x | | | |
| 3 | *Acrostichum aureum* L. | x | x | | | | x | x | | x |
| 4 | *Alibertia edulis* (Rich.) A. Rich. | | | | x | x | | | | |
| 5 | *Annona glabra* L. | | | x | | | x | x | | x |
| 6 | *Ardisia compressa* Kunth | | | | x | x | | | | |
| 7 | *Ardisia revoluta* Kunth | | | | x | | | | | |
| 8 | *Attalea butyracea* (Mutis ex L. f.) Wess. Boer | x | | | x | | | | | |
| 9 | *Avicennia germinans* (L.) L. | | x | | | | | | x | |
| 10 | *Bignonia obovata* (Kunth) Spreng. | | | | | x | x | x | | |
| 11 | *Bonellia cavanillesii* Bertero ex Colla | | | | | | | | | x |
| 12 | *Brosimum alicastrum* Sw. | | | | x | | x | | | |
| 13 | *Bursera simaruba* (L.) Sarg. | | | | | x | x | | | |
| 14 | *Coccoloba barbadensis* Jacq. | | | | | x | x | | | |
| 15 | *Combretum laxum* Jacq. | | | | | | | | | x |
| 16 | *Commelina diffusa* Burm. f | | | | | | | | | x |
| 17 | *Crinum erubescens* Aiton | | | x | | | | | | |
| 18 | *Crossopetalum rhacoma* Crantz | | | | | | | | | x |
| 19 | *Dalbergia brownei* (Jacq.) Schinz | x | x | | x | | | x | x | x |
| 20 | *Daphnopsis americana* (Mill.) J.R. Johnst. | x | | | | | | | | |
| 21 | *Dendropanax arboreus* (L.) Decne. & Planchon | | | | | | | | x | x |
| 22 | *Dioscorea convolvulacea* Schltdl. & Cham. | | | | | | | | x | |
| 23 | *Diospyros digyna* Jacq. | x | | x | x | x | x | x | | |
| 24 | *Eugenia capuli* (Schltdl. & Cham.) Hook. & Arn | | | | | x | | | x | |
| 25 | *Eugenia oerstediana* O. Berg | | | | x | | | | | |
| 26 | *Ficus aurea* Nutt. | | | x | | | | | | |
| 27 | *Ficus insipida* Willd. subsp. Insipida | x | | x | x | | x | | x | |
| 28 | *Ficus maxima* Mill. | | | x | x | x | | | | |

| | Species | Apompal | Laguna Grande-Chica | La Mancha | Ciénaga del Fuérte | Galindo | Boquilla | Mandinga | Estero Dulce | Río Blanco |
|---|---|---|---|---|---|---|---|---|---|---|
| 29 | *Ficus obtusifolia* Kunth | x | | | x | | | | | |
| 30 | *Ficus pertusa* L. f. | | | | | x | x | | | |
| 31 | *Guatteria galeottiana* Baill. | | | | x | | | | | |
| 32 | *Hampea nutricia* Fryxell | | | | x | x | | | | |
| 33 | *Heliconia latispatha* Benth. | x | | | | | | | | |
| 34 | *Hippocratea celastroides* Kunth | x | x | | x | | | | | |
| 35 | *Hippocratea volubilis* L. | | | | | | | | | x |
| 36 | *Inga paterno* Harms | | | | | x | | | | |
| 37 | *Inga vera* Willd. | x | | | x | | | | x | |
| 38 | *Ipomoea anisomeres* B.L. Rob. & Bartlett | | | | | | | | x | x |
| 39 | *Laguncularia racemosa* (L.) Gaerth. F. | x | | | | | | | x | |
| 40 | *Leersia* sp. | | | | | | | | | x |
| 41 | *Machaerium falciforme* Rudd | | | | | | | | | x |
| 42 | Malvaceae | | | | | | | | | |
| 43 | *Malvaviscus arboreus* Cav. | | | | x | | x | | x | x |
| 44 | *Microgramma nitida* (J. Sm.) A.R. Sm. | | | | | | | | | x |
| 45 | *Nectandra salicifolia* (Kunth) Nees | | | | | | x | | | |
| 46 | *Pachira aquatica* Aubl. | x | x | x | x | | | | x | x |
| 47 | *Palicourea nigricans* K. Krause | | | | x | | | | x | |
| 48 | *Parathesis psychotrioides* Lundell | | | | x | | | | | |
| 49 | *Passiflora biflora* Lam. | | | x | | | | | | x |
| 50 | *Paullinia pinnata* L. | x | | | x | | | | | |
| 51 | *Petiveria alliacea* L. | | | | x | | | | | |
| 52 | *Picramnia antidesma* Sw. | | | | x | | | | | |
| 53 | *Piper amalago* L. | | | x | | | | | | |
| 54 | *Piper nitidum* Sw. | x | | x | | | | | | |
| 55 | *Pisonia aculeata* L. | | | | x | | | | | |
| 56 | *Pithecellobium latifolium* (L.) Benth | | | | x | | | | | |
| 57 | *Pithecellobium recordii* (Britton & Rose) Standl | | | | | | | | x | |

| | Species | Apompal | Laguna Grande-Chica | La Mancha | Ciénaga del Fuérte | Galindo | Boquilla | Mandinga | Estero Dulce | Río Blanco |
|---|---|---|---|---|---|---|---|---|---|---|
| 58 | *Pithecellobium* sp. | | | | | | | x | | |
| 59 | *Pleuranthodendron lindenii* (Turcz.) Sleumer | | | | | | x | | x | |
| 60 | *Polygonum longiocreatum* Bartlett | | | | | | | | | x |
| 61 | *Pontederia sagittata* C. Presl | | | | | | | | x | x |
| 62 | *Psychotria trichotoma* M. Martens & Galeotti | | | | x | | | | | |
| 63 | *Rapanea myricoides* (Schltdl.) Lundell | | | | | | | | | x |
| 64 | *Rhabdadenia biflora* (Jacq.) Müll. Arg. | | x | | | | | | x | x |
| 65 | *Rhizophora mangle* L. | | x | | | | | | | |
| 66 | *Sabal mexicana* Mart. | | | | | | x | x | | x |
| 67 | *Sapium nitidum* (Monach.) Lundell | x | | | | | | | | |
| 68 | *Scleria lithosperma* (L.) Sw. | x | | | | | | | | |
| 69 | *Smilax domingensis* Willd. | | | | | | | | | x |
| 70 | *Smilax mollis* Humb. & Bonpl. ex Willd. | | | x | | | | | | |
| 71 | *Smilax* sp. | x | | | | | | | | |
| 72 | *Spathiphyllum cochlearispathum* (Liebm.) Engl. | | | x | | | x | | | |
| 73 | *Syngonium podophyllum* Schott | x | | x | x | x | x | x | | |
| 74 | *Tabebuia rosea* (Bertol.) DC. | x | | x | | | x | | | |
| 75 | *Tabernaemontana alba* Mill. | x | | | x | | | | | |
| 76 | *Thalia geniculata* L. | | | | | | | | x | x |
| 77 | *Thelypteris serrata* (Cav.) Alston | x | | x | x | | | | | |
| 78 | *Trichilia havanensis* Jacq. | | | | | x | x | | | |
| 79 | *Trophis mexicana* (Liebm.) Bureau | | | x | | | | | | |
| 80 | *Urechites andrieuxii* Müll. Arg. | | x | | | x | | | x | |
| 81 | *Zanthoxylum caribaeum* Lam. | | | | | | | x | | |

**Appendix 3:** Literature-based comparison of the leaf litter production in different types of temperate and tropical forested wetlands in different regions of the world. GW = groundwater.

**A: Temperate wetlands**

| Location (country) | Type of wetland | Species | Litterfall productivity ($g\ m^{-2}\ y^{-1}$) | Water level range (cm) [min–max] | Salinity ($g\ L^{-1}$) | Reference |
|---|---|---|---|---|---|---|
| Des Allemads, AL (USA) | Bottomland hardwood | *Taxodium distichum, Nyssa aquatica* | 574 | - | - | Conner & Day 1976 |
| | Cypress-Tupelo | *Nyssa aquatica, Taxodium distichum* | 620 | - | - | Conner & Day 1976 |
| Tar River, NC (USA) | Tupelo swamp | *Taxodium distichum* | 609–677 | - | - | Brinson 1977 |
| Creeping Swamp, NC (USA) | Floodplain swamp | Not available | 523 | - | - | Mulholland 1979 |
| Dismal Swamp, VA (USA) | Cedar swamp | *Chamaecyparis thyoides* | 757 | - | - | Dabel & Day 1977 |
| Dismal Swamp, VA (USA) | Maple-gum swamp | *Liquidambar styraciflua* | 659 | - | - | Dabel & Day 1977 |
| Dismal Swamp, VA (USA) | Cypress swamp | *Taxodium distichum* | 678 | - | - | Dabel & Day 1977 |
| Dismal Swamp, VA (USA) | Mixed hardwood swamp | *Quercus* spp., *Nyssa sylvatica* | 653 | - | - | Dabel & Day 1977 |
| Okefenokee, GA (USA) | Cypress swamp | *T. distichum* | 328 | 15–100 | - | Schlesinger 1978 |
| Heron Pond, IL (USA) | Cypress Tupelo | *Nyssa aquatica, Taxodium distichum* | 448 | 0–152 | - | Mitsch *et al*. 1977 |
| Alachua County, FL (USA) | Floodplain swamp | Not available | 521 | - | - | Brown 1978 |
| Big Cypress Swamp, FL (USA) | Drained swamp | *Nyssa aquatica* | 120 | -116–12 | - | Carter *et al*. 1973 |
| Big Cypress Swamp, FL (USA) | Undrained swamp | *Nyssa aquatica* | 485 | -100–61 | - | Carter *et al*. 1973 |
| Kisatchie National Forest, LA (USA) | Alluvial-floodplain bottom-land hardwood forest | *Quercus pagoda, Q. nigra, Liquidambar styraciflua* | 687–1040 | -175–25 | - | Meier *et al*. 2006 |
| Apalachicola River, FL (USA) | Non-tidal freshwater forested wetlands | *Fraxinus caroliniana, Nyssa aquatica, N. ogeche* | 664.9 | - | - | Anderson & Lockaby 2011 |
| Apalachicola River, FL (USA) | Tidal freshwater forested wetlands | *Acer rubrum, Fraxinus profunda, Ogeechee tupelo, Nyssa sylvatica var. biflora, Persea palustris, Taxodium distichum, Ulmus americana* | 381.1 | - | - | Anderson & Lockaby 2011 |
| Strawberry Swamp, Hobcaw Barony, SC (USA) | Tidal freshwater forested wetlands | *Taxodium distichum* | 470 | 0–100 | 0.8–6.3 | Liu *et al*. 2017 |

**B: Tropical wetlands (mangroves)**

| Location (country) | Type of wetland | Species | Litterfall productivity ($g\ m^{-2}\ y^{-1}$) | Water level range (cm) [min–max] | Salinity ($g\ L^{-1}$) | Reference |
|---|---|---|---|---|---|---|
| Rookery Bay, southwest FL (USA) | Mangrove | *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* | 504–751 | flooding tides (≈ 8 cm/tide) | 35–50 | Twilley *et al*. 1986 |
| Fort Myers, southwest FL (USA) | Mangrove | *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* | 351–868 | flooding tides (≈ 8 cm/tide) | 60–85 | Twilley *et al*. 1986 |
| Laguna de Términos, Campeche (México) | Mangrove | *Rhizophora mangle*, *Avicennia germinans* | 536–1116 | 0–50 (tidal) | 25–70 (interstitial) | Coronado-Molina 2000 |
| Laguna La Mancha, Veracruz (México) | Mangrove | *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* | 905 | - | - | Rico-Gray & Lot 1983 |
| Laguna La Mancha, Veracruz (México) | Mangrove, fringe and basin | *Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle* | 692–967 | 0–82 | 21.3–32.5 | Utrera-López & Moreno-Casasola 2008 |
| Laguna La Mancha, Veracruz (México) | Mangrove, relic riverine | *Rhizophora mangle* | 1350 | 0–77 | 2.1–10.6 | Utrera-López & Moreno-Casasola 2008 |
| Yaqui, Mayo and Fuerte, Gulf of California, Hermosillo (Mexico) | Mangrove, | *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* | 712–1506 | 14–20 (tidal) | 36.3–46.1 | Sánchez-Andrés *et al*. 2010 |
| Laguna La Mancha, Veracruz (México) | Mangrove, fringe and basin | *Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle* | 1068–2734 | - | 9.2–41 (dry season) 8.5–30 (rainy season) | Agraz Hernández *et al*. 2011 |
| Laguna de Términos, Campeche (México) | Mangrove | *Rhizophora mangle* | 1160–1838 | - | 10–50 (interstitial) | Agraz Hernández *et al*. 2015 |
| Barra de Navidad Lagoon, Jalisco | Mangrove | *Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle*, *Conocarpus erectus* | 229 | 0–28 | 1.7–38.9 (GW) | Mendoza-Morales *et al*. 2016 |
| Laguna Mecoacan, Tabasco (México) | Mangrove | *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa* | 515 | - | 9.1–20.4 (surface) 22–56 (interstitial) | Torres *et al*. 2017 |
| Centla Wetlands Biosphere Reserve, Tabasco (Mexico) | Mangrove | *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa* | 469–904 | -160–40 | 2.9–30 (surface) 29 ± 1.4 (interstitial) | Torres *et al*. 2018 |
| Balandra, La Paz Bay, BC (Mexico) | Mangrove | *Rhizophora mangle*, *Laguncularia racemosa*, *Avicennia germinans* | 698.5 | - | 44.9 ± 6.6 (interstitial) | Ochoa-Gomez 2014 |

**C: Tropical wetlands (swamps)**

| Location (country) | Type of wetland | Species | Litterfall productivity (g m$^{-2}$ y$^{-1}$) | Water level range (cm) [min–max] | Salinity (g L$^{-1}$) | Reference |
|---|---|---|---|---|---|---|
| The Pantanal, Mato Grosso (Brazil) | Seasonally flooded semi-deciduous forests | *Vochysia divergens, Duroia cf. eriopila, Trichilia catigua, Mouriri guianensis* | 753–1027 | 35–50 | - | Haase 1999 |
| Kosrae Island (Micronesia) | Freshwater peatland | *Terminalia carolinensis, Horsfieldianum nunu, Barringtonia racemosa* | 1106–1137 | -0.1–3.4 | - | Chimner & Ewel 2005 |
| Central Amazon forest (terra firme), Manaus (Brazil) | Tropical evergreen forest | not specified (destructively sampled trees) | 730–830 (litterfall)<br>1290 (above-ground) | -<br>- | -<br>- | Chambers *et al*. 2001 |
| Puerto Rico (USA) | Swamp forest (riverine and basin) | *Pterocarpus officinalis* | 870–1190 | - | - | Alvarez-Lopez 1990 |
| (Guadeloupe) | Mangrove and swamp forest | not available | 1050–1420 | - | - | Febvay & Kermarrec 1978 |
| Ciénaga del Fuerte, Veracruz (Mexico) | Swamp forest | *Pachira aquatica, Ficus insipida, F. maxima, Hippocratea celastroides, Dalbergia brownei* | 1376 | -42–53 | 0.21 (surface)<br>0.59 (GW) | Infante Mata *et al*. 2012 |
| Laguna Chica, Veracruz (Mexico) | Swamp forest | *Pachira aquatica, Hippocratea celastroides, Dalbergia brownei* | 1485 | -44–26 | 2.1 (surface)<br>10.8 (GW) | Infante Mata *et al*. 2012 |
| La Mancha, Veracruz (Mexico) | Swamp forest | *Annona glabra, Diospyros digyna* | 971 | -24–59 | 0.47 (surface)<br>0.4 (GW) | Infante Mata *et al*. 2012 |
| Apompal, Veracruz (Mexico) | Swamp forest | *Pachira aquatica, Ficus maxima, Roystonea dunlapiana* | 933 | -10–70 | 0.17 (surface)<br>0.15 (GW) | Infante Mata *et al*. 2012 |
| El Salado, Veracruz (Mexico) | Swamp forest | *Pachira aquatica, Annona glabra* | 1250 | -27–10 | 0.23 (surface)<br>0.27 (GW) | Infante Mata *et al*. 2012 |