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Floristic composition and soil characteristics of tropical freshwater forested wetlands of Veracruz on the coastal plain of the Gulf of Mexico

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ABSTRACT

We studied the influence of geomorphological setting and soil properties on the vegetation structure, composition and diversity of five forested coastal wetlands in Veracruz on the Gulf of Mexico. These swamps are located on floodplains and in dune depressions. We recorded 109 woody and herbaceous species. The most frequent species were the trees *Pachira aquatica*, *Annona glabra*, *Diospyros digyna* and *Ficus insipida* subsp. *insipida*, the lianas *Dalbergia brownei* and *Hippocratea celastroides* and the hemi-epiphyte *Syngonium podophyllum*. The Shannon-*H* diversity index varied from 2.659 to 3.373, density from 1750 to 2289 stems ha^{-1} and basal area from 32.7 to 76.42 m^2 ha^{-1}. The classification analysis defined two groups: one corresponded to forested wetlands along the floodplain (Apompal, Cienaga, Chica) and the other included Mancha and Salado, in dune depressions. PCA ordination of soil parameters during the rainy season explained 67.0% and during the dry season 69.1% of the total variance. In the rainy season Mancha and Salado samples remain close together because they have lower Mg, Na, K, % Total C and % Total N values. Apompal and Chica samples remain close to each other because of their high levels of % Total C, % Total N, Mg, Na and high soil water content. Cienaga samples are separated from the others because of high values of P, Ca and Eh as well as high water levels. In general, soil parameter ordination during the dry season showed that redox potential, P, water level and water content decreased in the forested wetlands and Na values increased in Chica. The soil textures identified were clay, sandy clay loam, sandy loam and clay loam; clay texture dominated alluvial processes in the floodplain (e.g., Cienaga). The forested wetlands in the floodplains had similar vegetation and the same happened in the dune depressions but soil characteristics were more variable in both cases. Plant diversity in floodplains tends to be relatively high, and the presence of adjacent tropical forests probably increases its richness, except in cases in which there are stressing factors, such as salinity. The forested wetlands studied showed dominant floristic elements, which extend north into Florida such as *A. glabra* and *Ficus aurea*. Other dominant elements such as *P. aquatica* are also found in Central and South America. The forested wetlands studied are subjected to continuous deforestation to transform the land into farming or ranching activities, this being a common practice throughout the distribution range of these forests.

1. Introduction

Tropical forested wetlands provide connectivity between coastal ecosystems, which is critical in flood control and storage of organic matter, sediment retention, among other functions (Ewel, 2010). These forested wetlands are located in extensive floodplains such as the Amazon (Kubitzki, 1989; Teixeira et al., 2011), in depressions where the water table is exposed as in dune lakes (Moreno-Casasola et al., 2009), on the periphery of coastal lagoons (Lot and Novelo, 1990), as small patches of vegetation in the Everglades (Gunderson and Loftus, 1993), forming Petenes in the Yucatan Peninsula (Olmsted and Durán, 1986), or in narrow plains as in the case of the Pacific islands (Allen et al., 2005; Ellison, 2009). Many of these swamps in subtropical and tropical areas and in coastal tropical plains are frequently found upland from mangroves, and they have received little attention (Ewel, 2010).

Forested wetlands are characterized by the presence of tree elements with morphological adaptations (buttresses, knee roots) to

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scarcity of oxygen, and the presence of palms, which can become the dominant elements and lianas. The height of these forests usually ranges from 10 to 25–30 m. Despite the physiognomic similarities among forested wetlands in each region, each is characterized by a particular plant composition: for example in the southern United States dominant species are *Taxodium distichum* var. *nutens* and *Nyssa sylvatica* var. *biflora* (Brown et al., 1984), in the coastal Gulf of Mexico *Pachira aquatica* and *Annona glabra* (Lot and Novelo, 1990), in the Yucatan Peninsula *Bucida spinosa* and *Haematoxylum campechianum* dominate (Olmsted and Durán, 1986), in the Guyanas and Caribbean region, including Puerto Rico the most conspicuous species are *Pterocarpus officinalis* and *Symphonia globulifera* (Alvarez-Lopez, 1990; Migeot and Imbert, 2011), in the Pacific Islands one can find *Terminalia carolinensis*, *Campnosperma brevipetiolatum*, *Calophyllum vexans* (Allen et al., 2005; Ellison, 2009) and in the southern part of Australia *Melaleuca* spp. (Finlayson et al., 1993; Zoete, 2001). The description of the structure of these forests and their relationship with environmental parameters such as soils, hydrology and geomorphology has established the characteristics of the main types of forested wetlands and their functions (Chimner and Ewel, 2005; Hupp et al., 2009; Klimas et al., 2009; Middleton, 2009), but there are still few examples in the tropical and subtropical regions. Knowledge of the structure and species composition of these ecosystems will set the basis for determining and comparing their diversity (Myers, 1990; Zoete, 2001), connectivity and interactions with adjacent ecosystems (Mitsch and Gosselink, 2000), and will permit the establishment of guidelines for their conservation (King et al., 2009) and restoration (Middleton, 2002; Toth et al., 2002), role in carbon storage and productivity rates which is exported to mangroves and adjacent water bodies.

Historically, the main human activities that have transformed these ecosystems are flow alteration by dams (De la Lanza-Espino and Cáceres-Martínez, 1994; Jansson et al., 2000; Millennium Ecosystem Assessment, 2005), water contamination (Keddy, 2002; Tockner and Stanford, 2002) and changes in land use (MacKenzie, 2008; Ewel, 2010) that have reduced their distribution and altered the function and quality of the environmental services they provide.

Coastal tropical wetlands of the Gulf of Mexico are supplied with freshwater flowing from the highlands (and rainwater) and, in some cases, saltwater intrusion from the coastal lagoons. This mixture of salt- and freshwater creates a salinity gradient that facilitates the establishment of diverse types of wetlands. From high to low levels of salinity, mangroves (*Rhizophora mangle*, *Laguncularia racemosa*, *Avicennia germinans*, *Conocarpus erectus*), freshwater forested wetlands (*P. aquatica*, *A. glabra* and *Ficus* spp.) and freshwater/brackish marsh species (*Sagittaria lancifolia*, *Pontederia sagittata*, *Thalia geniculata*, *Cyperus giganteus*, *Typha domingensis*) can be found in this region. The freshwater wetlands in Veracruz have been severely degraded, mainly by a transformation of all of these types of wetlands into flooded pastures and the introduction of exotic species such as the African grass *Echinochloa pyramidalis* (López-Rosas et al., 2005, 2006; Moreno-Casasola and Infante, 2010; Moreno-Casasola et al., 2010). More recently, urbanization has also become an important cause of wetland transformation.

Regional forested wetlands have received little attention. Emphasis has been on the study of different aspects of mangrove ecology (Rico-Gray and Lot, 1983; López-Portillo and Ezcurra, 2002; Hernández-Trejo et al., 2006; Utrera-López and Moreno-Casasola, 2008). There is some information describing the floristic composition of the freshwater forested wetlands (Orozco and Lot, 1976; Lot and Novelo, 1990) and less on their functionality (Infante, 2004; Yetter, 2004; Infante and Moreno-Casasola, 2005; Moreno-Casasola et al., 2009). Today, there are few remnants of forested wetlands, and there is a growing need for more detailed study on their composition and vegetation structure, seed and seedling ecology, productivity, hydrology and soil characteristics.

Wetlands exist on landforms that allow the accumulation of water (Jackson, 2006). Swamps in Veracruz are found both on floodplains and in depressions of coastal dune systems, and each type of forest maintains a particular soil type and hydroperiod as a result of differences in the main sources of water (Mitsch and Gosselink, 2000; Kolka and Thompson, 2006). Floodplains are identified by flood pulses and the inflow of surface water (Middleton, 2002); the hydroperiod of forested wetlands in depressions depends on fluctuations of the water table (Yetter, 2004).

Hydroperiod is a crucial component in the functioning of wetlands (Junk et al., 1989; Mitsch and Gosselink, 2000; Richardson et al., 2001; Jackson, 2006). In coastal areas of the Gulf of Mexico, freshwater forested wetlands have increased water levels during the rainy season, and the species that inhabit them have adapted their phenologies by adjusting the waterborne dispersion of their seeds to periods of flooding; both *P. aquatica* and *A. glabra*, two of the dominant trees of these flooded forests, have adopted this strategy (Infante and Moreno-Casasola, 2005). Biogeochemical processes in the soil are also dominated by the annual cycle of flooding-drying that occurs in tropical wetlands, as has been found in Brazil's forested wetlands (Piedade et al., 2010) and in Guyana's (van Andel, 2003). Water inflow enriches wetlands with nutrients (Lodge et al., 1994; Mitsch and Gosselink, 2000; Middleton, 2002) but also causes a decrease in oxygen and runoff of both beneficial and toxic compounds to plants (Kadlec and Wallace, 2009). Wetland plants have adapted to withstand periods of flooding through anatomical and physiological adaptations that allow them to endure the presence of toxins and low oxygen conditions in the soil (Cronk and Fennessy, 2001). When the dry period returns, the functioning of wetland soils responds to the return of oxygenated conditions that allow for the microbial activity necessary for the decomposition of organic matter and the mineralization of compounds that are toxic to plants (Collins and Kuehl, 2001; Boon, 2006; Reddy and DeLaune, 2008).

The objectives of the study were to (i) characterize the floristic composition, structure and diversity of wetland forests located in floodplains and dune depressions in the southern Gulf Coast of Mexico and (ii) characterize the soil properties and flooding level of these wetlands during the rainy season and dry season. We developed the following hypotheses with regard to the vegetation and soil properties of the tropical freshwater forested wetlands under study:

i. The structure and composition of vegetation differs between wetlands in floodplains and in flooded depressions in coastal dunes. Diversity will be higher in forested wetlands on floodplains. Forested wetlands that remain flooded for longer periods of time, i.e. in depressions, will have lower diversity values.
ii. The soil texture of the floodplain forests will be dominated by fluvial materials and that of the dune depressions by sand.
iii. In floodplain forests, we expect higher concentrations of exchangeable cations because these forests are exposed to nutrient input by inflow from the land and the overflow of rivers. In the forests located in dune depressions, the main change in water level is through the elevation of groundwater, and thus nutrient input from runoff is less important, thus exchangeable cations will have lower values.
iv. The forested wetlands that remain flooded for a longer time show higher values of carbon and nitrogen storage in the soil.

2. Materials and methods

2.1. Study site

Field studies were conducted on five swamps on the coastal plain of the Gulf of Mexico in the state of Veracruz. The study sites, ranging from north to south, include Cienaga del Fuerte (Municipality of Tecolutla), Laguna Chica (Vega de Alatorre), La Mancha (Actopan), Laguna La Apompal (Jamapa) and El Salado (Alvarado), the southernmost site located close to the Port of Veracruz (Fig. 1). The location and environmental characteristics for each study site are shown in Table 1.

The climate of the coastal plain of the Gulf of Mexico has three seasons: a rainy period extending from July to October, cold fronts with strong winds and rain between November and February and the dry season between March and June (López-Rosas et al., 2006). Mean annual temperature is 22–25 °C (IMTA, 2007). Annual precipitation fluctuates between 1200 and 1650 mm, with 80% of the annual precipitation falling between June and September (Fig. 1). The sites differ in their geomorphological setting, soil characteristics (Table 1), inundation area and flooding times.

2.2. Sampling procedures and field surveys

Species composition for tree and shrub strata and vegetation cover were measured in 10 × 10 m plots, with 9–12 plots per site (Teixeira et al., 2011); herbs were evaluated in three 2 × 2 m plots within each of the 10 × 10 m plots. Cover was estimated using the Westhoff and van der Maarel (1978) cover-abundance scale. The flooded forests were dominated by a few species of large trees,

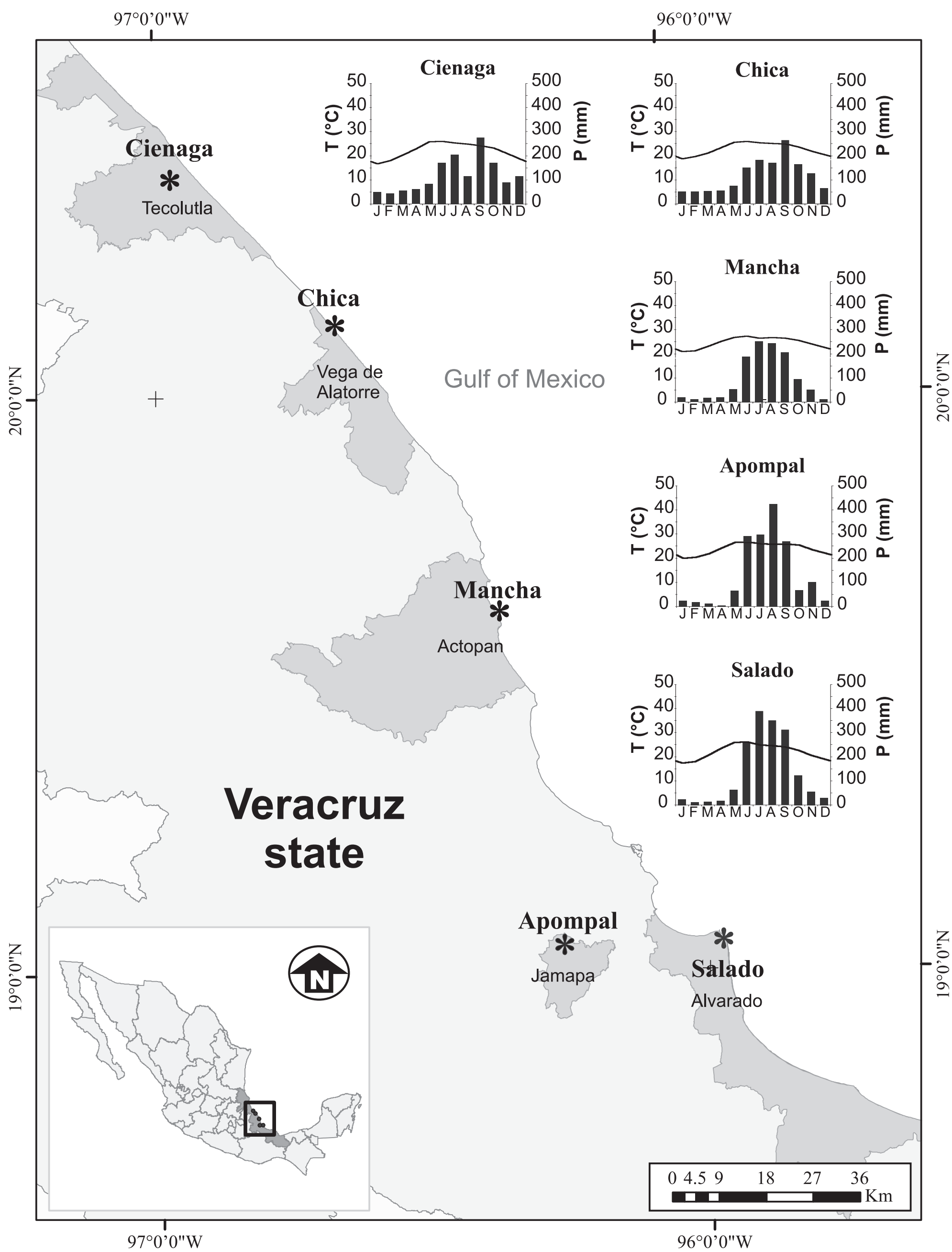

Fig. 1. Location of the study sites in the coastal plain of the Gulf of Mexico and climate diagrams for each area; P (precipitation in mm), T (temperature, °C), data taken from Eric III (IMTA, 2007).

Table 1
Description of the environmental characteristics of the forested wetlands studied on the coastal plain of Veracruz.

	Cienaga	Chica	Mancha	Apompal	Salado
Location	20°18′34.80″N 96°54′56.20″W	20°05′47.8″N 96°41′23.8″W	19°35′52.91″N 96°22′53.81″W	19°01′19.39″N 96°17′6.61″W	19°02′4.40″N 95°59′1.52″W
Geomorphology[a]	Fluvio-accumulative surface	Perilacustrine accumulative surface	Accumulative intradunal depression	Boggy-fluvial accumulative surface	Accumulative intradunal depression bordering a coastal plain
Soil type[a]	Fluvic Gleysoil	Humic Gleysoil	Humic Gleysoil	Fluvi-gleic Histosol	Histo-gleic Arenosol
Associated water flow	Floodplain and river	Floodplain, fringing a coastal lagoon	Phreatic water	Floodplain and river	Phreatic water
Annual precipitation[b] (mm)	1436.3	1397.7	1155.9	1646.3	1591.5
Superficial water salinity[c] (g L^{-1})	0.21 ± 0.01	2.06 ± 0.55	0.47 ± 0.08	0.17 ± 0.02	0.27 ± 0.02
Groundwater salinity[c] (g L^{-1})	0.59 ± 0.27	10.79 ± 1.37	0.40 ± 0.07	0.15 ± 0.02	0.27 ± 0.02
Bordering ecosystems	Marshes, citrus cultivars, inundated pastures, mangroves towards the coast	Marshes, inundated pastures, mangroves	Tropical dry forest, dune lake and marshes, dune vegetation	Marshes, inundated pastures, mango cultivars	Tropical dry forest, watermelon cultivars, pasture lands

[a] Data obtained from field work in each study area.
[b] Eric III (IMTA, 2007).
[c] The salinity was measured with an YSI 550 multiparameter at each site.

and the plot size allowed for the presence of several trees and shrubs. Each plot was systematically surveyed by identifying and measuring the diameter at breast height (DBH) of trees, shrubs and climbers with stems over 3 cm DBH. If a tree was multicaulous, each stem was considered to be an individual. Buttressed trees were measured with a ladder 10 cm above the top of the buttresses.

2.3. Plant collection

Plant collections, when possible, were made of all species growing in the plots. In addition, flowering and fruiting material was collected outside the plots to match not-flowering specimens collected from within the plots. The plant material was deposited at the Herbarium XAL of the Instituto de Ecología, A.C., Xalapa, Veracruz. A complete list of all identifiable species found in the five tropical forested wetlands is given with full authority in the Appendix.

2.4. Soil samples

One soil sample was taken in five of the vegetation plots in each site, both during the rainy season (October 2005) and the dry season (June 2006). Soil samples were taken from the top 15 cm. Available P was obtained using the Bray and Kurtz extraction method (Bray and Kurtz, 1945) and Olsen's method (Olsen and Dean, 1965). Exchangeable Ca, Mg, K and Na were obtained by mixing 33 mL of 1 N ammonium acetate with a 5 g soil sample (Chapman, 1965). The filtered extract was analyzed with an inductive coupled plasma atomic emission spectrometer (Lanyon and Heald, 1982) for Ca and Mg and by flame photometry for K and Na (Knudsen et al., 1982). Soil pH was measured with a glass electrode in a well-mixed 2:1 solution of deionized water and soil (Jackson, 1964). Total C and N were determined using dry combustion (LECO 2002, LECO Corporation, St. Joseph, Michigan, USA). Soil texture was analyzed using the hydrometer method (Bouyoucos, 1962).

Water content was obtained by taking 15 cm deep soil samples and keeping them in aluminum boxes. For each sample, we recorded the wet weight; dry weight was obtained after drying for 48 h at 80 °C. Final data for water content were calculated by subtracting the dry weight from the wet weight, dividing by the dry weight and multiplying by 100 (Wilke, 2005).

2.5. Redox potential

Soil redox potential (Eh) was measured in each forested wetland, in both the rainy and dry seasons, in five plots at a soil depth of 15 cm using three platinum electrodes, one calomel reference electrode (Corning 476340) and a digital pH/ORP Barnant meter. Platinum electrodes were calibrated in the laboratory with quinhydrone (Sigma Q-1001) in a pH 4.0 buffer solution (Bohn, 1971). To calculate Eh, +244 mV was added to each mV reading. We used an average of three redox values for each plot in our analysis.

2.6. Water level

A water-level tape (Solinst Mini 101) was used to measure the height of the water level inside the five monitoring wells located in each study site. Monitoring wells were made from PVC pipe that was 13 mm in diameter and 3 m in length, and they were installed to a depth of 1.5 m. Twenty centimeters at the end of the PVC pipe were slotted at 2-cm intervals and wrapped with Nytex™ microfilament mesh held into place with stainless steel wire. The end of the well was closed. Water level was measured in October 2005 and June 2006. The wells were never dry during the study period. Monitoring wells were not referenced to a common datum, therefore height of groundwater is relative to the soil surface.

2.7. Data processing

A relative importance value (RIV) was used to compare the species composition of the plots (Cottam and Curtis, 1956). The RIV of a species was defined as the sum of its relative dominance (Rdom), its relative density (Rden) and its relative frequency (Rfreq), using the formula RIV = Rdom + Rden + Rfreq. The last three indices are calculated using the following equations:

$$\text{Relative dominance}(\text{Rdom}) = \text{total basal area for a species/total basal area for all species} \times 100\% \quad (\text{basal area} = \pi^{*}(\text{DBH}/2)^2)$$

$$\text{Relative density (Rden)} = \text{number of individuals of a species/total number of individuals} \times 100\%$$

$$\text{Relative frequency (Rfreq)} = \text{frequency of a species/sum frequencies of all species} \times 100\%$$

The frequency of a species is defined as the number of subplots (10 × 10 m) in which it is present. The theoretical range for Rdom, Rden and Rfreq is 0 to 100%. Thus, the RIV of a species may vary between 0% and 300%.

A matrix with cover-abundance values per species and per plot (109 species × 51 plots) was subjected to Ward's hierarchical classification using relative Euclidian distance as a measure of similarity. The PC-ORD program version 5 (McCune and Mefford, 1999) was used.

The estimation of species richness as a measure of the sampling effort carried out at each site was analyzed using nonparametric methods $Chao_2$ and Jack-knife 1 (program Bio Diversity Pro9-McAleece et al., 1999). Alpha diversity, using the Shannon index, was calculated using the PAST program (Hammer et al., 2001) and this was compared between sites through a one-way ANOVA (Stat Soft Inc., 2001). Beta diversity, using the Sorensen index, was calculated with the program EstimateS, version 8.2 (Colwell, 2009).

Histograms classed based on the values for diameter at breast height were used to evaluate the vegetation structure of each site. The tree density per diameter class was adjusted to 1 ha to make graphical comparison between sites possible.

Soil textural classes were analyzed according to the soil textural triangle (Saxton et al., 1986; Sprecher, 2001). Soil bulk density (oven-dry weight per volume) was determined after drying soil samples of 198 cm^3 in volume at 105 °C for 24 h (Hausenbuiller, 1972). We applied a one-way ANOVA by soil texture and bulk density. After a significant group effect was detected ($P < 0.05$), multiple comparisons were applied using the Tukey method to identify significant differences among groups (Zar, 1996). The statistical package Statistica, version 6 (Stat Soft Inc., 2001) was used.

Soil data (exchangeable Ca, Mg, K, P and Na, % Total N, % Total C and C/N, pH soil, Eh, water content and highest level of water measured) were compared among sites by a two-way ANOVA (factor sites with five forests; factor season with dry conditions and rainy conditions). The N and C percentage data were arcsine transformed for linearity and subjected to an analysis of variance. After a significant group effect was detected ($P < 0.05$), multiple comparisons were applied using the Tukey method to identify significant differences among groups (Zar, 1996).

To determine the structure of the soil parameters in the forested wetlands, we used two ordinations (one for the rainy season and another for the dry season) applying a Principal Component Analysis (PCA) using a correlation-biplot and a relative Euclidean distance as similarity measure (program PC-ORD version 5, McCune and Mefford, 1999). Matrices were built with data from the five soil samples of each forested wetland. Values for Mg, Na, K, Ca, P, % Total C, % Total N, C/N, soil pH, water content, water level and Eh (25 soil samples × 12 parameters) were incorporated in the environmental matrix.

3. Results

3.1. Floristic composition of freshwater tropical forested wetlands

We identified a total of 109 species belonging to 52 families. The family Moraceae was the best represented with nine species, Fabaceae with seven species, Rubiaceae and Araceae with five species and Myrtaceae, Primulaceae and Malvaceae with four species each (Appendix). Trees comprised 45 species, followed by shrubs with 23, herbs with 21 species and climbers-lianas with 17 species. Hemi-epiphytes were represented by only three species (Appendix).

We found 45 species in Cienaga, 32 in Apompal, 44 in Mancha, 20 in Salado and 12 in Chica. The most frequent species were the trees *P. aquatica*, *Ficus insipida* subsp. *insipida*, *A. glabra* and the lianas *Dalbergia brownei*, *Hippocratea celastroides* and *Rhabdadenia biflora*.

The estimation of species richness of tropical forested wetlands through $Chao_2$ and Jack-knife 1 methods showed that the number of species expected in flooded forests was higher than the number that was actually observed. The sites that showed the greatest differences between both values were Cienaga and Mancha (Table 2).

3.2. Alpha and beta diversity

The Shannon-*H* diversity indices (mean ± standard error) for Cienaga (3.321 ± 0.128), Mancha (3.373 ± 0.131) and Apompal (3.142 ± 0.139) were higher than the values obtained for Salado (2.659 ± 0.101) and Chica (2.247 ± 0.074) ($F_{(4, 46)} = 19.19$; $P < 0.0001$).

Beta diversity (Table 3) showed that the flooded forests differed in species composition. The highest similarity values were recorded between Cienaga and Apompal and between Apompal and Salado. At the other extreme, the lowest similarities were found between Mancha and Chica and Cienaga and Chica.

3.3. Vegetation structure

Cienaga: this site had three well-developed strata based on tree height. The high tree stratum (18–25 m) is formed by *P. aquatica* and several species of *Ficus*. The medium stratum (6–18 m) is formed by *Pithecellobium latifolium* and *Trophis racemosa*. The shrub stratum (2–6 m) is formed by *Ardisia revoluta*, *A. compressa*, *Palicourea nigricans* and *Parathesis psychotrioides*, and the herb stratum was dominated by *Thelypteris serrata*, *Scleria lithosperma* and *Lithachne pauciflora*. The lianas *H. celastroides* and *D. brownei* grow mainly on the canopy of the trees, and the hemi-epiphyte *Syngonium podophyllum* grows on the buttresses and trunks of *P. aquatica* (Table 4). Tree density is 1750 individuals per hectare with a tree basal area of 71.15 m^2 ha^{-1} (Table 4). Species with the highest RIVs include *P. aquatica* (103.61%), *P. latifolium* (44.88%), *H. celastroides* (42.99%) and *Attalea liebmannii*, *F. insipida* subsp. *insipida* and *A. revoluta* (16% each) (Appendix). Fig. 2 shows that 60% of the stems recorded

Table 2
Area sampled per site, species richness observed and estimated by nonparametric methods $Chao_2$ and Jack-knife 1.

	Area (m^2)	Estimator $Chao_2$	Estimator Jack-knife1	Observed number or species
Cienaga	1000	63	62	45
Apompal	900	34	37	32
Chica	1200	13	13	12
Mancha	1000	64	59	44
Salado	1000	22	24	20

Table 3
Beta diversity showing similarities between the forested wetlands of Veracruz on the coastal plain of the Gulf of Mexico.

	Chica	Mancha	Apompal	Salado
Cienaga	<u>0.105</u>	0.135	**0.364**	0.277
Chica		<u>0.071</u>	0.227	0.250
Mancha			0.263	0.250
Apompal				**0.385**

Bold numbers indicate high similarity values and low values are underlined.

Table 4
Density, basal area and importance value of the main species of Cienaga, Apompal and Chica forested wetlands located on the floodplains.

Species	Absolute density (ind. ha^{-1})	Basal area (m^2 ha^{-1})	Relative frequency (%)	Relative density (%)	Relative dominance (%)	Importance value (%)
Cienaga						
Pachira aquatica	410	46.71	14.55	23.43	65.64	103.61
Pithecellobium latifolium	410	3.62	16.36	23.43	5.09	44.88
Hippocratea celastroides	370	3.90	16.36	21.14	5.48	42.99
Ardisia revoluta	160	4.04	7.27	9.14	5.68	16.96
Attalea liebmannii	70	0.06	7.27	4.00	0.09	16.50
Ficus insipida subsp. *insipida*	20	9.61	1.82	1.14	13.51	16.47
Dalbergia brownei	70	0.41	7.27	4.00	0.58	11.86
Trophis racemosa	60	2.35	1.82	3.43	3.31	5.70
Parathesis psychotrioides	30	0.26	3.64	1.71	0.36	5.61
Ficus maxima	10	0.02	1.82	0.57	0.03	5.38
Total other species (10)	140	0.17	21.84	7.98	0.23	30.05
Total	1750	71.15	100	100	100	300
Apompal						
Pachira aquatica	1178	58.56	18.37	40.77	76.62	135.75
Hippocratea celastroides	533	2.11	16.33	18.46	2.77	37.56
Dalbergia brownei	444	1.42	16.33	15.38	1.87	33.58
Hasseltia laxiflora	267	0.34	10.20	9.23	0.46	19.89
Attalea liebmannii	67	6.40	8.16	2.31	8.38	18.86
Roystonea dunlapiana	89	5.19	4.08	3.08	6.80	13.96
Parathesis aff. *brevipes*	156	0.048	4.08	5.38	0.06	9.53
Ficus trigonata	33	1.37	4.08	1.15	1.81	7.04
Tabernaemontana alba	44	0.039	4.08	1.54	0.05	5.67
Diospyros digyna	22	0.005	4.08	0.77	0.01	4.86
Total other species (5)	56	0.939	10.21	1.93	1.17	13.30
Total	2889	76.42	100	100	100	300
Chica						
Pachira aquatica	1117	38.38	30.77	46.53	80.90	158.20
Laguncularia racemosa	358	6.06	10.26	14.93	12.77	37.96
Hippocratea celastroides	233	0.42	17.95	9.72	0.88	28.56
Rhabdadenia biflora	258	0.38	15.38	10.76	0.80	26.95
Bignoniaceae	117	0.72	7.69	4.86	1.51	14.06
Rhizophora mangle	150	1.02	5.13	6.25	2.15	13.53
Dalbergia brownei	67	0.12	7.69	2.78	0.25	10.72
Hibiscus pernambucensis	83	0.19	2.56	3.47	0.39	6.43
Avicennia germinans	17	0.17	2.56	0.69	0.35	3.60
Total	2400	47.44	100	100	100	300

Species are ranked in order of decreasing importance value with respect to importance values of all the species (see Appendix).

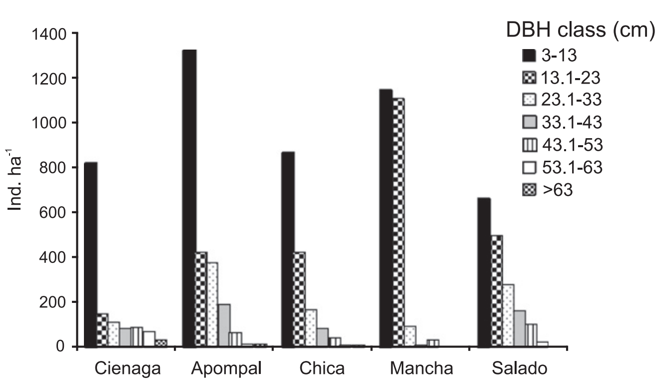

Fig. 2. Number of individuals per hectare in each of the diameter classes (DBH $\geqslant$ 3) in each tropical freshwater forested wetland studied.

in 1 ha had a diameter of 3–13 cm, 25% between 13.1 and 43.1, and 15% were represented by large trees over 43.1 cm of DBH.

Apompal: this tropical swamp did not show such a clear stratification. *P. aquatica* is found in all stages of development and can be present both in the shrub and tree strata. The 20–25 m tree stratum is dominated by *P. aquatica* and the palm *Roystonea dunlapiana*. The 12–20 m stratum comprises the palm *A. liebmannii* and the figs *Ficus aurea* and *Ficus obtusifolia*. The low tree stratum (6–12 m) has *Sapium nitidum* and *Hasseltia laxiflora*. In the shrub stratum (2–5 m), *Parathesis* aff. *brevipes*, *Diospyros digyna*, *H. laxiflora* and *Acrostichum aureum* are frequent. The herbaceous stratum is represented by *Boehmeria ramiflora*, *T. serrata* and *Heliconia latispatha*. The lianas in the tree canopy are *H. celastroides* and *D. brownei*. Tree density in Apompal is higher than in Cienaga, with 2889 individuals per hectare and a basal area of 76.42 m^2 ha^{-1} (Table 4). The highest RIVs were found for *P. aquatica* (135.75%), *H. celastroides* (37.56%), *D. brownei* (33.58%), *H. laxiflora* (19.89%), *A. liebmannii* (18.86%) and *R. dunlapiana* (13.96%) (Table 4 and Appendix). With respect to the diameter of the trees in the Apompal, all size classes were represented. The trees with a 3–13 cm DBH are the most frequent with 1322 individuals per hectare (55%), those between 13.1 and 43 cm DBH accounted for 41%, and trees over 43 cm DBH comprised 3.7% (Fig. 2).

Chica: this flooded forest had an inland boundary with a freshwater marsh (*C. giganteus*, *T. domingensis*) and formed an ecotone with the mangroves surrounding the coastal lagoon. The tree layer of 10–12 m has *P. aquatica* as the dominant species as well as some individuals of *R. mangle* and *L. racemosa*. The shrub layer consists of a few patches of *Hibiscus pernambucensis*, which reached 3 m in height, lianas (*H. celastroides*, *D. brownei* and *R. biflora*, which have the ability to climb and grow on the tree canopy) and young *P. aquatica* trees. The herbaceous layer is absent. Tree density is 2400 individuals per hectare with a basal area of 47.44 m^2 ha^{-1} (Table 4). Species with the highest RIVs include *P. aquatica* (158.20%), *L.*

racemosa (37.96%), *H. celastroides* (28.56%), and *R. biflora* (26.95%) (Table 4 and Appendix); 54% of the trees measured in Chica are from 3 to 13 cm DBH, 42% are from 13.1 to 43 cm, and only 3.6% of the trees were over 43 cm DBH (Fig. 2).

Mancha: the trees of this forested wetland attained a height of 10–12 m. The tree layer was composed of *A. glabra*, *Salix humboldtiana*, *F. insipida* subsp. *insipida* and *Ficus cotinifolia*. The shrub stratum has a height of 1.5–4 m and consists of *Piper amalago*, *P. nitidum*, *Acacia cornigera* and *Trichilia havanensis*. The herbaceous layer, exuberant reaching a height of 1.5 m, and is represented by *Crinum erubescens* and some patches of *A. aureum*, *Boehmeria cylindrica* and the floating *Pistia stratiotes*. Tree density was 2421 individuals per hectare with a basal area of 32.7 m^2 ha^{-1} (Table 5). Species with the highest RIVs are *A. glabra* (159.11%), *S. humboldtiana* (13.61%), *F. insipida* subsp. *insipida* (12.28%), *F. cotinifolia* (11.58%) and *D. digyna* (11.55%) (Table 5 and Appendix). The tree diameter classes' best represented in the forest of Mancha is the 3–13 cm class, with an estimate of 1146 individuals per hectare, slightly under 48%; the 13.1–23 cm class, with 1107 individuals per hectare (46%) and the 23.1–53 cm class, with 130 individuals per hectare (5.4%). No trees over 53 cm DBH were found (Fig. 2).

Salado: the heights of the tallest trees in this swamp were approximately 15 m. The tree canopy (10–15 m) was dominated by *P. aquatica*, *A. glabra* and *F. insipida* subsp. *insipida*. In the 5–10 m stratum, *Dendropanax arboreus* and *D. digyna* were frequent as well as juveniles of *P. aquatica* and *A. glabra*. The shrub stratum was represented by *Piper nitidum* and *S. nitidum*. The herbaceous stratum was represented by *Spathiphyllum* spp. and the hemi-epiphyte *S. podophyllum*. The more important lianas are *D. brownei*, *H. celastroides* and *Combretum laxum*. Tree density was 2230 individuals per hectare with a basal area of 74.73 m^2 ha^{-1} (Table 5). Species with the highest RIVs are *P. aquatica* (129.28%), *A. glabra* (53.41%), *D. arboreus* (22.21%), *D. brownei* (19.57%), *P. nitidum* (15.40%) and *H. celastroides* (12.93%) (Table 5 and Appendix). The trees with a 3–13 cm DBH account for 38%, individuals from 13.1 to 43 cm diameter account for 54.6% and those between 43 and 63 cm DBH were represented by 7%. No trees larger than 63 cm DBH were identified (Fig. 2).

3.4. Hierarchical classification of freshwater forested wetlands vegetation

Five sub-groupings were differentiated in a dendrogram from Ward's hierarchical classification (linkage level = 1.6; Fig. 3), corresponding to the plots from each site. Group I corresponds to Apompal and Cienaga forested wetlands and groups the samples at a level of similarity of 40%. The plots from Chica merged with Group I, with a similarity level of 20%. Finally, the plots from Mancha and Salado merge to form Group II, with a similarity level of 30%.

3.5. Soil properties of freshwater forested wetlands

The soils of Mancha, Apompal and Chica were composed mainly of sand (54.3–74.0%), Cienaga was dominated by clay (52.2%), and Salado has a combination of sand and clay (42.4% and 32.7%, respectively). The silt content is similar in all sites at 18.6–27.1% (Table 6). Bulk density varies between 0.18 and 1.08 g cm^{-3} (Table 6).

Soil parameters showing significant variation between seasons and sites included Na, Ca, P, % Total C, % Total N, water level, water content and redox potential (Eh) and water level above the soil

Table 5
Density, basal area and importance value of the main species of Mancha and Salado forested wetlands in the dune depressions.

Species	Absolute density (ind. ha^{-1})	Basal area (m^2 ha^{-1})	Relative frequency (%)	Relative density (%)	Relative dominance (%)	Importance value (%)
Mancha						
Annona glabra	1677	22.96	19.67	69.21	70.23	159.11
Salix humboldtiana	38	2.86	3.28	1.59	8.75	13.61
Ficus insipida subsp. *insipida*	69	1.47	4.92	2.86	4.51	12.28
Ficus cotinifolia	38	0.59	8.20	1.59	1.79	11.58
Diospyros digyna	54	0.91	6.56	2.22	2.77	11.55
Tabebuia rosea	62	0.38	6.56	2.54	1.18	10.27
Ginoria nudiflora	46	0.85	3.28	1.90	2.60	7.78
Trichilia havanensis	31	0.30	4.92	1.27	0.93	7.12
Piper amalago	77	0.19	3.28	3.17	0.58	7.03
Pachira aquatica	15	0.13	3.28	0.63	0.39	4.30
Enterolobium cyclocarpum	8	0.95	1.64	0.32	2.89	4.85
Bursera simaruba	31	0.07	3.28	1.27	0.21	4.76
Coccoloba liebmannii	15	0.20	3.28	0.63	0.61	4.52
Acacia cornigera	38	0.07	3.28	1.59	0.21	5.08
Cestrum scandens	15	0.03	3.28	0.63	0.10	4.02
Total other species (12)	207	0.74	21.32	8.56	2.27	32.14
Total	2421	32.7	100	100	100	300
Salado						
Pachira aquatica	810	56.61	17.24	36.32	75.72	129.28
Annona glabra	550	9.87	15.52	24.66	13.22	53.41
Dendropanax arboreus	140	0.31	15.52	6.28	0.42	22.21
Dalbergia brownei	230	1.76	6.90	10.31	2.36	19.57
Piper nitidum	150	0.038	8.62	6.73	0.05	15.40
Hippocratea celastroides	130	0.149	6.90	5.83	0.20	12.93
Sapium nitidum	70	0.116	8.62	3.14	0.16	11.92
Ficus insipida subsp. *insipida*	20	4.41	1.72	0.90	5.91	8.53
Diospyros digyna	30	1.11	5.17	1.35	1.48	8.00
Combretum laxum	50	0.332	5.17	2.24	0.45	7.86
Total other species (3)	50	0.0279	8.62	2.24	0.03	10.89
Total	2230	74.73	100	100	100	300

Species are ranked in order of decreasing importance value with respect to importance values of all the species (see Appendix).

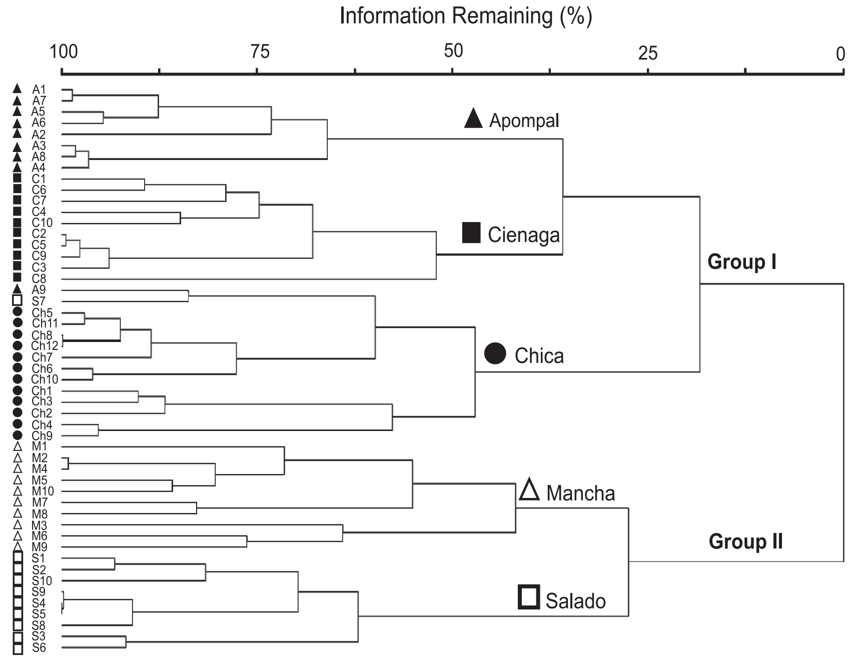

Fig. 3. Dendrogram (using Wards hierarchical classification) showing the grouping of samples from the five freshwater swamps, based on the species cover-abundance values. Chaining value was 1.61. A. Apompal; C. Cienaga, Ch. Chica; M. Mancha and S. Salado.

Table 6
Soil texture and bulk density of the five tropical freshwater forested wetlands studied on the coastal plain of the Gulf of Mexico.

Forested wetland	Sand (%) Mean (S.E.)	Clay (%) Mean (S.E.)	Silt (%) Mean (S.E.)	Bulk density (g cm^{-3}) Mean (S.E.)	Soil textural classes[a]
Cienaga	20.70 (1.60)c	52.22 (6.70)a	27.08 (5.85)	0.18 (0.02)b	Clay
Apompal	65.86 (8.29)ab	14.87 (4.82)bc	19.26 (3.63)	0.22 (0.09)b	Sandy loam
Chica	54.34 (8.18)ab	25.45 (5.26)b	20.22 (3.29)	0.33 (0.18)b	Sandy clay loam
Mancha	74.02 (2.81)a	7.34 (1.05)c	18.64 (2.06)	0.47 (0.13)ab	Sandy loam
Salado	42.41 (2.59)bc	32.72 (5.40)ab	24.87 (4.16)	1.08 (0.09)a	Clay loam
F-value	14.68***	13.15***	0.90 n.s.	11.41**	

n.s., not significant.
Different letters indicate significant differences.
** $P < 0.01$.
*** $P < 0.001$.
[a] According the soil textural triangle (Sprecher, 2001) and bulk density calculator based on the US texture triangle (Saxton et al., 1986).

(Table 7 and Fig. 4). Mg, K, C/N and pH varied among forest sites. During the dry season, Na increases, but Ca and P decrease.

PCA ordination of soil parameters during the rainy season explained 67.0% of the total cumulative variance. Axis 1 explained 42.1% of the variance (Eigenvalue 5.058), and Axis 2 contributed with 24.9% (Eingenvalue 2.983) (Fig. 5a). Soil pH correlated positively with Axis 1 and Mg, Na, % Total C, % Total N and water content were negatively correlated. C/N correlated positively with Axis 2, and K, Ca, P and Eh were negative (Table 8 and Fig. 5a). These *V* vectors are the correlation coefficients between scores for rows in the main matrix and the column variables. Mancha and Salado samples, the two forested wetlands set in dune depressions, are close because of their presentation of lower Mg, Na, K, % Total C and % Total N values. Apompal and Chica samples remain close to each other because of their high levels of % Total C, % Total N, Mg, Na and high soil water contents. Cienaga samples are separated from samples of other forests because of a high value of P and Ca and a high water level and Eh (Fig. 5a).

Soil parameter ordination during the dry season explained 69.1% of the accumulated variance. Axis 1 contributed with 39.1% of variance (Eigenvalue 4.688) and Axis 2 with 30.0% (Eingenvalue 3.606) (Fig. 5b). The parameters positively correlated with Axis 1 were Ca and soil pH; Mg, Na, % Total C, % Total N and C/N were negatively correlated. With respect to Axis 2, P and Eh were positively correlated and water content and water level were negatively correlated (Table 8 and Fig. 5b). Soil samples of Mancha are separated due to higher pH and Ca values. Apompal maintained high levels of % Total C, % Total N, and C/N at times of higher water content in the soil and flooding above the ground for a longer period of time. Chica increases its Na values during the dry season. Finally, Cienaga and Salado separates from the other forests because of low values of Mg, N and C.

4. Discussion

4.1. Floristic composition and structure of freshwater tropical forested wetlands

The forested freshwater wetlands of Mexico are more similar in species composition to those found in Central and South America (Bacon, 1990; van Andel, 2003; Koponen et al., 2004; Teixeira et al., 2011) than those of more northern latitudes (Ewel and Odum, 1984; Sharitz and Mitsch, 1993; Mitsch and Gosselink,

Table 7
Two-way ANOVA by exchangeable cations (Mg, Na, K, Ca, P), % total C, % total N, C/N, pH, water content, water level and Eh of soils of the tropical freshwater forested wetlands on the coastal plain of the Gulf of Mexico.

Source	d.f.	Mg		Na		K		Ca		P		C		N		C/N		Soil pH		Water content		Water level		Eh	
		M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*	M.S.	*F*
Season (S)	1	0.42	0.32 n.s.	45.15	125.99***	0.00	0.01 n.s.	370.60	51.73 ***	3053.85	130.98***	370.60	51.73***	16.00	11.42*	26.77	8.10*	7.12	36.91***	188,307	13.84**	54120.50	575.21***	389079.59	104.20***
Forested wetlands (FW)	4	93.04	71.61***	34.73	96.91***	1.03	13.46***	328.12	45.80***	627.67	26.92***	328.12	45.80***	19.59	13.98***	30.15	9.13***	6.86	35.60***	312601.63	22.99***	3101.32	32.96***	100115.55	26.81***
S × FW	4	3.04	2.34 n.s.	12.25	34.19 ***	0.09	1.23 n.s.	60.18	8.40 ***	329.95	14.15 ***	60.18	8.40 ***	6.21	4.43*	6.01	1.82 n.s.	0.49	2.55 n.s.	13604.11	6.41**	2207.00	23.46***	90834.20	24.33***
Error	40	1.30		0.36		0.08		7.16		23.32		7.16		1.40		3.30		0.19		57.16		94.09		3733.81	

n.s., not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

2000), except in southern Florida, where they share two of the dominant species, *A. glabra*, pond apple, and *F. aurea*, Florida strangler fig (Gunderson and Loftus, 1993). The forested wetlands are characterized by their tree layer, which is dominated by a few species, but the shrub and herbaceous layers may be more varied. Table 9 shows the species that characterize tropical forested wetlands in coastal regions of America, the Caribbean Region, the Pacific Islands and Australia. Structural parameters such as diversity, tree height, density and basal area were compared.

Some genera identified in this study are common in the forested wetlands of the American tropics (Table 9). Among them are the tree genera *Tabernaemontana* (Apocynaceae), *Tabebuia* (Bignoniaceae), *Diospyros* (Ebenaceae), *Inga* (Fabaceae) and *Ficus* (Moraceae); the shrubs *Piper* (Piperaceae), *Alibertia*, *Palicourea* and *Psychotria* (Rubiaceae); the lianas *Paullinia* (Sapindaceae), *Hippocratea* (Celastraceae), *Dalbergia* (Fabaceae) and the herbs *Philodendron*, *Spathiphyllum* and *Syngonium* (Araceae) (van Andel, 2003; Migeot and Imbert, 2011; Teixeira et al., 2011).

Some of the species recorded in our sites have also been observed in the swamps of more tropical latitudes but not as the dominant species; for example, the tree *A. glabra* in the Antilles (Alvarez-Lopez, 1990; Imbert et al., 2000), *Ficus maxima* and *P. aquatica* in Guyana (van Andel, 2003), *P. aquatica* in the forested wetland of Várzea and Igapó in Amazonia (Kubitzki, 1989).

Lianas are important structural components of the *Pachira* swamps and are also found in other tropical forested wetlands, such as those formed by *P. officinalis* Jacq. (Imbert et al., 2000). Their presence has been recognized as a constant life form component of tropical forested wetlands (Ascencio, 1994; van Andel, 2003; Moreno-Casasola et al., 2009), although they are not represented in all temperate forested wetlands (Conner and Day, 1982; Lugo et al., 1988; Mitsch and Gosselink, 2000; Cronk and Fennessy, 2001; Middleton, 2002). Actually, there are a number of lianas in baldcypress swamps, including great quantities of *Rhus toxicodendron*, *Vitis* spp., and *Smilax* spp. (Allen et al., 2007; Schnitzer and Bongers, 2011).

Some species were only found in one of the swamp sites, giving these sites particular compositions that helped separate them in the classification analysis. For example, *Parathesis* aff. *brevipes*, *Syzygium jambos* and *R. dunlapiana* were only found in Apompal. Cienaga was the only site with *P. latifolium*, *P. psychotrioides* and *A. revoluta*, and in Salado and Mancha with *A. glabra* and *P. nitidum*. Nevertheless, the floodplains of Cienaga and Apompal shared dominant species (the tree *P. aquatica* and the lianas *H. celastroides* and *D. brownei)*. Chica is situated in a small floodplain draining to a coastal lagoon and was the only site where *P. aquatica* formed an ecotone with mangrove species such as *R. mangle* and *L. racemosa*. On the shore of the dune lake in Mancha, the dominant species was *A. glabra,* and in Salado, the dominant species were *P. aquatica* and *A. glabra*. We found that species composition is related to geomorphological characteristics: similar species compositions were found between forested wetlands on floodplains (Cienaga and Apompal, together with Chica), forming Group 1 of the dendrogram (Fig. 3). The second group is found on dune depressions (Salado and Mancha), corroborating what we expected in our hypothesis (Hypothesis 1).

P. aquatica showed the highest RIV in the tropical forested wetlands of Veracruz, similar to the values reported by Ascencio (1994), who studied the structure of a *Pachira* forest farther south along the coast of the Gulf of Mexico (in Huimanguillo, Tabasco). He found, for this same species, an RIV ranging from 186.06 to 203.61%, higher than the values we found. Another species that Ascencio (1994) found was *P. latifolium,* with a RIV of 27% (we reported 44.88% in Cienaga). Thus, in general, the tropical forested wetlands show a clear dominance of a few species (Bacon, 1990; Imbert et al., 2000; Moreno-Casasola et al., 2009) that define the

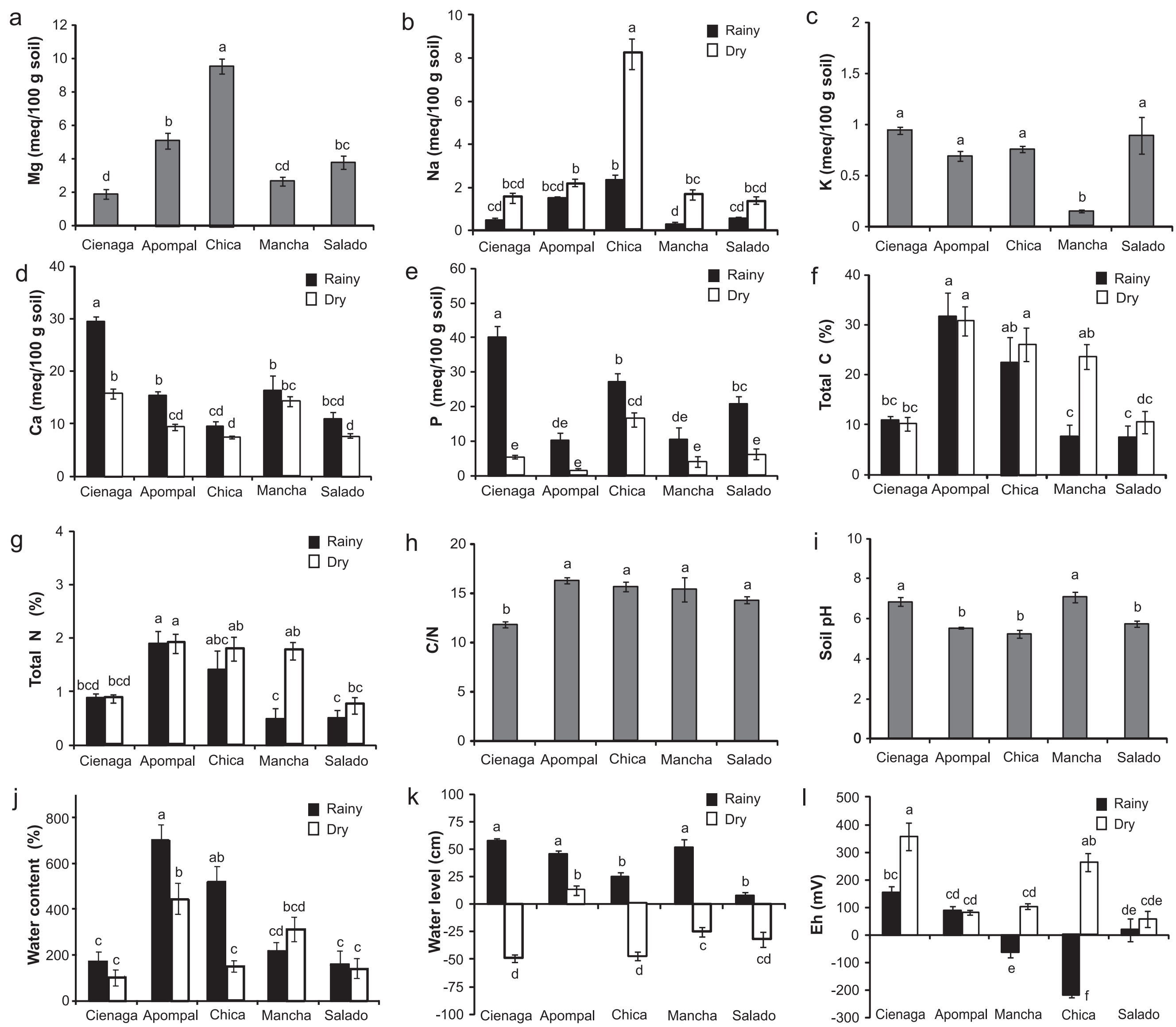

Fig. 4. Mean value (±S.E.) of soil properties in the five forested tropical freshwater wetlands studied. (a) Mg; (b) Na; (c) K; (d) Ca; (e) P; (f) Total C; (g) Total N; (h) C/N; (i) Soil pH; (j) Water content; (k) Water level and (l) Eh. Parameter values between forested wetlands were compared (graph with one bar by site) as well as the interaction of the forests with the season (graph with two bars by site) when differences were significant at $P < 0.05$. Table 7 shows two-way ANOVA values.

physiognomy of the swamp along the coastal plains of the Gulf of Mexico. Other examples showing the same trend are the forested wetlands of *H. campechianum* L. (known as tintal) and *Metopium brownei* (Jacq.) Urb. (known as chechenal) on the Yucatan Peninsula (Olmsted and Durán, 1986; Lot and Novelo, 1990; Olmsted, 1993). The same was found for other tropical American sites: *Tabebuia insignis* (Miq.) Sandwith (Quackal swamp), *Euterpe oleracea* Mart. (Manicole swamp) and *Mora excelsa* Benth. (Mora swamp) in Guyana (van Andel, 2003) and *P. officinalis* swamps in Guadeloupe (Imbert et al., 2000) and in Puerto Rico (Alvarez-Lopez, 1990). Even palms can be the characteristic elements of tropical forested wetlands: *Acoelorraphe wrightii* (Griseb. and H. Wendl.) H. Wendl. ex Becc. (tasistal) in the southeast of Mexico, *R. dunlapiana* in Quintana Roo and Veracruz, Mexico (Lot and Novelo, 1990) and palm swamps in Central America (Ellison, 2004).

Tree height in tropical swamps is very variable (Table 9). We classified tropical forested wetlands as low forests (10–15 m) and medium forests (20–25 m), following the botanical classification system used in Mexico (Miranda and Hernández, 1963). In general the highest forests were those of *P. officinalis* and *M. excelsa* with 30–45 m trees (located in Kariako, Northwest Guyana), the subtropical forested wetlands with *T. distichum* var. *nutens* attaining 30 m, those of Mexico with 25 m (*P. aquatica* and *R. dunlapiana*), Micronesia with 28 m (*T. carolinensis*), Brazil (*Calophyllum brasilense*, *Euterpe edulis*) and Australia (*Melaleuca* spp.). The average height was 20 m (Table 9). There are also very low forests with a height of less than 10 m such as the ones found in the Yucatan Peninsula (*A. wrightii*) and the Cypress scrub in Florida (6 m high trees).

With regard to tree density per hectare, we found both higher (2889 individuals ha^{-1}) and lower values (1750) than those reported for the forests of *Pachira* in Huimanguillo with 2100 ind. ha^{-1} (Ascencio, 1994). However, higher densities were found in the *P. officinalis* forest in Guadaloupe with 3598 stems ha^{-1} (Migeot and Imbert, 2011) but less basal area (55.33 m^2 ha^{-1}) with respect to Cienaga, Apompal and Salado (Table 9).

Trees with a larger diameter were found in Cienaga, Chica and Apompal, all of them located on floodplains and mainly corresponding to *P. aquatica* and *Ficus* spp. dominance. Mancha and Salado are located in dune depressions where *A. glabra* dominates

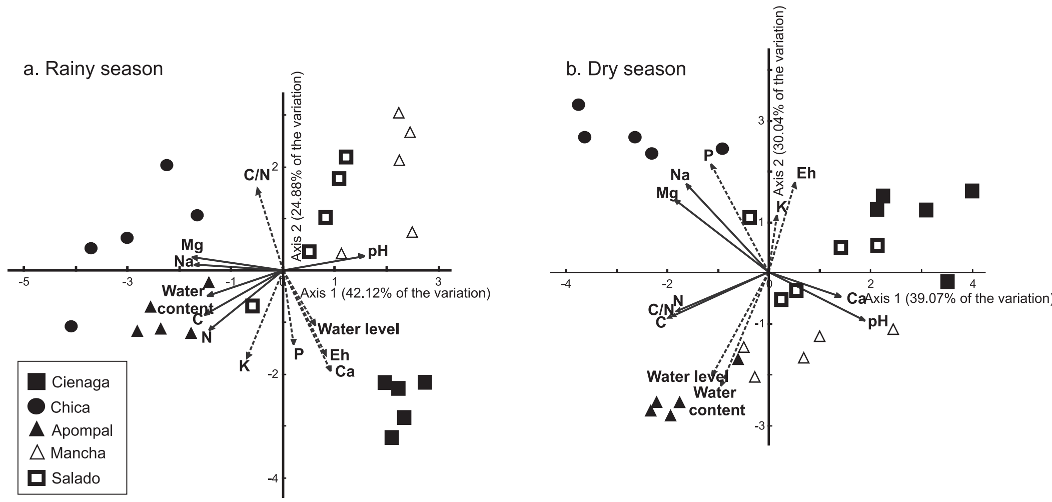

Fig. 5. PCA ordination for the soil parameters in the forested wetlands during the rainy season (a) and the dry season (b). Percentage variation explained by the first two axis was 67.0% and 69.1% respectively. Solid lines indicate the correlation with Axis 1, dotted line indicates correlation with Axis 2. Table 8 shows correlation values of parameters for Axis 1 and Axis 2.

Table 8
First 2 Eigenvectors (*V* vectors), each scaled to its standard deviation, obtained in the PCA ordination for the soil parameters in the forested wetlands, in the rainy and dry season.

Soil parameter	Rainy season		Dry season	
	Axis 1	Axis 2	Axis 1	Axis 2
Mg	−0.9438	0.1047	−0.7779	0.5275
Na	−0.9222	0.0003	−0.6881	0.6432
K	−0.366	−0.7011	0.0662	**0.4144**
Ca	0.4933	−0.8055	**0.5965**	−0.1775
P	0.1129	−0.5944	−0.4782	**0.7876**
% Total C	−0.8128	−0.353	−0.8409	−0.3308
% Total N	−0.7690	−0.4808	−0.7736	−0.2856
C/N	−0.267	**0.6471**	−0.8059	−0.3223
Soil pH	**0.8432**	0.1100	**0.7973**	−0.3488
Water content	−0.7796	−0.2028	−0.4725	−0.7525
Water level	0.3355	−0.4377	−0.3998	−0.8246
Eh	0.4145	−0.6778	0.2171	**0.6538**

Bold numbers indicate positively correlated parameters, and underlined values indicate the negatively correlated, for each axis.

and shows smaller DBH values. The DBH of trees in floodplain forests dominated by *P. aquatica* may be greater than 63 cm (forested wetlands of Huimanguillo- Ascencio, 1994), but when compared with the DBH of other wetland tropical trees such as *E. edulis* and *C. brasiliense* in Itirapina, Brazil (<23 cm), trees in the floodplains of the Gulf of Mexico have larger diameters. However, in Kosrae, Micronesia, buttressed trees such as *T. carolinensis* and *Horsfieldia numu* reach, on average, 59 and 54 cm DBH, respectively, and heights of up to 32 m (Chimner and Ewel, 2005) so that the structure of this forest may be similar to the forested wetlands dominated by *P. aquatica* and *Ficus* spp. reported in this study.

4.2. Alpha and beta diversity

The number of species that make up the forested wetlands is variable. Three to nine species were reported in the subtropical forested wetlands of Georgia and Florida. The number of species in tropical wetlands of the Gulf of Mexico increased to 12–78 and Brazil with 55; the highest number of species was recorded in the swamps in Guyana (98–102 species). Diversity values in the forested wetlands of Mexico (2.247–3.321) were similar to those of Brazil (2.244–2.810), however the values found in the insular forested wetlands (Guadeloupe, French West Indies) decreased to 1.390 (Table 9).

The tropical freshwater forested wetlands of the coastal plain of Mexico have been cleared, and the land has been used for agriculture and pasture for livestock (Moreno-Casasola, 2008) creating a highly fragmented landscape. Today, the remnants of these flooded forests are embedded among herbaceous wetlands (Cienaga, Apompal), in small areas fringing mangroves (Chica) and in some protected areas (Mancha, Cienaga). There are no laws protecting them (there is only protection for mangroves species-NOM-059-SEMARNAT-2010) so that logging occurs right up to the edge of the mangroves.

The five forests in the present study vary in the number and abundance of species. We believe that among the causes producing these differences is seed dispersal through water (hydrochory). Sites with greater influence by water runoff are Cienaga and Apompal, and as a result, they receive and distribute seeds with each flood pulse, which has also been observed in Amazonia (Piedade et al., 2010). While both of these forests are located in floodplains, Cienaga has a drought period of 6 months while Apompal stays flooded all year, and the anoxia in the soil of the latter theoretically restricts the establishment of many species, allowing only for species morphologically and physiologically adapted to these stressful conditions. Permanent soil flooding would result in an expected decrease in diversity; however, contrary to what we expected, Apompal showed a relatively high diversity value (3.142).

The forested wetland with the lowest species number was Chica, also on a floodplain. Unlike the other four freshwater forested wetlands, this one forms an ecotone with the mangrove, being more abundant towards the areas with lower salinity values. Brackish water from the adjoining coastal lagoon can influence the area during the rainy season, when there are superficial water overflows (2.06 g L^{-1}), and in the dry season, when the water levels have lowered and the groundwater (10.79 g L^{-1}) has more influence on the soil. Salinity would be the limiting factor for the establishment of species, in this case allowing for the establishment of a monodominant stand of *P. aquatica*, which tolerates brackish water. Salinity has been recognized by Mitsch and Gosselink (2000) as a factor that decreases diversity in coastal wetlands.

In Mancha and Salado, where flooding is produced by the rising of the water table, seeds are distributed only within the

Table 9
Tree species composition of the tropical freshwater forested wetlands in different parts of the world and the structural characteristics of the vegetation.

Site	Dominant species	Diversity (H)	Total species	Density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Mean height (m)	Annual rainfall (mm)	Reference
United States								
Okefenokee, Georgia 31°04′N, 82°16′W Pond cypress swamp	*Taxodium distichum* var. *nutans, Nyssa sylvatica* var. *biflora, Acer rubrum, Magnolia virginiana, Persea borbonia*		4–9 5	1891 1739	70.4 53.3	18–30	1340	Schlesinger (1978) and Best (1984)
Florida, 29.5°N Cypress dome Mature	*Taxodium distichum* var. *nutans, Nyssa sylvatica* var. *biflora, Acer rubrum, Magnolia virginiana, Persea borbonia*		6	3951	70.8	20	1420	Brown (1981)
Naples, Florida, 26°00′N, 81°45′W Scrub Cypress	*Taxodium distichum* var. *nutans, Ilex cassine, Myrica cerifera*		3	2496	21.9	6	1330	Brown et al. (1984)
Mexico								
Cienaga, Tecolutla, Veracruz 20°18′34.80″N, 96°54′56.20″W	*Pachira aquatica, Pithecellobium latifolium, Hippocratea celastroides, Ardisia revoluta, Attalea liebmannii, Ficus insipida* subsp. *insipida*	3.321	45	1750	71.15	25	1436.3	This study
Chica, Vega Alatorre, Veracruz 20°05′47.8″N, 96°41′23.8″W	*Pachira aquatica, Laguncularia racemosa, Hippocratea celastroides, Rhabdadenia biflora, Rhizophora mangle, Dalbergia brownei*	2.247	12	2400	47.44	12	1397.7	This study
Mancha, Actopan, Veracruz 19°35′52.91″N 96°22′53.81″W	*Annona glabra, Salix humboldtiana, Ficus insipida* subsp. *insipida, Ficus cotinifolia, Diospyros digyna*	3.373	44	2421	32.70	12	1155.9	This study
Apompal, Jamapa, Veracruz 19°01′19.39″N, 96°17′6.61″W	*Pachira aquatica, Hippocratea celastroides, Dalbergia brownei, Hasseltia laxiflora, Attalea liebmannii, Roystonea dunlapiana*	3.142	34	2889	76.42	25	1646.3	This study
Salado, Alvarado, Veracruz 19°02′4.40″N, 95°59′1.52″W	*Pachira aquatica, Annona glabra, Dendropanax arboreus, Dalbergia brownei, Piper nitidum, Hippocratea celastroides*	2.659	20	2230	74.73	15	1591.5	This study
Huimanguillo, Tabasco 18°00′51″N, 93°56′45″W	*Pachira aquatica, Pithecellobium latifolium, Casearia* sp., *Parathesis psychotrioides*		78	2100	56.75	18	2543.6	Ascencio (1994)
Sian Ka'an, Quintana Roo, 19°05′N, 87°42′W	(A) *Haematoxylum campechianum, Bucida spinosa, Dalbergia glabra* (B) *Acoelorraphe wrightii*		A. 53 B. 12	A. 13,733 B. 362		A. 11–12 B. 4–5	1100–1300	Olmsted and Durán (1986)
Central America								
Laguna Tortugero, Costa Rica, 10°37′N, 83°32′W	*Raphia taedigera, Manicaria saccifera, Pithecellobium latifolium, Pterocarpus officinalis, Carapa guianensis, Pachira aquatica*		9–13	520–910	2.27 *Raphia* 31.34 *Manicaria*	10–15	5061	Myers (1990)
Antilles								
Puerto Rico A. Huamaco 18°09′N, 65°45′W B. Patillas, 17°58′N, 65°58′W	(A) *Pterocarpus officinalis* (B) *Pterocarpus officinalis, Annona glabra, Calophyllum calaba, Clusia rosea, Ficus citrifolia, Ficus sintenisii, Laguncularia racemosa*		A. 1 B. 6	A. 1770 B. 1910	A. 43 B. 54.8	A. 27 B. 18	1789	Alvarez-Lopez (1990)
Bay of the Grand Cul-de-Sac Marin, Guadeloupe, French West Indies 16°17′N, 61°31′W	*Pterocarpus officinalis, Sterculia caribaea, Symphonia globulifera, Chrysobalanus icaco, Coccoloba swartzii, Calophyllum calaba, Guettarda scabra, Inga laurina, Tabernaemontana citrifolia, Cassipourea guianensis*		68	3598	55.33	17	1800	Migeot and Imbert (2011)
Bay of the Grand Cul-de-Sac Marin, Guadeloupe, French West Indies 16°17′N, 60°31′W	*Pterocarpus officinalis, Sterculia caribaea, Stylogine lateriflora, Dalbergia monetaria, Hippocratea volubilis, Polypodium latum, Pisonia fragrans, Symphonia globulifera*	1.390	107		35–79	11–23	1200–2500	Imbert et al. (2000)
South America								
Sinnamary River Basin, French Guyana 5°15′N, 52°56′W	*Pterocarpus officinalis, Malouetia tamaquarina, Taralea oppositifolia, Caryocar microcarpum, Licania heteromorpha, Licania macrophylla, Caraipa* sp., *Diospyros guianensis,*		63	1467	69.6	3–7	3000	Koponen et al. (2004)
Northwest Guyana A. Kariako 7°23′N, 59°43′W	(A) *Mora excelsa, Pterocarpus officinalis* subsp. *officinalis, Eschweilera wachenheimii, Diospyros guianensis* var. *guianensis*		A. 102	A. 321	A. 33.66	A. 30–45	2750	van Andel (2003)
B. Santa Rosa 7°41′N, 58°55′W	(B) *Tabebuia insignis* var. *monophylla, Symphonia globulifera, Macrosamanea pubiramea* var. *pubiramea, Pachira*		B. 75	B. 946	B. 24.99	B.12		

(continued on next page)

Table 9 (*continued*)

Site	Dominant species	Diversity (H)	Total species	Density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Mean height (m)	Annual rainfall (mm)	Reference
	aquatica							
C. Assakata 7°44′N, 59°04′W	(C) *Pentaclethra macroloba, Symphonia globulifera, Euterpe oleracea, Pterocarpus officinalis* subsp. *officinalis*		C. 98 Total 228	C. 664	C. 35.88	C.15		
Itirapina, São Paulo, Brazil, 22°15′54″S, 47°40′51″W	*Calophyllum brasiliense, Protium spruceanum, Euterpe edulis, Xylopia emarginata, Tapirira guianensis, Styrax pohlii*		37			6–8	1523	Teixeira et al. (2011)
Santa Genebra Municipal Reserve, Brazil 22°44′S, 47°06′W	*Euterpe edulis, Syagrus romanzoffiana*			844	21.9	16	1360	Souza and Martins (2005)
Sao José Farm, municipality of Rio Claro, São Paulo, Brazil 22°22′S, 47°28′W	*Euterpe edulis, Calophyllum brasiliense, Calyptranthes concinna, Magnolia ovata, Geonoma brevispatha*	2.810			54.6	10–20	1456	Teixeira et al. (2008)
Linha XV de Novembro, Vale do Sol, Brazil 29°34′S, 52°40′W	*Gymnanthes concolor, Euterpe edulis, Sorocea bonplandii, Pachystroma longifolium, Trichilia claussenii*	2.244 2.633	55	1855	41.94	20	1367	Jarenkow and Waechter (2001)
Micronesia								
Yela and Yewak, Kosrae, Micronesia 5°19′N, 163°00′E	*Terminalia carolinensis, Barringtonia racemosa, Campnosperma brevipetiolatum, Areca catechu, Dendrocnide kusaiana, Ficus tinctoria, Hibiscus tiliaceus, Horsfieldia nunu, Inocarpus fagifer, Ixora casei, Morinda citrifolia*		27	555–2912	29–46.5	24–28	5500	Allen et al. (2005)
Australia								
Moreton Region, Queensland 27°30′S, 153°30′E (30 sites)	*Melaleuca quinquenervia, Eucalyptus robusta, Casuarina glauca*			1726 mean 5000 max 360 min	49 mean 97 max 19 min	18 mean 29 max 13 min		Zoete (2001)
Magela Creek, Leichhardt Billabong, Northern Territory 12°27′S, 132°8′E	*Melaleuca cajuputi, Melaleuca viridiflora*			294		22	1560	Finlayson et al. (1993)

maximum limits of the flooded depression. An additional source of forest species may be the tropical forest of the surrounding territory, as suggested by Teixeira et al. (2011) for the swamps of Itirapina, Brazil. In such cases, seed dispersal is accomplished mainly through zoochory by mammals and birds and anemochory (personal observation). The establishment of these species occurs during times of less flooding and on the buttresses or branches of *A. glabra* in the case of *F. cotinifolia* (strangling fig). Another factor contributing to the establishment of forest species from the mainland is the microtopography that exists in these wetlands (Flores-Verdugo et al., 2007), creating microhabitats favoring species with different levels of tolerance to inundation (Piedade et al., 2010). For example, on the border of the flooded depressions where occasional flooding with freshwater takes place, species tolerant to flooding for short periods may become established without problems. La Mancha, in particular, showed a high diversity value (3.373) because it forms a gradient with a tropical forest on higher ground.

We can conclude that forests in floodplains show higher diversity values and duration of flooding is not a limiting factor. Established species that can tolerate low oxygen conditions in the soil can form species-rich communities. These numbers increase when communities form gradients with other tropical forests and can decrease when there are stressing factors such as salinity.

4.3. Soils of freshwater forested wetlands

We hypothesized (Hypothesis 2) that soil texture of the forests located in floodplains would be dominated by fluvial materials; however, high amounts of clay were only found in Cienaga and in Salado. In the latter, contrary to our expectation that it would have a sand-dominated soil, the soils of this swamp located in a dune depression may reflect the influence of flooding from the nearby coastal plain, and because of the high fragmentation and change in soil use, flow communication has been hindered (Table 1). The soils of the other swamps were dominated by sand, a sediment of marine and eolic origin common in coastal plains with dune systems (Kolka and Thompson, 2006). When considering the carbon content and soil texture (Sprecher, 2001; USDA-NRCS, 2006), we found that the forests of Mancha, Apompal and Chica were classified as swamps with organic soil material, and Cienaga and Salado were classified as having mineral soils. These differences in the soil were also reflected in the soil density and its water storage capacity. Forested wetlands on organic soils were those with higher values such that the soils of these forests could be considered as "very poorly drained" (Tiner, 1999; Jackson, 2006).

In general, the concentrations of exchangeable cations were higher in flooded forest with surface water inflows, produced either by the overflowing of rivers (Cienaga and Apompal) or because of the influence of saltwater (Chica) with respect to the swamps in dune depressions, where the main water source is the phreatic table (Mancha and Salado). This result is consistent with what we hypothesized (Hypothesis 3) and coincides with data that have been reported for several forested wetlands influenced by other types of wetlands (Howard-Williams, 1985) and agricultural areas (Givnish et al., 2008). Nevertheless, it is important to note the differences in soils between the flooded forests and the possible causes of variation that occurred between seasons.

Regarding seasonal variations, the concentration of P in the soil was consistently higher in all of the forests during the rainy season due to P inputs from runoff (Howard-Williams, 1985). In the forests adjacent to agricultural fields (Cienaga, Chica and Salado), fertilizer use may be an important source of P. Other causes of increasing P include its release *in situ* because it is found forming complexes with Fe, Al, Ca and Mg and is released by the reduction of these compounds when redox potential decreases (Manahan, 2000). The soil composition of wetlands influences the form of phosphorous; in mineral soils, up to 80% can be inorganic, and up to 50% can be inorganic in organic soils (Reddy and DeLaune, 2008). P decreases during the dry season; it is probably used by wetland plants when water level decreases and is also immobilized through the formation of Fe and Al compounds at pH = 5.5 and with Ca at pH $\geqslant$ 6 (Manahan, 2000). Ca retention at higher pH is reflected in Mancha and Cienaga soils in the dry season (Fig. 5b). Nevertheless, the greatest concentration of Ca recorded was in Cienaga during the rains, which may be explained in part by its combination with P and in part because it is a cation strongly absorbed by clay soil colloids (Kolka and Thompson, 2006), which dominate the soil texture in this forested wetland.

Soil pH ranged from 4.6 to 5.9 (strongly acid to moderately acidic) in Apompal, Chica and Salado and between 6.4 and 7.7 (slightly acid to moderately alkaline) in Mancha and Cienaga. The latter forested wetlands have a higher pH due to the high Ca content. This feature allows them a greater capacity to buffer redox potential decrease during seasons when the soil remains anaerobic. These pH values are frequent in this type of vegetation (Moreno-Casasola et al., 2009); however, the drainage and drying of these wetlands or the alteration of their hydroperiod can cause a decrease in the pH and a resultant breakup and liberation of toxic compounds, causing fish death and preventing plant establishment (Batzer and Sharitz, 2006), a trend that was observed in soil when pH decreased slightly during the dry season.

In general, the soil of the flooded forests has low concentrations of Na, as their main source of water is fresh, except that of Chica, which had a higher concentration of Na and Mg due to the influence of the neighboring brackish coastal lagoon. Tiner (1999) recognizes the seawater as a source of these nutrients in the soil of coastal wetlands. This phenomenon was very marked during the dry season, when Na concentrates in the soil of Chica, making them distinct from the soils of the other forested freshwater wetlands studied (Fig. 5b).

Potassium is in lower concentrations in Mancha than in the other forests because the main source of K in the soil is clay (Fisher and Binkley, 2000), and in this site, clay is a minor component (7%). Loss by water percolating through the large pores that exist in a sandy soil may be another cause (Jackson, 2006). The K in Mancha could be considered as the limiting nutrient for productivity. N may also limit productivity according to the C/N ratios found in other swamps (Cienaga and Salado).

The Eh values found in the first 20 cm of soil indicate a predominance of reduction processes of Fe^{+3} and SO_4^{2-} because the water level, even in the dry season, is very near the soil surface. Only during the dry season in Cienaga did Eh correspond to NO_3 processes because the soil was partially oxidized. Methanogenic processes (reduction of CO_2: CH_4) were recorded only in the soil of Chica (Eh −220 mV) during the rainy season. We believe that the vegetation of these forests is able to oxidize the rhizosphere. The translocation of oxygen by plants takes place from the stems to the roots and is performed by aerenchyma tissue; once the oxygen diffuses into the soil, it promotes oxidation in areas close to the root (Cronk and Fennessy, 2001). The freshwater forested wetlands regulate the processes of oxidation–reduction in the soil, avoiding redox potential levels that indicate methane production; vegetation provides oxygen through roots and the shade of the trees (which keep the soil and water temperature similar during the wet and dry season), which must be influencing the production of very low levels of methanogenesis. This condition is lost by clearing the forests and allowing the sun's rays to penetrate directly to the ground, increasing the temperature and causing an increase in reduction reactions in flooded areas. This scenario is produced when forested wetlands are replaced by grasslands for cattle ranching. Another harmful effect is the drying of the soil of these forests and the oxidation of organic matter that results in lowering the pH, producing the acidification of soil and groundwater from nearby communities.

In biological terms, the increase of Na in the soil during the dry season in the forested wetlands in Chica causes a decline in the number of species and the formation of an ecotone with the mangroves. Another significant interaction between forests and seasons is a lower content of Ca and P in the soil during the dry season indicating that it is a period in which these elements are available to plants for assimilation (Boon, 2006); this represents a pulse of nutrient release. Plants also have adapted their life cycle to the periods of flooding and drying during the rainy season, by releasing seeds and propagules dispersed by water (hydrochory), which germinate when the water level decreases (Junk, 1989).

With respect to the hypothesis (No. 4) stating that the forested wetlands that remain flooded for a longer time will show more carbon and nitrogen storage in the soil, and will have lower diversity values, we found that the highest contents of C and N were in fact found in the soils of the forests that remained flooded longer: Apompal, Chica and Mancha. Nevertheless, the presence of high carbon and nitrogen did not show a relationship with the diversity of the forests wetlands.

The difference in the N and C content in forested wetlands is partly due to factors such as water content and the level of flooding; they modify redox potential (Eh) between seasons, allowing redox processes to be carried out in wetlands (Vepraskas and Faulkner, 2001; Lohse et al., 2009). In Cienaga and Salado, the water content in the soil is low, and the soil remains dry for a few months, which allows for the oxidation of C and N. In contrast, the high water content in the soil of the flooded forests of Chica, Mancha and Apompal reduces the rate of nitrogen mineralization and decomposition of organic matter, which is reflected in higher contents of these nutrients in the drier forests. Prolonged saturated and anaerobic conditions in wetland soils slow organic matter decomposition and lead to organic matter accumulation (Kolka and Thompson, 2006).

5. Conclusions

Species composition was related to geomorphological characteristics: similar species compositions were found between forested wetlands on floodplains and within dune depressions. Trees showed larger DBH values in the former. In general, the tropical forested wetlands showed a clear dominance of a few species. The tree *P. aquatica* showed the highest RIV, and lianas were an important structural component.

Tropical forested wetlands of the coastal plain of the Gulf of Mexico are distinct from other tropical flooded forests; species composition differs and two species show a clear dominance, *P. aquatica* and *A. glabra*. In Central America *P. officinalis* becomes the dominant species in these types of forested wetlands (Ellison, 2004). With respect to the subtropical forested wetlands of the northern Gulf of Mexico (e.g., Florida) the swamps of Veracruz have a greater number of species. The forested wetlands of the Yucatan Peninsula are located on a calcareous platform and soils are thin; wetland soils of these wetlands in Veracruz have a strong component of either sand or clay and generally with abundant or-

Appendix Table 1A

Species found in the five study areas and their importance value. An X indicates the presence of herbaceous and shrub species in the sites. Botanical nomenclature follows Missouri Botanical Garden's VAST (VAScular Tropicos) nomenclatural database (http://www.tropicos.org/Home.aspx).

Species	Biological form	Cienaga	Apompal	Chica	Mancha	Salado
Pachira aquatica Aubl. (Malvaceae)	T	103.61	135.75	158.20	4.3	129.28
Hippocratea celastroides Kunth (Celastraceae)	C	42.99	37.56	28.56	–	12.93
Dalbergia brownei (Jacq.) Schinz (Fabaceae)	C	11.86	33.58	10.72	–	19.57
Attalea liebmannii (Becc.) Zona (Arecaceae)	T	16.50	18.86	–	–	–
Ficus insipida Willd. subsp. *insipida* (Moraceae)	T	16.47	2.74	–	12.28	8.53
Pithecellobium latifolium (L.) Benth. (Fabaceae))	T	44.88	–	–	–	–
Ardisia revoluta Kunth (Primulaceae)	S	16.96	–	–	–	–
Trophis racemosa (L.) Urb. (Moraceae)	T	5.70	–	–	–	X
Parathesis psychotrioides Lundell (Primulaceae)	S	5.61	–	–	–	–
Ficus maxima Mill. (Moraceae)	T	5.38	–	–	–	–
Unidentified species 1 (Bignoniaceae)	C	4.86	–	–	–	–
Cissus biformifolia Standl. (Vitaceae)	C	4.82	–	–	–	–
Tabernaemontana alba Mill. (Apocynaceae)	T	3.01	5.67	–	–	X
Palicourea nigricans K. Krause (Rubiaceae)	S	2.97	–	–	–	–
Hasseltia laxiflora (Benth.) Eichler (Salicaceae)	T	2.41	19.89	–	–	–
Brosimum alicastrum Sw. (Moraceae)	T	2.40	–	–	–	–
Ardisia compressa Kunth (Primulaceae)	S	2.40	–	–	–	–
Tournefortia hirsutissima L. (Boraginaceae)	C	2.40	–	–	–	–
Eugenia oerstediana O. Berg (Myrtaceae)	S	2.39	–	–	–	–
Alibertia edulis (Rich.) A. Rich. ex DC. (Rubiaceae)	T	2.39	–	–	–	–
Arrabidaea mollissima (Kunth) Bureau and K. Schum. (Bignoniaceae)	C	X	–	–	–	–
Capparis frondosa Jacq. (Capparaceae)	S	X	–	–	–	–
Cionosicys macranthus (Pittier) C. Jeffrey (Cucurbitaceae)	H	X	–	–	–	–
Cupania dentata DC. (Sapindaceae)	T	X	–	–	–	–
Diospyros digyna Jacq. (Ebenaceae)	T	X	4.86	–	11.55	8.00
Guatteria galeottiana Baill. (Annonaceae)	T	X	–	–	–	–
Hamelia patens Jacq. (Rubiaceae)	H	X	–	–	–	–
Hampea nutricia Fryxell (Malvaceae)	S	X	–	–	–	–
Inga vera Willd. (Fabaceae)	T	X	X	–	–	–
Lithachne pauciflora (Sw.) P. Beauv. (Poaceae)	H	X	–	–	–	–
Malvaviscus arboreus Cav. (Malvaceae)	S	X	–	–	–	–
Mikania micrantha Kunth (Asteraceae)	H	X	–	–	–	–
Paullinia pinnata L. (Sapindaceae)	C	X	X	–	–	–
Petiveria alliacea L. (Phytolaccaceae)	S	X	–	–	–	–
Philodendron guttiferum Kunth (Araceae)	HE	X	–	–	–	–
Picramnia antidesma Sw. (Picramniaceae)	C	X	–	–	–	2.18
Pisonia aculeata L. (Nyctaginaceae)	S	X	–	–	–	–
Psychotria trichotoma M. Martens and Galeotti (Rubiaceae)	S	X	–	–	–	–
Rourea glabra Kunth (Connaraceae)	S	X	–	–	–	–
Scleria lithosperma (L.) Sw. (Cyperaceae)	H	X	X	–	–	–
Smilax mollis Humb. and Bonpl. ex Willd. (Smilacaceae)	C	X	X	–	X	–
Syngonium podophyllum Schott (Araceae)	HE	X	X	–	X	X
Thelypteris serrata (Cav.) Alston (Thelypteridaceae)	H	X	X	–	X	–
Unidentified species 2 (Poaceae)	H	X	–	–	–	–
Unidentified species 3 (Poaceae)	H	X	–	–	–	–
Avicennia germinans (L.) L. (Acanthaceae)	T	–	–	3.60	–	–
Hibiscus pernambucensis Arruda (Malvaceae)	S	–	–	6.43	–	–
Rhizophora mangle L. (Rhizophoraceae)	T	–	–	13.53	–	–
Unidentified species 4 (Bignoniaceae)	L	–	–	14.06	–	–
Rhabdadenia biflora (Jacq.) Müll. Arg. (Apocynaceae)	L	–	–	26.95	–	–
Laguncularia racemosa (L.) C.F. Gaertn. (Combretaceae)	T	–	–	37.96	–	X
Acrostichum aureum L. (Pteridaceae)	H	–	X	X	–	–
Ipomoea tiliacea (Willd.) Choisy (Convolvulaceae)	H	–	X	X	X	–
Urechites andrieuxii Müll. Arg. (Apocynaceae)	L	–	–	X	–	–
Acacia cornigera (L.) Willd. (Fabaceae)	S	–	–	–	5.08	6.55
Acalypha sp. (Euphorbiaceae)	T	–	X	–	–	–
Annona glabra L. (Annonaceae)	T	–	–	–	159.11	53.41
Unidentified species 5 (Apocynaceae)	C	–	X	–	–	–
Boehmeria cylindrica (L.) Sw. (Urticaceae)	H	–	–	–	X	–
Boehmeria ramiflora Jacq. (Urticaceae)	H	–	X	–	–	–
Bursera simaruba (L.) Sarg. (Burseraceae)	T	–	–	–	4.76	–
Byrsonima crassifolia (L.) Kunth (Malpighiaceae)	S	–	–	–	3.52	–
Casearia guevarana Cast.-Campos and E. Medina (Salicaceae)	T	–	–	–	2.38	–
Cedrela odorata L. (Meliaceae)	T	–	–	–	X	–
Celtis caudata Planch. (Cannabaceae)	T	–	–	–	2.38	–
Cestrum scandens Vahl (Solanaceae)	S	–	–	–	4.02	–
Coccoloba barbadensis Jacq. (Polygonaceae)	T	–	–	–	–	2.18
Coccoloba liebmannii Lindau (Polygonaceae)	T	–	–	–	4.52	–
Combretum laxum Jacq. (Combretaceae)	C	–	–	–	–	7.86
Crinum erubescens Aiton (Amaryllidaceae)	H	–	–	–	X	–
Daphnopsis americana (Mill.) J.R. Johnst. (Thymelaeaceae)	S	–	X	–	–	–
Dendropanax arboreus (L.) Decne. and Planch. (Araliaceae)	T	–	–	–	–	22.21
Desmopsis trunciflora (Schltdl. and Cham.) G.E. Schatz (Annonaceae)	T	–	–	–	–	2.34

Appendix Table 1A (*continued*)

Species	Biological form	Cienaga	Apompal	Chica	Mancha	Salado
Diphysa robinioides Benth. (Fabaceae)	T	–	–	–	2.07	–
Enterolobium cyclocarpum (Jacq.) Griseb. (Fabaceae)	T	–	–	–	4.85	–
Erythrina herbacea L. (Fabaceae)	S	–	–	–	2.02	–
Ficus aurea Nutt. (Moraceae)	T	–	–	–	4.02	–
Ficus cotinifolia Kunt (Moraceae)	T	–	–	–	11.58	–
Ficus obtusifolia Kunth (Moraceae)	T	–	3.22	–	2.32	X
Ficus trigonata L. (Moraceae)	T	–	7.04	–	–	–
Ginoria nudiflora (Hemsl.) Koehne (Lythraceae)	T	–	–	–	7.78	–
Heliconia latispatha Benth. (Heliconiaceae)	H	–	X	–	–	–
Hyperbaena mexicana Miers (Menispermaceae)	T	–	–	–	2.33	–
Microgramma nitida (J. Sm.) A.R. Sm. (Polypodiaceae)	HE	–	–	–	–	X
Nectandra ambigens (S.F. Blake) C.K. Allen (Lauraceae)	T	–	–	–	X	–
Ocotea cernua (Nees) Mez (Lauraceae)	S	–	–	–	3.96	–
Parathesis aff. *brevipes* Lundell (Primulaceae)	T	–	9.53	–	–	–
Passiflora sp. (Passifloraceae)	H	–	–	–	X	–
Passiflora biflora Lam. (Passifloraceae)	H	–	X	–	–	–
Passiflora filipes Benth. (Passifloraceae)	H	–	X	–	–	–
Pimenta dioica (L.) Merr. (Myrtaceae)	T	–	–	–	X	–
Piper amalago L. (Piperaceae)	S	–	–	–	7.03	–
Piper nitidum Sw. (Piperaceae)	S	–	X	–	2.31	15.40
Pistia stratiotes L. (Araceae)	H	–	–	–	X	–
Pontederia sagittata C. Presl (Pontederiaceae)	H	–	–	–	X	–
Psidium guava Griseb. (Myrtaceae)	T	–	–	–	2.49	–
Psychotria erythrocarpa Schltdl. (Rubiaceae)	S	–	–	–	X	–
Roystonea dunlapiana P.H. Allen (Arecaceae)	T	–	13.96	–	–	–
Salix humboldtiana Willd. (Salicaceae)	T	–	–	–	13.61	–
Sapium nitidum (Monach.) Lundell (Euphorbiaceae)	T	–	4.90	–	–	11.92
Serjania racemosa Schumach. (Sapindaceae)	C	–	–	–	X	–
Sicydium schiedeanum Schltdl. (Cucurbitaceae)	C	–	–	–	X	–
Spathiphyllum cochlearispathum (Liebm.) Engl. (Araceae)	H	–	–	–	X	–
Spathiphyllum sp. (Araceae)	H	–	–	–	–	X
Tabebuia rosea (Bertol.) A. DC. (Bignoniaceae)	T	–	X	–	10.27	–
Trichilia havanensis Jacq. (Meliaceae)	T	–	–	–	7.12	–
Trophis mexicana (Liebm.) Bureau (Moraceae)	T	–	–	–	X	–
Unidentified species 6 (Vitaceae)	C	–	X	–	–	–
Syzygium jambos L. Alston (Myrtaceae)	S	–	2.43	–	–	–
Total		300	300	300	300	300

The six species identified only to family are indicated. T = tree; S = shrub; C = climber; H = herb; HE = hemi-epiphyte.

ganic matter, which allows them to retain more water. Several rivers drain into the southern coastal plain of the Gulf of Mexico forming floodplains, however the tropical forested wetlands are restricted to small areas of the plain because a great part of them have been felled and land is being used for cattle rising and agriculture. There is also a strong tidal influence causing the coexistence of mangrove forests which cover nowadays a larger area of the floodplain. Forested wetlands in Mexico are restricted to the coastal zone due to the proximity of the mountain to the coast, which does not occur in the Amazon region where the forests extend inland considerably. It is also noteworthy that mountain ranges in South America and Africa, being further inland, allow for extensive floodplains where these type of communities occupy great extensions (e.g., Orinoco floodplains in Venezuela, Amazonia, and Congo basin in Africa) (Parolin and Wittmann, 2010). On the other hand, in Mexico and Central America the mountain range is much closer to the sea, coastal plains are narrower and floodplains are less extensive. Allen et al. (2005), Ellison (2009) and Ewel (2010) reported a similar situation in Islands of Pacific Ocean (e.g., Papua New Guinea, Palau, New Caledonia, Pohnpei and Kosrae).

The five forests varied in the number and abundance of species. Forested wetlands in floodplains (Cienaga and Apompal) showed higher diversity values, and duration of flooding was not a limiting factor. The formation of a gradient towards a tropical forest on higher ground increased the number of species, and salinity was a limiting factor for the species diversity.

The freshwater forested wetlands were found both in organic and mineral soils. They play an important role in the coastal areas because their soils retain/percolate water and maintain carbon in large quantities in the form of organic matter. An increase in the concentration of Na of 8 meq/100 g of soil (as is the case of Chica) produces a decline in diversity and the presence of very few salt-tolerant species (e.g., *P. aquatica*, *A. glabra*, *H. celastroides*, *D. brownei*), causing conditions to change from a freshwater forested wetland to mangrove forest. This is a possible scenario of saline intrusion by excessive extraction of water, holding it in reservoirs and sea level rise.

Forested wetlands that remain flooded during a longer time allow carbon and nitrogen storage in the soil, and higher values were found in the soils of the forests that remained flooded longer because there is less decomposition of organic material. Exchangeable cations showed the effect of the main water source. Forests on floodplains had higher concentrations because of the nutrient input by inflow from the land and the overflow of rivers.

The vegetation of forested wetlands has adapted to the temporal soil cycles of flooding–drying and to the flooding patterns. Vegetation, in turn, has influenced the soils, converting some of them into organic soils as a result of the interaction of soil–water-vegetation for long periods of time. The alteration of any of these components can modify forest functioning and affect the quality of the environmental services they provide, resulting in negative impacts on the human populations that inhabit the southern coastal plain of the Gulf of Mexico.

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Appendix A

See Appendix Table 1A.

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