Recent advances in understanding Colombian mangroves

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A R T I C L E   I N F O

A B S T R A C T

Throughout the last 15 years, researchers at the National University of Colombia at Medellin have studied Colombian mangroves. Remote sensing, pollen analysis of superficial and deep sediments, Holocene coastal vegetation dynamics, sediment dating using ^{14}C and ^{210}Pb, sampling in temporary plots, sampling in temporary and permanent plots, and other techniques have been applied to elucidate long- and short-term mangrove community dynamics. The studied root fouling community is structured by several regulatory mechanisms; habitat heterogeneity increases species richness and abundance. Fringe mangroves were related to Ca concentration in the soil and the increased dominance of *Laguncularia race-mosa* and other nonmangrove tree species, while the riverine mangroves were associated with Mg concentration and the dominance of *Rhizophora mangle*. The seedling and mangrove tree distributions are determined by a complex gradient of natural and anthropogenic disturbances. Mangrove pollen from surface sediments and the existing vegetation and geomorphology are close interrelated. Plant pollen of mangrove and salt marsh reflects environmental and disturbance conditions, and also reveals forest types. Forest dynamics in both coasts and their sensitivity of to anthropogenic processes are well documented in the Late Quaternary fossil record. Our studies of short and long term allow us to predict the dynamics of mangroves under different scenarios of climate change and anthropogenic stress factors that are operating in Colombian coasts. Future research arises from these results on mangrove forests dynamics, sea-level rise at a fine scale using palynology, conservation biology, and carbon dynamics.

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1. Introduction

Mangrove trees grow along subtropical and tropical coasts, where they fulfill several valuable socioecological and economic services (Alongi, 2009). Mangrove forests are a valuable economic resource as important breeding grounds and nursery sites for various animal species, including offshore fish populations (Barbier, 2000; Nagelkerken et al., 2008). They stabilize coastal lands and offer protection against storms, tsunamis, and sea-level rise (e.g., Dahdouh-Guebas et al., 2005; Mukherjee et al., 2010). More than 90% of the world's mangroves are located in developing countries (Duke et al., 2007), where impoverished human populations depend on their resources for subsistence (Walters et al., 2008). In this context, a group of researchers at the National University of Colombia studied different aspects related to the goods and services of mangroves in Colombia.

Colombia is the only South American country with coastlines on the Pacific Ocean (1200 km) and the Caribbean Sea (>1800 km). Precipitation and tidal patterns vary between these coasts. There are two dry seasons each year along the Caribbean coast, where the average rainfall does not exceed 2500 mm year^{-1}. There is a rainfall gradient from the northeast to the western Caribbean, including the islands of San Andrés, Providencia, and Santa Catalina (Fig. 1) (Álvarez-León and Polanía, 1996; Lacerda et al., 2001). In contrast, heavy rains (>3000 mm year^{-1}) predominate the Pacific coast throughout the year, where the mean tidal range is about 3 m. These conditions guarantee nearly continuous strips of mangroves along the Pacific coast, whereas in the Caribbean, narrow strips of forests are linked to freshwater sources (Zamora et al., 2013).

Such patterns of rainfall, tides, and local geomorphology produce mangrove stands with different structures and species compositions. Mangrove species that comprise the canopy of Caribbean mangroves are *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* (L.) L. (black mangrove), *Laguncularia racemosa* (L.) C.F. Gaertn. (white mangrove), *Conocarpus erectus* L., *Pelliciera rhizo-phorae* Planch. & Triana, and the fern *Acrostichum aureum* L. Colombian Pacific mangroves are built of *Rhizophora racemosa* G. Mey., the putative hybrid *Rhizophora harrisonii* Leechm. (cf Cerón-

Fig. 1. Map of the distribution of mangroves and the study sites in Columbia.

Souza et al., 2010), and *Mora megistosperma* (Pittier) Britton & Rose. Mangrove stands south of the San Juan River are more developed than those of the northern coast (Sánchez-Páez et al., 2000; Lacerda et al., 2001).

Our sites are found throughout the Caribbean: San Andrés Island in the west, the Gulf of Urabá at the southern limit, Guajira Peninsula in the driest northeastern part, and Cispatá Bay on the central Colombian coast. The Caribbean Current flows from east to west past San Andrés Island and the Old Providence Archipelago, and then detours to the southwest at the Nicaraguan Rise to form a counterclockwise eddy in the southwestern Caribbean (Geister and Díaz, 1997). In the archipelago, sediment-laden runoff from the Central American continent fails to affect the transparency and salinity of its ocean waters. There have been few thorough investigations of our sites compared to the Ciénaga Grande de Santa Marta, the largest extent of mangrove forests in the Colombian

Caribbean, which is sadly famous for the loss of more than half of its mangroves since the 1950s (equivalent to >25,000 ha; Polanía et al., 2001; Rivera-Monroy et al., 2006; Vilardy et al., 2011) and for government efforts to recover the forests (Botero and Salzwedel, 1999; Polanía et al., 2001).

Academic studies on mangrove ecosystems have increased exponentially in recent years (e.g., Feller et al., 2010), not excepting Colombian mangrove ecosystems (Cortés-Castillo and Rangel-Ch, 2011). However, most of these studies comprise grey literature that has not been readily available to the international scientific community. Results published in international journals throughout the last two decades are improving the knowledge of goods and services supplied by Colombian mangroves and provide tools for species management (Espinosa et al., 2011; Blanco and Castaño, 2012). The objectives of our review were: (i) to characterize the fouling community of mangrove ecosystems (at San Andrés Island), (ii) to characterize vegetation composition and structure, and to relate vegetation to environmental variables (at San Andrés Island, Guajira Peninsula, and Cispatá Bay), and (iii) to predict mangrove stand dynamics under different climate change scenarios and anthropogenic stressors.

2. Material and methods

2.1. Associated fauna

Fouling communities were surveyed at two sites on San Andrés Island with different levels of anthropogenic stress (the island has >2000 inhabitants km^{-2}). San Andrés is a tiny oceanic island (area <30 km^2) more than 190 km away from the mainland and over 400 km southeast of Jamaica. San Andrés Island has had no connection with the mainland for the last 80 million years (Díaz et al., 1996). Londoño et al. (2002) and Vilardy and Polanía (2002) qualitatively and quantitatively characterized the mollusk and polychaete fauna associated with submerged *R. mangle* roots in three regions subjected to different levels of anthropogenic impact on San Andrés Island. They cut several *R. mangle* roots and took them to the laboratory to identify and characterize the Annelida—Mollusca—Crustacea community. They also measured the temperature, salinity, and dissolved oxygen and hydrocarbon contents of the water column. They characterized faunal communities using the Shannon Weaver diversity index. They compared the mollusk communities among locations by using the Bray—Curtis index for dominance and similarity, and compared polychaete communities by using two-way ANOVA (Londoño et al., 2002; Vilardy and Polanía, 2002). Also on San Andrés Island, Romero-Murillo and Polanía (2008) evaluated the early succession of Annelida—Mollusca—Crustacea communities using 130 branches as pseudo-root substrate for 188 days. They used the Bray—Curtis similarity index, graphical analysis of dendrograms, and multidimensional nonmetric scaling to compare group dynamics under different levels of stress.

2.2. Mangrove vegetation and its relationship with the environment

Mangrove ecosystem structure has been related to physical and chemical factors not only in continental forest stands in the Gulf of Urabá, the Turbo river basin and the Ranchería River delta, but also at San Andrés Island. We assessed forest structure along transects perpendicular to the coastline in 400-m^2 quadrats and/or circular 500-m^2 plots, within which all trees (DBH > 2.5 cm) were measured and identified. In each plot, we also measured pore-water pH and salinity, flooding level, organic matter content, and soil granulometry. We used canonical correspondence analysis to determine correlations among forest composition and environmental variables. Mangrove types were identified according to the Lugo and Snedaker (1974) physiographic classification. In addition, we assessed the spatio-temporal dynamics of natural regeneration of mangroves using four 1-m^2 subplots in each plot, which were distributed in basin mangroves of the Turbo River basin and the Ranchería River delta. In these subplots, we measured mortality, recruitment, and survival during at least three periods.

2.3. Mangrove dynamics and climate change

We analyzed forest dynamics over short- (years to decades) and long-term (centuries to millennia) time scales. Over short time scales, we used maps, remote sensing, and GIS to evaluate changes in mangrove extent and forest composition at Guajira Peninsula. Changes were related to climate by using a series of measurements, such as temperature and precipitation. In the Ranchería River delta, we assessed mangrove productivity, tree diameter growth, and litterfall during a 2-year period.

We reconstructed vegetation and environmental change over previous centuries and millennia by using palynological analysis. We retrieved sediment cores from an oceanic basin and a continental swamp in the Pacific, and from coastal lagoons and mangrove soils on San Andrés Island, the Cispatá lagoon complex, the Ranchería River delta, and the Navio Quebrado lagoon at Guajira Peninsula. We built time scales by interpolating ages obtained from ^{14}C and ^{210}Pb dates. We chemically treated sediment samples, taken every 5 cm from each core, with standard methods for palynological analysis (Faegri and Iversen, 1989). We counted at least 250 pollen grains in each sample with the microscope. We analyzed changes along each core on pollen diagrams. We made zonations of diagrams by using cluster analysis and canonical correspondence analysis.

We validated the mangrove pollen by performing a palynological analysis of surface sediments from mangroves and the floors of shallow estuarine lagoons. Palynological analysis provided a tool to reconstruct the sea level, as well as environmental and floristic changes of mangrove stands. We related the spatial distribution of pollen to specific environmental features of different mangrove types by using canonical correspondence analysis.

2.4. Prospective

Ruiz-Ochoa et al. (2008) analyzed time series of rainfall, sea level, Sinú River water flow (since 1931), and sea surface temperature (monthly 1953—2000). They also compared aerial photographs (1981 and 1989) and satellite images (1986—2000) for changes in the area of water bodies and vegetation. They surveyed and compared salinity and the structure of mangrove forest stands (from INVEMAR data 2002—2005), took instrumental measures of organic matter content and percentages of mud and sand contents, and collected foraminifera taxa from the deltaic plain.

2.5. Management

Although Colombia exports flowers and other genetically important products, it lacks clear official regulations for nontimber forest products at the national level. Regional environmental agencies should set minimum requirements to allow the removal of nontimber forest products, and each product should be specifically studied before its export can eventually be approved.

Colombia's National Environmental System includes the Ministry of Environment, the Housing and Territorial Development, and so-called autonomous regional corporations, which are environmental local agencies that are supposed to ensure the rational and sustainable use of natural resources. Likewise, there are numerous

other state agencies with different capacities, whose regulation can lead to contradicting regulations. Within this context, García and Polanía (2007) analyzed the regulatory framework, including resolutions MAVDT No. 1602/1995 and 020/1996, which states that corporations must develop studies to establish management zones for each ecosystem and identify ways of managing their resources (resolutions MAVDT No. 0924/1997, 233/1999, 0694/2000 and 0721/2002). They compared basic technical information and proposed a conceptual framework.

3. Results and discussion

3.1. Associated fauna

R. mangle, the dominant species in Caribbean mangroves, is characterized by long prop-roots that extend into deeper water and support diverse communities of epibiotic algae and invertebrates below the lower low water line (Farnsworth and Ellison, 1996). As with many other subtidal fouling communities, patterns of distribution and abundance of mangrove-root epibionts are controlled by larval recruitment dynamics at local scales and by physical factors, current regimes, and stochastic events at larger scales (Farnsworth and Ellison, 1996).

The series of studies that we initiated to verify the diversity of the fouling community on a western Caribbean oceanic island surrounded by oligotrophic seas is relevant to island biogeography theory (Macarthur and Wilson, 1967). The habitat, with characteristics such as strong shading, a rich food supply, and substrate heterogeneity, offers plenty of refuges for different species. A salient feature of the community was the large variability at a fine scale (within field samples). A clumped distribution of benthic organisms is a typical feature in communities of multispecies benthic habitats. The large spatiotemporal variability of the community structures is probably why neither zones nor seasons formed clear groups in the analysis.

Vilardy and Polanía (2002) collected 5771 individuals from 21 species in 17 mollusk families and 5 genera of 11 polychaete species, all common to other regions of the Great Caribbean Basin. Romero-Murillo and Polanía (2008) identified 34,175 individuals (>77% annelids) in their study of the succession of the fouling community. New colonizing species even after 188 days revealed that the process could be longer than they expected.

Successional processes might be affected by the climate cycles of the island. Reduced precipitation and increased salinity before and stable conditions after sampling could have generated greater abundance and diversity. Romero-Murillo and Polanía (2008) demonstrated that only species adapted to extreme conditions (e.g., oily wastes, sewage, and water level decrease) are found in some of the most affected sites in Hooker Bay. Londoño et al. (2002) had already related these conditions to the presence of the annelid *Neanthes* sp., whereas Vilardy and Polanía (2002) studied mollusk species (e.g., *Neritina virginea*).

The relatively rough and unstable habitat in the intertidal region is predominantly populated by opportunists characterized by rapid growth and turnover (e.g., *Spirorbis* sp.). High numbers of individuals demonstrate the importance of the mangrove forest ecosystem as an energy source for estuarine and marine food webs. Filter-feeder opportunists can obtain food easier in areas with stronger stream flow that occur in response to wind patterns. *Polydora* sp., found by Moreno (2002) during a rainy season, have not recently been recorded in the area. Reyes and Campos (1992a), as well as Hernández-Alcántara and Solís-Weiss (1995) have suggested that precipitation may be important in regulating this species, which could explain its appearance only during a rainy season.

This mangrove fouling community had lower species diversity than communities from Caribbean mainland sites (Batista, 1980; Cifuentes, 1980; Reyes and Campos, 1992a,b; Hernández-Alcántara and Solís-Weiss, 1995; Moreno, 2002). This tiny isolated island is less likely to receive immigrants than other less isolated but larger sites (*sensu* Macarthur and Wilson, 1967). Although we observed differences among sites that were more or less impacted by human activities, they were not significant. The vast array of species seems to be representative of the community at San Andrés Island; according to the Chao 1 index, the species richness of San Andrés Island corresponds to 48% of the species identified at Honda Bay (for day 132) and 98% of the species at Hooker Bay (day 57) (Romero-Murillo and Polanía, 2008).

Red mangrove roots at San Andrés Island provide a very complex living space, which seems to be controlled by many factors that operate on different scales. Frequent tides supply the mangrove root system with fresh nutrients, which assures a continuous input of food resources. Thus, food supply should not be a limiting factor, especially because the epifauna are typically limited by the available space. These findings suggest three groups of regulatory mechanisms that structure the root fouling community: (i) microhabitat, (ii) competition for space, and (iii) local flow conditions and neighboring habitats. Potentially available area for settlement is a limiting factor for species richness and abundance. Some sessile organisms are obviously attractive for mobile species and provide habitat for other cryptic species. Habitat heterogeneity increases species richness and abundance as some common species acquire a heterogeneous distribution (Fig. 2). Recruitment and species composition may be influenced by water flow, whereas the proximity and type of neighboring habitat seem to affect species composition. The loose trophic structure of this community does not seem to be explicitly controlled by the feeding pressure of resident large organisms.

A broader understanding of trophic, substrate, and refuge functions of mangroves is of prime interest as tropical coastlines continue to be disturbed by natural and anthropogenic factors. Therefore, further investigation of the fouling communities is necessary to develop realistic predictions about global climate change, conservation, and the potential for ecosystem restoration.

3.2. Mangrove vegetation and its relationship with the environment

Mangrove forest composition and structure on San Andrés Island were not homogeneous along the eastern coast (Urrego et al., 2009a). They identified two physiographic types of mangrove forests: riverine and fringe. The dominant species of riverine mangroves were *L. racemosa* and *C. erectus*. *A. germinans* was dominant in fringe mangroves. *R. mangle* was abundant in both communities. We related mangrove structural development and stand distribution to an environmental gradient; fringe mangroves were primarily found in areas of lower freshwater availability (flooding), greater pore-water salinity, and organic soils. We did not detect a clear zonation pattern in San Andrés Island mangroves; instead, natural and anthropogenic disturbances and the regional species pool strongly influenced coastal mangroves. The differentiation of forest types was based on not only the dominance of true mangrove species, but also associated species growing in adjacent upland forests. The presence of *L. racemosa* was noteworthy as an indication of less preserved forest stands.

Bolívar and Vélez (2004) described the environmental gradient at San Andrés Island, which influenced the distribution of vegetation, especially along the transition from mangroves to adjacent upland forests. Anthropogenic impacts were mainly responsible for this gradient, as some small farm units and residential homes were found next to mangroves. There were three distinct groups along this gradient: (i) *R. mangle*, *L. racemosa*, and *A. germinans*; (ii)
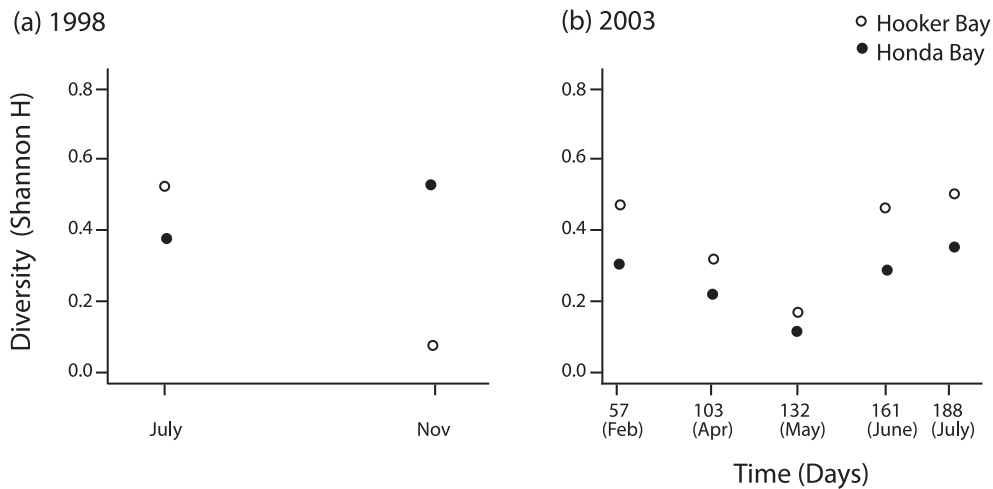
Fig. 2. Diversity of the fouling mollusk and annelid communities of *R. mangle* roots in Honda Bay and Hooker Bay, San Andrés Island, Colombia in (a) 1998 (Vilardy and Polanía, 2002; Londoño et al., 2202) and (b) 2003 (Romero-Murillo and Polanía, 2008).

mangrove and upland forest species, including *Annona glabra* L., *Ficus trigonata* L., *Hibiscus tiliaceus* L., *Eugenia* sp., and *Dalbergia* sp.; and (iii) exclusively upland species, including, but not limited to, *Melicoccus bijugatus* Jacq., *Guazuma ulmifolia* Lam., *Casearia aculeata* Jacq., *Psidium guajava* L., and *Spondias mombin* L. These intensively logged and fragmented forests differ from natural, original forests.

In Caribbean continental mangroves, the structure and composition followed a gradient of increased seasonality of precipitation and salinity from west to east. Urrego et al. (2014) found three mangroves types along the Gulf of Urabá, the largest entrance of the Caribbean Sea into the continental Colombian coast. Basin mangroves dominated by *A. germinans* were located on the eastern side of the Gulf and were related to mineral soils, predominantly composed of sand and clay, and high sediment loads transported by the Turbo River, whose river bed shifted in 1954. Fringe and riverine mangroves were found on organic soils with lower pore-water salinity. Although we could not establish a clear limit between both mangrove types, they were arranged along an environmental gradient in the ordination diagram. This arrangement was also related to differences in vegetation structure and composition. Whereas fringe mangroves were related to Ca concentration in the soil and the increased dominance of *L. racemosa* and other nonmangrove tree species, the riverine mangroves were associated with Mg concentration in the soil and the dominance of *R. mangle* for all tree sizes. The location of riverine mangroves in the northeastern part of the Gulf closer to the open sea and very intense anthropogenic disturbance in the fringes strongly influenced forest structure, composition, and nutrient availability in the soil.

Hoyos et al. (2013) analyzed the dynamics of natural regeneration in basin mangroves of the Gulf of Urabá. *A. germinans* dominated the regeneration, exhibited high mortality rates, and suffered attack by *Junonia evarete* Cramer caterpillars. *R. mangle* seedlings had the greatest survivorship and *L. racemosa* exhibited the greatest mortality. Regeneration of these species responded to a complex gradient of natural and anthropogenic disturbances, especially increased rainfall during the rainy season and higher sea levels during storm surges that led to increased mortality. Recruitment increased during the dry season. Logging of *R. mangle* and increased sedimentation rates also affected seedling survivorship. This research demonstrates that seedling and tree distributions in these mangroves are determined by variables that operate at two spatial scales. Blanco et al. (2012) warned that mangroves (basin more

than fringe types) are visibly threatened by selective logging for poles, planks, and pilings, as well as conversion to pasture.

Vásquez (2000) recorded basin and riverine mangroves in the Ranchería River delta in the northeastern Colombian Caribbean. Due to low annual precipitation (600 mm), a long dry season (8 months), and a lack of permanent freshwater flows, salinity recorded in basin mangroves dominated by *A. germinans* in La Guajira region was greater than in the Gulf of Urabá. *L. racemosa*, *R. mangle*, and *C. erectus* are also found in riverine mangroves but in lower relative abundances. Nonmangrove forest species that colonize these mangroves, such as *Prosopis juliflora* (Sw.) DC, *Capparis odoratissima* Jacq., and *Rhabdadenia biflora* (Jacq.) Müll. Arg., belong to adjacent dry forest and, therefore, benefit from such a long dry season. Mangrove structural parameters, range in tree density, and species composition varied with level of anthropogenic disturbance, as in mangroves of the Gulf of Urabá and San Andrés Island.

Different morphologies of *R. mangle*, *A. germinans*, and *L. racemosa* in the Rancheria River delta (Lema et al., 2003) were related to differences in the timing of dispersal and distribution along the riverbed. According to Lema et al. (2003), small and abundant propagules of *A. germinans* and *L. racemosa* drifted down river and were mostly lost from the system after 2 weeks. Naturally accumulated *A. germinans* propagules were the most abundant and were consumed by cattle, ants, and crabs. Larger *R. mangle* propagules were much less frequent and were reduced by animal consumption, but remained for over 1 month in the forest, where 1% of them rooted and established. Nevertheless, high recruitment and salinity of mangrove soils are responsible for the dominance of *A. germinans* in forest stands of the Ranchería River delta.

The Riito branch (Rancheria River, Guajira Peninsula) mangroves exhibited increased structural development compared to Valle de los Cangrejos (Vásquez, 2000). Mangrove structural parameters, range in tree density, and species composition varied with levels of anthropogenic disturbance, including the Riohacha sewage system, garbage dumping, coal wastes, and extraction of forest products. Assessing these parameters was contingent on the size of the sampling unit, which was variable. Initial results revealed complex vegetation structure and dynamics that are congruent with Feller et al. (2010).

At the Rancheria river delta tree productivity was 20.2 Mg ha^{-1} year^{-1}, annual litter production rate averaged 12.9 Mg ha^{-1}, and biomass increase was estimated as 7.4 Mg ha^{-1} year^{-1} (Lema et al., 2003; Lema and Polanía, 2005, 2007). Mangrove seedling

survivorship was low, and development was slow due to the indiscriminant use of wood by people. Plant regeneration was exposed to browsing by goats and donkeys (Lema et al., 2003).

On the basis of differences in the proportions of different species of mangrove pollen, we identified four vegetation groups in Cispatá Bay that belonged to geomorphological settings (Castaño et al., 2010), as has been previously recognized in existing vegetation (Ulloa-Delgado et al., 2004). In the first group, *R. mangle* pollen had the highest percentage (>65%), followed by *L. racemosa* and *A. germinans*. This group was found in the littoral zone with the oldest and most developed mangroves. In the second group, *R. mangle* pollen (35–50%) typified estuarine mangroves. Logging was present in some sites. Lower percentages (<25%) were detected from the third group of highly degraded piedmont mangroves and forests in the transition zone between mangroves and the mainland. A fourth group was represented by salt marsh species (especially herbs and aquatic vegetation) that characterized the coastline of the bay (Urrego et al., 2009b). This classification shows the close relationship between mangrove pollen from surface sediments and existing vegetation and geomorphology.

Pollen from mangrove surface sediments of San Andrés Island also reflected the three mangrove types recorded by Urrego et al. (2009a) in the existing vegetation. Existing vegetation was reflected by the pollen of not only mangrove species (*R. mangle*, *L. racemosa*, *A. germinans*, *C. erectus*) but also some coastal plants (Amaranthaceae, Cyperaceae, and Poaceae), and was correlated with environmental features of each vegetation type. As *R. mangle* pollen was present in all samples, it did not contribute to the differentiation of forest types. Instead, *A. germinans* pollen represented fringe mangroves and high salinity sites, and *C. erectus* pollen represented landward mangroves and soils with high pH (>7). *L. racemosa* pollen and *A. aureum* spores were allied with disturbed mangrove forests with frequent logging, as in Cispatá Bay (Urrego et al., 2010). Urrego et al. (2009b, 2010) demonstrated the ability of mangrove and salt marsh plant pollen to represent environmental and disturbance conditions, as well as the composition of the present mangrove species. These studies show that pollen can be interpreted to reveal mangrove forest types.

3.3. Mangrove dynamics and climate change

Molina (2009) identified basin, fringe, and mixed mangroves at Bahía Portete (Guajira Peninsula) based on remote sensing. Mangroves had expanded 98 ha over the past 50 years (i.e., 2.3 ha year^{-1}), and basin mangroves dominated by *A. germinans* showed the greatest increase (1.3 ha year^{-1}). However, mangrove coverage between 1995 and 2003 decreased at a rate of 0.2 ha year^{-1}. Greater losses in fringe mangroves and an increased area of basin mangroves can be related to sea-level rise and increased mean air temperatures (related to current climate change; *sensu* Campbell et al., 2010).

3.3.1. Reconstruction of mangrove forest history over the last 900 years

We reconstructed vegetation and environmental changes during the last millennium from palynological analysis of several sediment cores retrieved from mangroves of the Colombian Caribbean. In two sediment cores from the Cispatá lagoon complex, Castaño et al. (2010) analyzed stratigraphy, palynological sequences, calcite concentrations, and carbon-to-nitrogen ratios to reconstruct mangrove dynamics over the last 900 years. Different sections reflected fluvial-marine dynamics, particularly the Sinú River Delta movements and sea-level changes. Fern spores dominated the pollen spectrum between 1064 AD and 1142 AD. Colonization of herbaceous species consistent with delta progradation

started in 1142 AD and has continued to the present. Mangrove establishment only began around 1717 AD. Sediment and pollen analyses provided evidence of mangrove migration since 1849 AD (when the delta expanded to Cispatá Bay), seawater intrusion around 1900 AD, and delta migration to its current position around 1938 AD. These conditions and the gradual increase in sea level since then have favored mangrove expansion inside Cispatá Bay.

Based on pollen records, sedimentology, and ^{14}C dating of Bahía Honda (San Andrés Island), we detected the following changes during the last 400 years. First, there was a loss of approximately 2000 years of the fossil record, possibly due to a hurricane that occurred around 1600 AD. This phenomenon devastated forest vegetation and facilitated the expansion of pioneer species, notably herbs and vines. Second, an early recovery of mangroves and coastal vegetation occurred within several decades (likely until 1700 AD). Third, mangrove stands expanded in response to increased moisture in the regional climate during the last phase of the Little Ice Age (1700–1850 AD). Finally, we related a reduction in mangroves around 1850 AD to the expansion of coconut plantations in the island at the expense of natural vegetation. In 1960 AD, mangroves recovered again as the economy of the island changed to commercial trade, and as environmental conditions returned to those similar to Cispatá Bay (González et al., 2010).

In the Pacific, we used two sediments cores to reconstruct the history of the vegetation at short time scales. Ramírez and Urrego (2002) examined changes in vegetation along the Colombian Pacific coast at the San Juan River delta. Palynological analysis of a section covering the last 1300 years was used to determine how local geomorphological processes affected coastal vegetation, including mangroves. A seismic event caused subsidence, tidal flooding, and salinization in this delta. These conditions, combined with sediment transportation by the San Juan River delta, benefited mangrove colonization at sites where freshwater wetlands were present. The environmental mosaic originated in fluvial dynamics, an extensive drainage network, and local tectonic processes that shaped coastal vegetation, especially mangroves on the coasts and swamp forests inland (Urrego and Del Valle, 2002).

3.3.2. Long time scales (pollen)

Pollen sequences from two sediment cores retrieved from Guajira Peninsula revealed the environmental and mangrove history over the last 6000 years (Urrego et al., 2013). Sea-level rise in the early Holocene led to the formation of the Navio Quebrado lagoon and colonization of mangroves. However, mangroves were established only after the sea level stabilized in the Caribbean 3000 years BP. The importance of available freshwater to survive caused a reduction in the number of mangroves and a change from *Rhizophora*- to *Avicennia*-dominated forest. These changes occurred during a severe dry period in the Caribbean, recorded 2850 to 2450 years BP, which increased water and soil salinity. Greater precipitation and the input of fluvial sediment after 2500 years BP led to the recovery of *Rhizophora*-dominated mangroves. During the last 150 years, the palynological record of mangroves around this lagoon and at the Ranchería River delta recorded contrasting responses to a rise in sea level. Whereas mangroves expanded landward in the Ranchería River delta and in other progradational coastal environments, there was a net loss of mangrove vegetation around the Navio Quebrado Lagoon, likely from coastal erosion and the absence of a continuous input of freshwater. The anthropogenic fingerprint may obscure identification of additional changes in mangrove vegetation during the last 150 years.

González et al. (2006) conducted the first palynological analysis of marine sediment cores in areas near the equatorial Colombian Pacific coast (Panamá Basin). Analysis of the two cores revealed the continuous presence of six vegetation groups during the last 39,000

years. Palynological analysis recorded the main climatic changes since then: specifically, the driest, coldest period around the Last Glacial Maximum (28,120–14,500 years BP) with the lowest sea levels; a transitional phase that preceded the Holocene when precipitation and sea levels increased; and the onset of the Holocene (11,300–5600 years BP) with the highest sea levels and moisture conditions, which allowed mangroves to colonize and establish in the Colombian Pacific. This study synchronizes climate changes in marine and continental records of the late Quaternary.

3.4. Prospective

Salinity ranged from 5.4 to 40, depending on location and climate. Some changes in salinity were detected in both saltpans and water bodies (>28% of its maximum surface in 10 years). Ruiz-Ochoa et al. (2008) drew attention to the difference in organic matter content of surface soils (1.4–92.1%, positive correlation with marine influence) and mud (1.4–99.6%, negative correlation with marine influence). The foram study confirmed this gradient; abundance was higher near the sea. Representatives of the suborder Textulariina were found closer to mainland, whereas those of Rotaliina were generally found in the most saline areas.

There were significant direct correlations (Pearson's R; p-value < 0.05) between mangrove tree density and mud content of surface sediments (0.75), between mangrove tree density and number of foraminifera (0.96), and between foraminifera and mud content (Pearson's R = 0.78). There were significant negative correlations between quadratic mean tree diameter and vegetation density (−0.89), between mean sand particle size and number of foraminifera, and between mean sand particle size and organic matter content (−0.73). These results allowed Ruiz-Ochoa et al. (2008) to build four scenarios of the long-term impact of the construction of the Urrá dam on vegetation structure (discussed below).

We found no significant correlation between rainfall and El Nino for the Colombian Caribbean coast, although there may be more frequent La Niña events in the coming decades. Since the deltaic plain has a great capacity to absorb the Sinú River flow, and the construction of the Urrá dam reduced the mean and range of the flow, occasional floods can be related mainly to storm surges and heavy precipitation events. The rise in sea level (25 cm between 1959 and 1993 at the nearest tide gauge) and the effects of flow regulation from the Urrá dam resulted in conditions that allowed Ruiz-Ochoa et al. (2008) to build the four prospective scenarios based on one of two assumptions: either the interaction between the Sinú River and the lagoon system will remain stable, or the two branches that drain the system will clog.

In the first and most probable scenario, the shoreline will erode, fringe mangroves will collapse, vegetation will die, and swamps and marshes will remain flooded. Low salinity and constant flooding that predict this first scenario match the optimal growth conditions of *L. racemosa* (Medina, 1999; Sobrado, 2007) and *C. erectus* (Medina, 1999). Consequently, these two species would colonize available space more aggressively. A second less likely scenario predicts a reduction in rainfall, consequent salinization of the lagoon system and receding coastline, and a breach of the Mestizos sandbar mangroves by tidal action. The third scenario predicts a lack of flow from the Sinú River into the lagoon system, which would then be fed only by local precipitation and river flooding, creating conditions that would not tolerated by mangroves. The fourth scenario proposes water stress and consequent mangrove death, establishment of salt marshes, and lack of flow for nutrient exchange. All scenarios involve mangrove losses and represent potential risks to local residents. Ruiz-Ochoa et al. (2008) propose the use of the foraminifera assemblages as early indicators of climate change. This work should be a serious warning to the government authorities to take protective measures.

3.5. Management issues

In theory, Colombian mangrove forests and their associated natural resources are protected and not open to exploitation. Nevertheless, some stakeholders, who had been traditionally engaged in agriculture, reoriented their livelihoods towards the extraction of forests and hydrobiological resources at Cispatá Bay while a management plan was being created. The implementation of this plan began in 2003 (CVS and INVEMAR, 2010).

Limitation of access to forests can affect stakeholders' livelihoods, but access to resources needs to be carefully monitored to ensure sustainable use. Additionally, there is interest in the commercial exploitation of *R. mangle* propagules for export as ornamentals to the USA in Chocó (Pacific coast), where a permit from the local environmental authority was requested. García and Polanía (2007) generated a conceptual framework for the possible use of *R. mangle* propagules as nontimber forest products in Colombia. These propagules are used in ponds, freshwater tanks, brackish water, houseplants, and for marine aquaria in the USA, since *R. mangle* flowers all year long. The low mortality rate of *R. mangle* seedlings and the long viability of propagules make them ideal export goods. The framework of García and Polanía (2007) includes the potential contribution of Colombian Pacific mangroves to this market.

Although the production of *Rhizophora* propagules varies with age (Bunt, 1995; >350,000 ha^{-1} year^{-1}, Clough et al., 2000), the relative effort put into reproductive structures varies between 10% and 40% of the total litterfall of *Rhizophora*. Collection, cleaning, and packing of *R. mangle* propagules were estimated to cost about US $0.062 altogether, whereas a two-leaf propagule could be found for sale online for US $0.43 (US $0.23 without leaves or roots; www.ebay.com).

Colombian legislation still shows large gaps in the use of nontimber forest products from both upland forests and mangroves. The García and Polanía (2007) proposal for establishing maximum extraction requirements could lead environmental authorities to grant appropriate export permits. Promoting the use of nontimber forest products can mean an equilibrium between conservation and sustainable use of tropical forests in countries where markets are expanding, not only for their potential contribution to GDP, but also because they can represent novel livelihood options for depressed rural communities. The production of *Rhizophora* propagules indicates that *R. mangle* propagules can be a viable option to achieve a balance between conservation and the sustainable use of these forest resources along the Colombian Pacific coast. Colombian natural resource management agencies should coordinate their activities with academic institutions to implement an acceptable mangrove forest policy.

4. Conclusions

Three groups of regulatory mechanisms structure the root fouling community at San Andres Island: (i) microhabitat, (ii) competition for space, and (iii) local flow conditions and neighboring habitats. There, habitat heterogeneity increases species richness and abundance as some common species acquire a heterogeneous distribution.

The mangrove types at the Gulf of Urabá were arranged along an environmental gradient, related to differences in vegetation structure and composition. Fringe mangroves were related to Ca concentration in the soil and the increased dominance of *L. racemosa* and other nonmangrove tree species. Riverine

mangroves were associated with Mg concentration in the soil and the dominance of *R. mangle* for all tree sizes. The seedling and tree distributions in these mangroves are determined by a complex gradient of natural and anthropogenic disturbances. Increased rainfall and higher sea levels during storm surges increase mortality. Recruitment increased during the dry season but logging of *R. mangle* and sedimentation also affected seedling survivorship.

A close relationship exists between mangrove pollen from surface sediments and the existing vegetation and geomorphology at the Cispatá Bay. Plant pollen of mangrove and salt marsh at San Andrés Island reflects environmental and disturbance conditions, and also reveals mangrove forest types.

Forest dynamics (e.g., loss of area) reflect the complexity of mangrove forests in the Caribbean and Pacific and the sensitivity of these forests to anthropogenic processes (e.g., landward activities or urban proximity to mangroves in the delta in Riohacha), aspects that are well documented in the Late Quaternary fossil record. Our studies of short and long term allow us to predict the dynamics of mangroves under different scenarios of climate change and anthropogenic stress factors that are operating in the Colombian coastal.

By constructing future mangrove development plans, we are optimistic that mangrove resources can be managed responsibly and sustainably. It is essential to continue scientific studies in this country to generate clearer mangrove management guidelines and to conserve natural resources. The results of mangrove forest research in Colombia summarized in this review can be applied to the consequences of global climate change, coastal management, conservation, and ecosystem restoration at national and global levels.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2015.01.001.

References

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

Álvarez-León, R., Polanía, J., 1996. Colombian Caribbean mangroves. Synthesis of their knowledge (in Spanish). Rev. Acad. Colomb. Cienc. Exactas Fís. Nat. 20, 447–464.

Barbier, E.B., 2000. Valuing the environment as input: review of applications to mangrove-fishery linkages. Ecol. Econ. 35 (1), 47–61.

Batista, V.E., 1980. Study of the Fouling Communities in Red Mangrove (*Rhizophora mangle* L.) Roots at Galeta Point, Atlantic Coast of Panama (in Spanish, BSc thesis). Universidad Jorge Tadeo Lozano.

Blanco, J.F., Castaño, M.C., 2012. Effect of mangrove conversion to grassland on the density and size of two gastropods at the Turbo River Delta (the Gulf of Urabá, Colombian Caribbean) (in Spanish). Rev. Biol. Trop. 60, 1707–1719.

Blanco, J.F., Estrada, E.A., Ortiz, L.F., Urrego, L.E., 2012. Ecosystem-wide impacts of deforestation in mangroves: the Urabá Gulf (Colombian Caribbean) case study. ISRN Ecol. 1–14.

Bolívar, J., Vélez, S., 2004. Comprehensive Zonation of the San Andrés Island Vegetation with Emphasis on the Mangrove-mainland Transition (in Spanish, BSc thesis). Universidad Nacional de Colombia Sede Medellín.

Botero, L., Salzwedel, H., 1999. Rehabilitation of the Cienaga Grande de Santa Marta, a mangrove-estuarine system in the Caribbean coast of Colombia. Ocean Coast. Manage. 42, 243–256.

Bunt, J.S., 1995. Continental scale patterns in mangrove litter fall. Hydrobiologia 295, 135–140.

Campbell, J., Taylor, M., Stephenson, T., Watson, R., Whyte, F., 2010. Future climate of the Caribbean from a regional climate model. Int. J. Climatol. 31, 1866–1878.

Castaño, A.R., Urrego, L.E., Bernal, G., 2010. Mangrove dynamics in the Cispata lagoon complex (Colombian Caribbean) during the last 900 years (in Spanish). Rev. Biol. Trop. Int. J. Trop. Biol. 58, 1347–1366.

Cerón-Souza, I., Rivera-Ocasio, E., Medina, E., Jiménez, J.A., McMillan, W.O., Bermingham, E., 2010. Hybridization and introgression in New World red mangroves, *Rhizophora* (Rhizophoraceae). Am. J. Bot. 97, 945–957.

Cifuentes, W., 1980. Contribution to the Knowledge of the Mangrove Ecosystem Structure, Flora, and Fauna at Cartagena Bay (in Spanish, BSc thesis). Universidad Jorge Tadeo Lozano.

Clough, B., Tan, D.T., Phuong, D.X., Buu, D.C., 2000. Canopy leaf area index and litter fall in stands of the mangrove *Rhizophora apiculata* of different age in the Mekong Delta, Vietnam. Aquat. Bot. 66, 311–320.

Cortés-Castillo, D.V., Rangel-Ch, J.O., 2011. Mangrove forests in a salinity gradient at the Cispatá Bay-Boca Tinajones, Cordoba Department, Colombia (in Spanish). Caldasia 33, 155–176.

CVS and INVEMAR, Corporación Autónoma Regional de Los Valles del Sinú y del San Jorge e Instituto de Investigaciones Marinas y Costeras, 2010. Comprehensive management plan for the integrated management district (IMD) Cispatá Bay-La Balsa-Tinajones in the estuarine Sinú river delta and surrounding areas, Córdoba Department (in Spanish). In: Rojas, G.X., Sierra-Correa, P. (Eds.), Serie de Publicaciones Especiales No. 18. INVEMAR, Santa Marta.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Lo Seen, D., Koedam, N., 2005. How effective were mangroves as a defence against the recent tsunami? Curr. Biol. 15, R443–R447.

Díaz, J.M., Díaz-Pulido, G., Garzón-Ferreira, J., Geister, J., Sánchez, J.A., Zea, S., 1996. Coral Reef Atlas of the Colombian Caribbean. In: Oceanic Reef Complexes, vol. I. Invemar, Santa Marta (in Spanish), Serie Publicaciones Especiales 2.

Duke, N.C., Meynecke, J.O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317 (5834), 41–42.

Espinosa, L.F., Parra, J.P., Villamil, C., 2011. Heavy metal determination in the geochemical fractions of surface sediments associated with the Cienaga Grande de Santa Marta mangroves, Colombia (in Spanish). Bol. Inv. Mar. Costeras 40, 7–23.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. Wiley, Chichester, England.

Farnsworth, E.J., Ellison, A.M., 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecol. Monogr. 66 (1), 45–66.

Feller, I.C., Lovelock, C.E., Berger, U., McKee, K.L., Joye, S.B., Ball, M.C., 2010. Biocomplexity in mangrove ecosystems. Annu. Rev. Mar. Sci. 2, 395–417.

García, S.C., Polanía, J., 2007. Conceptual framework for non-timber forest products in Colombian mangroves (in Spanish). Gest. Ambiente 10, 169–178.

Geister, J., Díaz, J.M., 1997. Field guide to the oceanic barrier reefs and atolls of the southwestern Caribbean (Archipiélago of San Andrés and Providencia, Colombia). In: Proc. 8th Int. Coral Reef Symp., vol. 1, pp. 235–262.

González, C., Urrego, L.E., Martínez, J.I., 2006. Late quaternary vegetation and climate change in the Panamanian Basin: palynological evidence from marine cores ODP 677B and TR 163–38. Palaeogr. Palaeoecol. 234, 62–80.

González, C., Urrego, L.E., Martínez, J.I., Polanía, J., Yokoyama, Y., 2010. Mangrove dynamics in the southwestern Caribbean since the 'Little Ice Age': a history of human and natural disturbances. Holocene 20, 849–861.

Hernández-Alcántara, P., Solís-Weiss, V., 1995. Some macrobenthic communities associated with *Rhizophora mangle* mangroves at the Terminos Lagoon, the Gulf of Mexico (in Spanish). Rev. Biol. Trop. 43, 117–129.

Hoyos, R., Urrego, L.E., Lema, T., 2013. Natural regeneration response in mangroves of the Gulf of Urabá (Colombia) to the environment and intra-annual climate variability (in Spanish). Rev. Biol. Trop. Int. J. Trop. Biol. 61, 1445–1461.

Lacerda, L.D., Conde, J.E., Kjerfve, B., Álvarez-León, R., Alarcón, C., Polanía, J., 2001. American mangroves. In: de Lacerda, L.D. (Ed.), Mangrove Ecosystem, Function and Management. Springer-Verlag, New York, pp. 1–62.

Lema, L., Polanía, J., 2005. Natural regeneration and production of the Rancheria River delta mangroves, Colombian Caribbean (in Spanish). Actual Biol. 27, 23–31.

Lema, L., Polanía, J., 2007. Structure and dynamics of the Rancheria River delta mangroves, Colombian Caribbean (in Spanish). Rev. Biol. Trop. Int. J. Trop. Biol. 55, 11–21.

Lema, L.F., Polanía, J., Urrego, L.E., 2003. Dispersal and establishment of mangrove species at the Rancheria River during the maximum fruiting period (in Spanish). Rev. Acad. Colomb. Cienc. Exactas Fís. Nat. 27, 94–104.

Londoño, M., Polanía, J., Vélez, I., 2002. Polychaetes of the mangrove-fouling community at the Colombian Archipelago of San Andrés and Old Providence, Western Caribbean. Wetl. Ecol. Manage. 10, 227–232.

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 39–64.

Macarthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, New Jersey, USA.

Medina, E., 1999. Mangrove physiology: the challenge of salt, heat, and light stress under recurrent flooding. In: Yánez-Arancibia, A., Lara-Domínguez, A.L. (Eds.), Ecosistemas de Manglar en América Tropical, pp. 109–126. Instituto de Ecología AC Xalapa, México. UICN/ORMA Costa Rica, NOAA/NMFS, Silver Spring, MD, USA.

Molina, O.E., 2009. The Dynamics of the Portete Bay Mangroves, Alta Guajira, at a Landscape Scale, and its Relationship with Climatic Variables Associated with Global and Regional Climate Change (in Spanish, MSc thesis). Universidad Nacional de Colombia Sede Medellín.

Moreno, P., 2002. The Annelida-Mollusca-Crustacea Taxocenosis Associated with *Rhizophora mangle* L. Submerged Roots at San Andrés Island, Colombian Caribbean (in Spanish, BSc thesis). Universidad de Bogotá Jorge Tadeo Lozano.

Mukherjee, N., Dahdouh-Guebas, F., Kapoor, V., Arthur, R., Koedam, N., Sridhar, A., Shanker, K., 2010. From bathymetry to bioshields: a review of post-tsunami ecological research in India and its implications for policy. Environ. Manage. 46, 329–339.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat. Bot. 89, 155–185.

Polanía, J.A., Santos-Martínez, J.E., Mancera-Pineda, L., Botero, A., 2001. The coastal lagoon Ciénaga Grande de Santa Marta, Colombia. In: Seeliger, U., Kjerfve, B. (Eds.), Coastal Marine Ecosystems of Latin America. Ecological Studies, vol. 144. Springer-Verlag, New York, pp. 33—46.

Ramírez, O., Urrego, L.E., 2002. Holocenic vegetation in the San Juan river Delta, Colombian Pacific. In: Correa Arango, I.D., Restrepo Ángel, J.D. (Eds.), Geology and Oceanography of the San Juan River Delta Colombian Pacific Littoral. Fondo Editorial Universidad EAFIT, , Medellin, Colombia, pp. 151—166 (in Spanish).

Reyes, R., Campos, N., 1992a. Macroinvertebrates colonizing *Rhizophora mangle* roots at Chengue Bay, Colombian Caribbean (in Spanish). An. Inst. Investig. Mar. Costeras Punta Betín 21, 101—116.

Reyes, R., Campos, N., 1992b. Molluscs, annelids and crustaceans associated with *Rhizophora mangle* Linnaeus roots at the Santa Marta region, Colombian Caribbean (in Spanish). Caldasia 17, 133—148.

Rivera-Monroy, V.H., Twilley, R.R., Mancera, E., Alcantara-Eguren, A., Castañeda-Moya, E., Casas Monroy, O., Reyes, P., Restrepo, J., Perdomo, L., Campos, E., Cotes, G., Viloria, E., 2006. Adventures and misadventures in Macondo: rehabilitation of the Cienaga Grande de Santa Marta, Colombia (in Spanish). Eco-tropicos 19, 72—93.

Romero-Murillo, P., Polanía, J., 2008. Early succession of the Mollusca-Annelida-Crustacea taxocenosis in the red mangrove submerged roots at the San Andrés Island, Colombian Caribbean (in Spanish). Rev. Biol. Mar. Ocean. 43, 63—74.

Ruiz-Ochoa, M., Bernal, G., Polanía, J., 2008. The influence of the Sinú River and the Caribbean Sea over the Cispatá lagoon system (in Spanish). Bol. Invest. Mar. Cost. 37, 31—51.

Sánchez-Páez, H., Ulloa-Delgado, G., Álvarez-León, R., 2000. Strategic Guidelines for the Conservation and Sustainable Use of the Colombian Mangroves (in Spanish). Ministerio del Medio Ambiente, ACOFORE, OIMT, Bogotá, Columbia.

Sobrado, M.A., 2007. Relationship of water transport to anatomical features in the mangrove *Laguncularia racemosa* grown under contrasting salinities. New. Phytol. 173, 584—591.

Ulloa-Delgado, G., Sánchez-Páez, H., Tavera-Escobar, T., 2004. Mangrove Restoration of the Colombian Caribbean (in Spanish) Project Report PD 60/01 Rev. I (F). Minambiente, CONIF. OIMT, Bogotá, Columbia.

Urrego, L.E., Del Valle, J.I., 2002. Reconstruction of succession in a "Guandal" forest (Colombian Pacific) during the recent Holocene (in Spanish). Caldasia 24, 425—443.

Urrego, L., Polanía, J., Buitrago, M.F., Cuartas, L.F., Lema, A., 2009a. Distribution of mangroves along environmental gradients on San Andrés Island (Colombian Caribbean). Bull. Mar. Sci. 85, 27—43.

Urrego, L., Bernal, G., Polanía, J., 2009b. Comparison of pollen distribution patterns in surface sediments of a Colombian Caribbean mangrove with geomorphology and vegetation. Rev. Palaeobot. Palynol. 156, 358—375.

Urrego, L.E., González, C., Urán, G., Polanía, J., 2010. Modern pollen rain in mangroves from San Andrés Island, Colombian Caribbean. Rev. Palaeobot. Palynol. 162, 168—182.

Urrego, L.E., Correa-Metrio, A., González, C., Castaño, A.R., Yokoyama, Y., 2013. Contrasting responses of two Caribbean mangroves to sea-level rise in the Guajira Peninsula (Colombian Caribbean). Palaeogeogr. Palaeoecol. 370, 92—102.

Urrego, L.E., Molina, E.C., Suárez, J., 2014. Environmental and anthropogenic influences on the distribution, structure, and floristic composition of mangrove forests of the Gulf of Urabá (Colombian Caribbean). Aquat. Bot. 114, 42—49.

Vásquez, J.L., 2000. The Structure of Two Mangrove Forests at Cangrejos Valley and Riíto, Ranchería River Delta, Colombian Caribbean (in Spanish, BSc thesis). Universidad Nacional de Colombia Sede Medellín.

Vilardy, S., Polanía, J., 2002. Mollusc fauna of the mangrove-root fouling community at the Colombian Archipelago of San Andrés and Old Providence. Wetl. Ecol. Manage. 10, 273—282.

Vilardy, S.P., González, J.A., Martín-López, B., Montes, C., 2011. Relationships between hydrological regime and ecosystem services supply in a Caribbean coastal wetland: a social-ecological approach. Hydrol. Sci. J. 56, 1423—1435.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: a review. Aquat. Bot. 89 (2), 220—236.

Zamora, A.P., Lozano, P., López, A.C., Hernández, M., Villamil, C., Agudelo, C.M., Gómez, M.C., Perdomo, L., Londoño, L.M., 2013. Management instruments for the ocean, islands, and coastal areas of Colombia: response indicators (in Spanish). In: INVEMAR. Informe del Estado de los Ambientes Marinos y Costeros, Santa Marta, Colombia.