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A Review of Sea-Level Rise Effect on Mangrove Forest Species: Anatomical and Morphological Modifications

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1. Introduction

Mangrove forests are among the most productive and biologically important ecosystems of the world, because they provide important and unique ecosystem goods and services to human society and coastal and marine systems, as stabilizing shorelines and reducing the devastating impact of natural disasters, providing breeding and nursing grounds for marine species, and food, medicine, fuel and building materials (Tomlinson, 1986; Giri et al., 2011).
Mangroves are taxonomically diverse trees and shrubs that have evolved independently through convergence (Hogarth, 1999). The principal genera are *Avicennia* (Avicenniaceae), *Laguncularia* and *Lumnitzera* (Combretaceae), *Nypa* (Palmae), *Bruguiera, Ceriops, Kandelia* and *Rhizophora* (Rhizophoraceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson, 1986). These plants have developed complex physiological, morphological and anatomical adaptations allowing survival and success in the high stress habitat where they inhabit (Hogarth, 1999). They can tolerate the stress of waterlogging and salinity prevailing in coastal environments influenced by tides and have adapted to wide salinity levels, may be influenced by local hydrology and episodic disturbance events (Doyle, 2003). The maximum concentration of soil water salinity that mangrove species can tolerate is suggested up to 155 ‰ with annual averages of 100 ‰ (Tomlinson, 1986).
Mangrove forests are generally distributed along tropical coastlines of America, Africa and Asia between 25° N and 25° S, although this range extends beyond due to the movement of unusually warm waters from the equator, including the east coast of Africa, Australia, and New Zealand (Hogarth, 1999; McLeod & Salm, 2006).
Nevertheless, sea-level rise in the future could be the biggest threat to mangrove ecosystems as climate change consequence (Giri et al., 2011). In the last century, sea-level has risen 10-20 cm mainly due to thermal expansion of the oceans and melting of glacial ice caused by global warming, with climate models predicting an accelerated rate of sea-level rise over coming decades from 0.09 to 0.88 m (McLeod & Salm, 2006). This will generate salinity concentration, along with rising CO_2, and temperature, determining future species distributions, abundances, and viability (Kareiva et al., 1993; Yáñez-Arancibia et al., 1998),

concerning worldwide from both scientific and policy perspectives (Alongi, 2008; Gilman et al., 2008; Semeniuk, 1994).

Increased surface temperature is expected to affect mangrove forests (Field, 1995). However, it is uncertain the effect of rising temperature when the interactive effects of changes in precipitation and other weather-related factors are considered (Alongi, 2008). In addition, temperature change in the tropics may not be as great as in boreal and temperate regions (Beaumont et al., 2011; Solomon et al., 2007). Responses of mangroves to rising temperature depend on reactions of individual plants, but such responses have not been addressed experimentally.

The chapter approach involve a review of worldwide studies regarding the association of mangroves morphological and anatomical traits variation with local and regional environmental factors, analyzing their stem, leaves, roots and growth, allowing to infer the effect of potential impacts of sea-level rise on their structure.

2. Morphological and anatomical adaptations of mangrove forest species to environmental factors

Mangrove species anatomical and morphological adaptations are relevant from ecological point of view, due to the particular environment where they inhabit, frequently flooded and highly saline (Tomlinson, 1986) (Fig. 1).

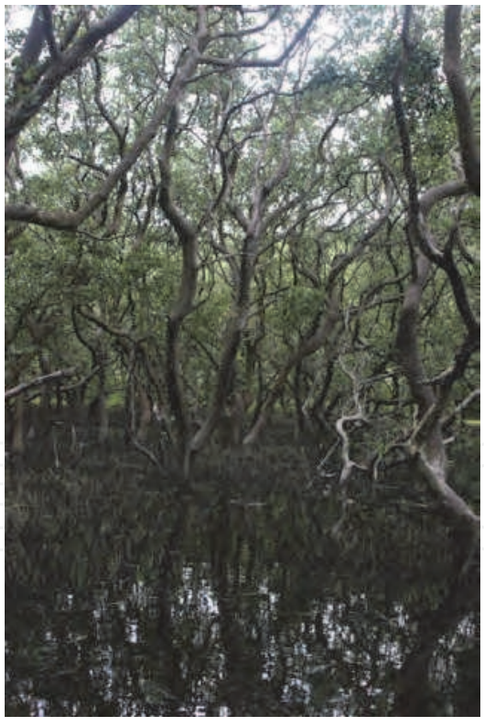


Fig. 1. Mangrove *Avicennia germinans* (L.) Stearn (Avicenniaceae) trees in the coastal lagoon "La Mancha", Veracruz, in the Gulf of Mexico (photo by Jorge López-Portillo).

There is in addition a group of species described as mangrove associates that comprises a large number of species typically occurring on the landward margin of the forest or non-mangrove habitats like salt marsh or lowland fresh water swamps that are completely or

partially flood tolerant (Hogarth, 1999) (Fig. 2). There is a long list of mangrove associates like *Hibiscus* and *Pavonia* (Malvaceae), *Amoora* (Meliaceae), *Ardisia* and *Myrsine* (Myrsinaceae), *Calamus* and *Phoenix* (Arecaeae), *Pandanus* (Pandanaceae), *Pouteria* (Sapotaceae), *Pachira* (Bombacaceae), *Ficus (*Moraceae), *Tabebuia* (Bignoniaceae), *Achrosticum* (Pteridaceae), *Annona* (Annonaceae), and others (Tomlinson, 1986).

The most typical adaptations of mangrove species are the aerial roots, stilt-roots, pneumatophores, root knees, and plank roots that have a higher proportion of gas space when waterlogged, mechanisms of salt exclusion by the roots, tolerance of high tissue salt concentrations and excretion of salt excess from leaves, vivipary or the development of the embryo in seed plants before they are dispersed, and seeds and propagules have different morphological adaptations that facilitate flotation (Baskin & Baskin, 2001; Hogarth, 1999; Tomlinson, 1986).



Fig. 2. Mangrove associate *Annona glabra* L. (Annonaceae) trees showing massive root system in the Everglades, Florida.

Trees vascular system has strong influence on leaves structure and function, carbon gain, nutrient use efficiency and growth rate. Diverse studies have revealed that mangroves show great plasticity in wood, bark and leaves structure as an adaptation to a wide gradient of water salinity, flooding level and waterlogging period. These modifications are important to account and understand the possible effects of the predicted sea-level rise as a consequence of global warming, because as all mangrove forests occur between high and low tide marks it is evident that they will be drastically influenced by any changes in sea-level.

3. Modifications of wood structure in response to environmental factors

Several studies have demonstrated that mangroves like *Bruguiera*, *Rhizophora, Laguncularia* and *Avicennia* trees stem vascular system, particularly wood anatomical traits as vessel density, grouping, diameter and length, as well as fiber wall thickness, are affected by variations on salinity and flooding level. (Table 1).

Anatomical traits	Species	Environmental factors	Reference
Vessel density	*Annona glabra* *Laguncularia racemosa* *Rhizophora mangle*	Salinity Flooding level Soil texture	Yáñez-Espinosa et al., 2001
	Laguncularia racemosa	Salinity Flooding level	Yáñez-Espinosa et al., 2004
	Rhizophora mucronata	Salinity	Schmitz et al., 2006
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Avicennia germinans	Salinity Flooding period	Yáñez-Espinosa et al., 2009
	Bruguiera gymnorrhiza	Flooding period	Xiao et al., 2010
Vessel diameter	*Rhizophora mangle*	Salinity Flooding level	Yáñez-Espinosa et al., 2001
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Avicennia marina	Flooding period	Xiao et al., 2009
	Rhizophora mucronata	Salinity	Schmitz et al., 2006
Vessel grouping	*Annona glabra*	Salinity Flooding level Soil texture	Yáñez-Espinosa et al., 2001
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
Vessel length	*Avicennia marina* *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Laguncularia racemosa	Salinity Flooding level	Yáñez-Espinosa et al., 2004
Fiber wall thickness	*Laguncularia racemosa*	Salinity	Yáñez-Espinosa et al., 2004
	Avicennia germinans	Salinity Flooding period	Yáñez-Espinosa et al., 2009
	Bruguiera gymnorrhiza	Flooding period	Xiao et al., 2010

Table 1. Mangrove and mangrove associate species wood anatomical characters affected by different environmental variables.

Vessel density increases from low- to high-salinity areas in all species, from high- to low-flooding level in most of them, and from temporal- to prolonged flooding period. Increasing vessel density with salinity can be explained by an interference with nutrient uptake and auxin physiology with higher soil water salinity (Schmitz et al., 2006).
Numerous vessels promote protection against cavitation in stressed environments, avoiding cavitation damage when flooding level is higher, because a sporadic drought could occur (Yáñez-Espinosa et al., 2004).
The concentration of salinity effects on vessel density could be observed in the relationship of *Rhizophora mucronata* 23–30 vessels $mm^{-2,}$ and *Avicennia marina* 78-68 vessels $mm^{-2,}$ ranging from 26.4–49.2‰ in Gazi Bay, Kenya (Robert et al., 2009; Schmitz et al., 2006); *Avicennia*

germinans 30 – 52 vessels mm^{-2}, ranging from 3.2 – 30‰ of soil water in La Mancha lagoon, México (Yáñez-Espinosa et al., 2009); *Laguncularia racemosa* 7-16 vessels $mm^{-2,}$ ranging from 6–9‰ in an estuarine river in Nayarit, México (Yáñez-Espinosa et al., 2004).

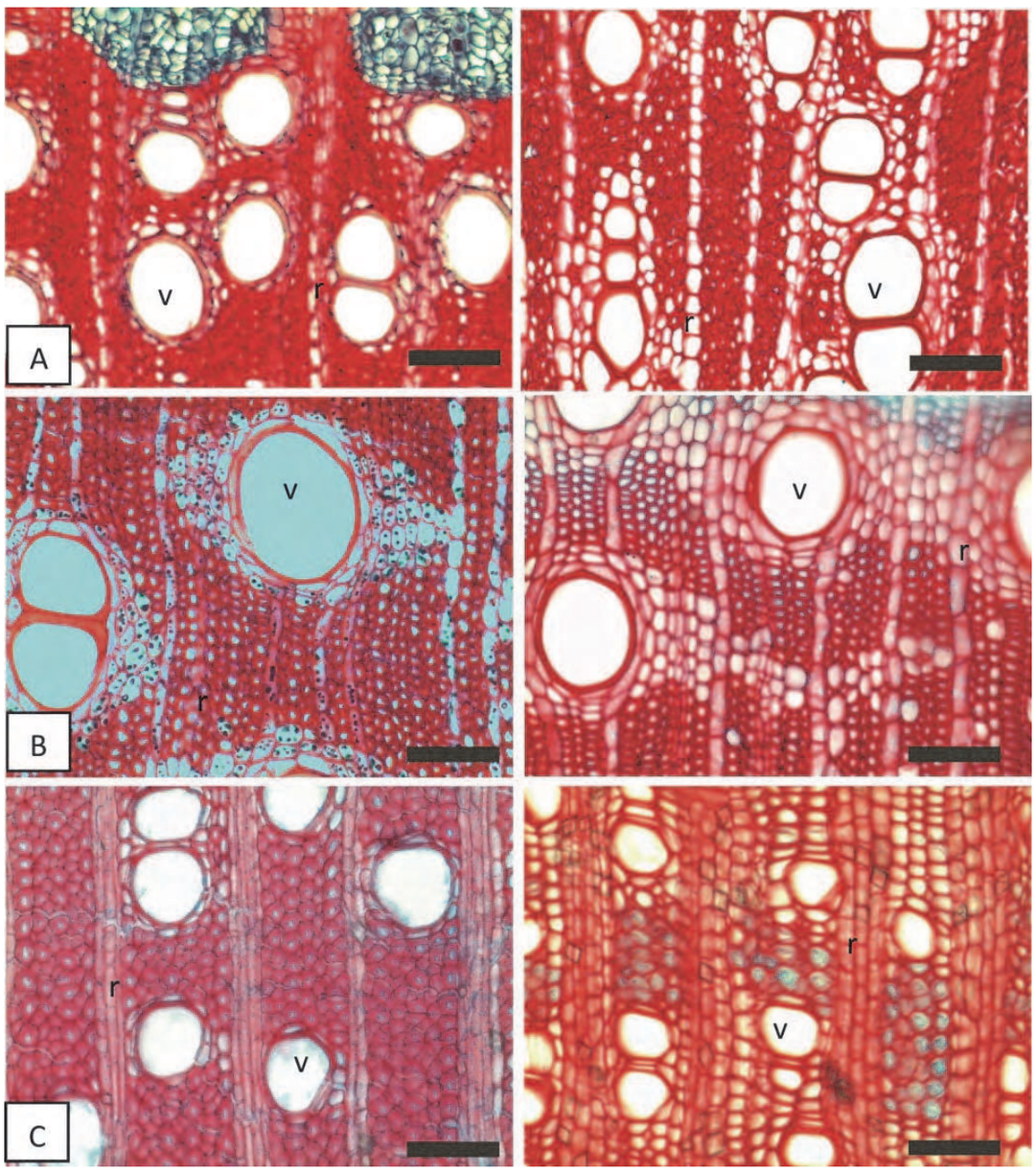


Fig. 3. *Avicennia germinans* (A), *Laguncularia racemosa* (B), and (C) *Rhizophora mangle* wood of trees growing in sites with lower (left) and higher (right) salinity. Differences in vessel density and diameter are present. Light microscope micrograph. Transverse section. v = vessel; r = wood ray; bar = 100 µm.

The stem water transport system consisting of a high vessel density, a high vessel grouping, small vessel diameters and short vessel elements in *Avicennia* and *Laguncularia* species, is contrasting with the water transport system of *Rhizophor*a species, suggesting to be safer

based on a physiological interpretation of the observed characteristics (Fig. 3). Structure modifications of *Bruguiera gymnorrhiza* seedlings of fiber wall thickness and length, and vessel diameter were reduced as flooding prolonged, suggesting distinct strategies for maintaining a balance between growth, conductive capacity, conductive safety and mechanical strength (Xiao et al., 2010). Lovelock et al. (2006a) suggest that over a range of species and sites, hydraulic conductivity in mangroves is constrained by salinity, with a variable relationship due to species differences (*Avicennia germinans* [2.13 kg m^{-1} s^{-1} $MPa^{-1} \cdot 10^{-4}$]; *L. racemosa* [0.81 kg m^{-1} s^{-1} $MPa^{-1} \cdot 10^{-4}$]), and to variation in nutrient availability.

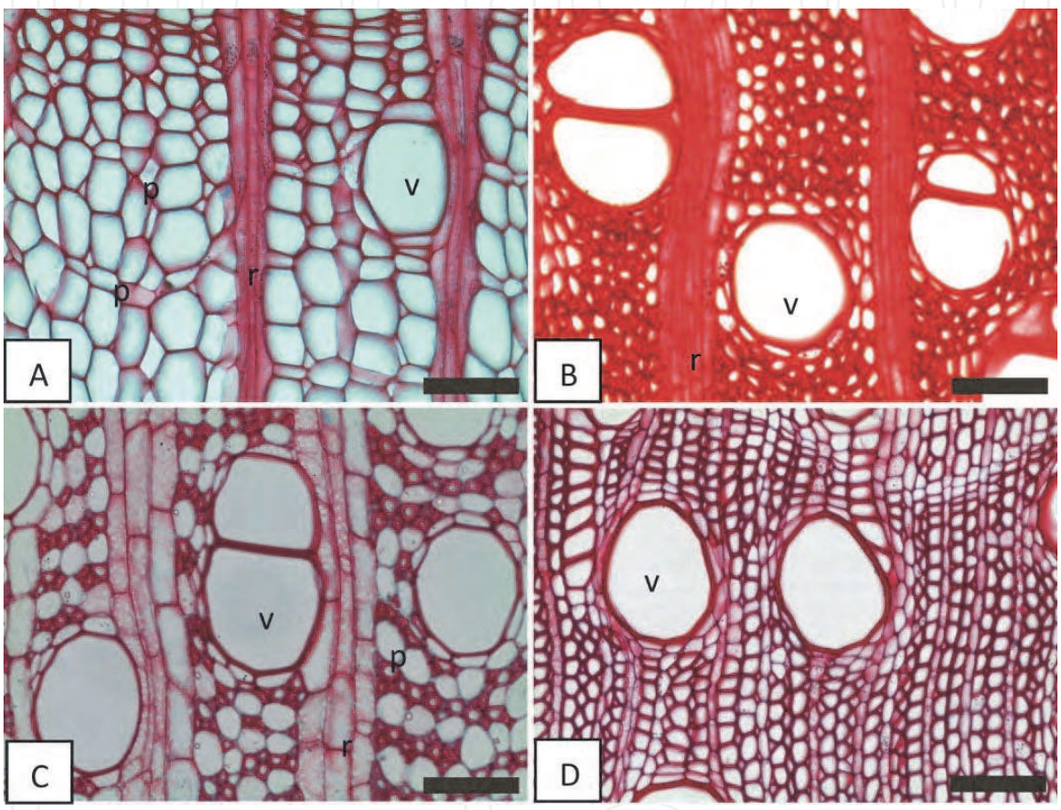


Fig. 4. The mangrove associate species *Annona glabra* (A), *Hibiscus tiliaceus* (B), *Pachira aquatica* (C), and *Rhabdadenia biflora* (D), showing vessels with wider tangential diameter than mangrove species. Light microscope micrograph. Transverse section. v = vessel; p = axial parenchyma; r = wood ray; bar = 100 µm.

Numerous mangrove associate species are more susceptible to modifications in flooding regime and salinity concentration, increasing vessel density like *Annona glabra*, from 4 to 7 vessels mm^{-2}. In general, vessel tangential diameter of mangrove associates is wider than those of mangrove species, suggesting an increment in vulnerability based on a physiological interpretation (Yáñez-Espinosa & Terrazas, 2001) (Fig. 4) (Table 2).
Nevertheless, abundant axial and radial parenchyma cells may be storing water in the stem, like *Annona*, *Pachira* and *Hibiscu*s species. This mechanism would compensate the effects of increased axial resistance on leaf water status, extracting water from storage in the stem and then sap flow would increase more slowly during the morning (Stratton et al., 2000).The mangrove associate vine, *Rhabdadenia biflora*, growing on *Avicennia germinans* mangrove tree

has scarce axial and radial parenchyma cells, however fiber diameter is wider like the other associate mangrove species.

Mangrove	Vessel tangential diameter (μm)	Mangrove associate	Vessel tangential diameter (μm)
Avicennia germinans	70	*Annona glabra*	93
Laguncularia racemosa	96	*Hibiscus tiliaceus*	122
Rhizophora mangle	73	*Pachira aquatica*	130
Conocarpus erectus	68	*Phyllanthus elsiae*	74
		Rhabdadenia biflora	93

Table 2. Comparison of average vessel tangential diameter from mangrove and mangrove associate species growing in Mexican mangrove forests (unpublished data).

Analysis of wood traits plasticity in some studies has identified hydraulic properties of trees as more plastic than those of leaf structural and physiological characters, concluding that hydraulic properties explain growth control.
The wide tolerance of mangroves wood traits to environmental gradient of salinity, soil texture and flooding conditions suggests that even if increases in relative sea level will eventually raise saturation and salinity conditions at ecotonal boundaries, mangroves are capable to advance or invade inland into freshwater marsh and swamp habitats (Doyle, 2003), modifying distribution and composition of the mangrove.

4. Modifications of bark structure in response to environmental factors

Prolonged flooding also affects bark anatomy of mangrove species, modifying the secondary phloem, rhytidome and periderm tissues, suggesting that prolonged flooding modifies vascular cambium and phellogen differently (Yáñez-Espinosa et al., 2008). Typical structural responses include formation of hypertrophied lenticels and adventitious root (Fig. 5), and increased aerenchyma development in the bark (Table 3).

Species	Rhytidome	Aerenchyma in rhytidome	Aerenchyma in collapsed phloem	Ray dilatation	Hypertro-phied lenticels	Adventitious roots
*Annona glabra**	++	++	++	++	++	++
*Hibiscus tiliaceus**	++	++	++	++	++	--
*Phyllanthus elsiae**	--	--	++	++	++	++
*Avicennia germinans**	--	--	--	--	++	--
*Laguncularia racemosa**	++	++	--	±±	++	±±
Conocarpus erectus•	++	++	--	±±	++	--
Pachira aquatica•	--	--	++	++	++	++

Table 3. Mangrove and mangrove associate species bark anatomical characters. ++ = present; -- = abscent; ±± = slightly present. * Data from Yáñez-Espinosa et al., 2008; • = Unpublished data.

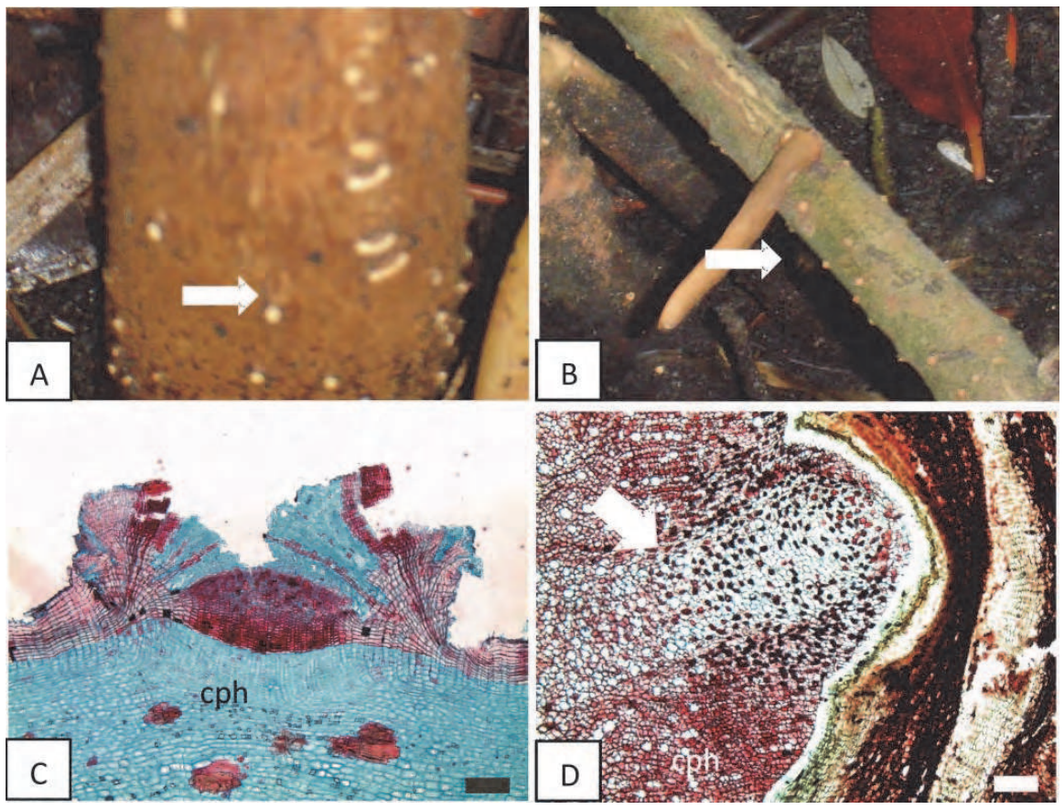


Fig. 5. Hypertrophied lenticels in the immersed portion of the stem of *Avicennia agerminans* (arrow) (A); and in the immersed stilt root of *Rhizophora mangle* (arrow) (B) macroscopic appearance; Light microscope micrograph. Transverse section. *Phyllanthus elsieae* hypertrophied lenticel in the immersed portion of the stem (C); *Annona glabra* adventitious root (arrow) in the immersed portion of the stem (D). p = periderm; cph = collapsed phloem; f = filling tissue; bar = 100 µm.

Mangrove species develop hypertrophied lenticels in the immersed portion of the stem, as well as mangrove associates tolerant to flooding, like *Annona glabra* (Mielke et al., 2005), excepting *Phyllanthus elsiae* (Euphorbiaceae), which develops hypertrophied lenticels above and below flooding level (Yáñez-Espinosa et al., 2008). Adventitious roots were present in the mangrove associate species *Annona glabra*, *Hibiscus tiliaceus*, *Pachira aquatica* and *Phyllanthus elsiae* (Mielke et al., 2005; Yáñez Espinosa et al., 2008). These species have not specialized roots like stilt roots or pneumatophores, then aeration depends on abundant hypertrophied lenticels and adventitious roots to tolerate prolonged or permanent flooding.
The importance of aerenchyma in the development of a continuous interconnected series of intercellular spaces is the most important adaptation to flooding in plants (Lambers et al., 1998). Trees without cork aerenchyma in their barks might develop larger air spaces in the phloem parenchyma, phelloderm or primary cortex (Roth, 1981), like *Rhizophora mangle* develops aerenchyma in phloem axial and radial parenchyma of collapsed region (Yáñez-Espinosa, unpublished data).
Although studies realized on bark rays show no statistical differences from short- to long-flooding period, mangrove species *Laguncularia racemosa*, *Avicennia germinans* and *Rhizophora mangle*, present shorter phloem rays under longer flooding period, may be associated with

the effect of prolonged flooding similar to that of drought. But mangrove associate *Annona glabra* tend to have lower rays under short-flooding period, may be due to anoxic conditions caused by prolonged flooding (Yáñez- Espinosa et al., 2001).
Increments in rays are related to enlargement of cells that could mobilize a higher oxygen volume and more photosynthates (Kozlowski et al., 1991). The intercellular space system of ray tissue is essential, because ray cells have indefinite viability and require gas exchange for metabolic activity (Carlquist, 1988) (Fig. 6).

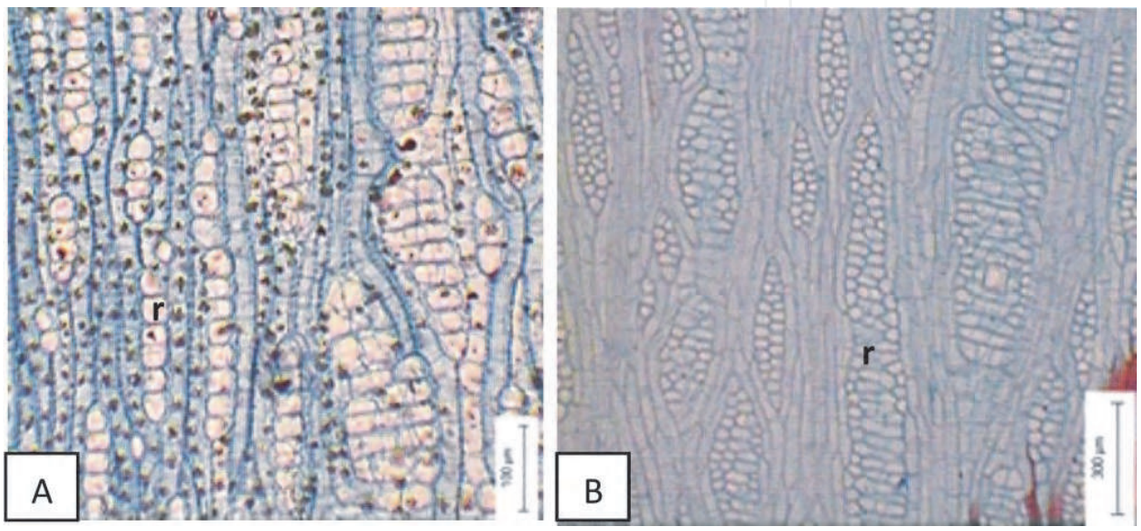


Fig. 6. Secondary phloem rays of *Laguncularia racemosa* (A) and *Annona glabra* (B) close to vascular cambium, showing a slightly dilatation. Light microscope micrograph. Tangential section. r = phloem ray.

Annona glabra, *Pachira aquatica* and *Hibiscus tiliaceus* develop aerenchyma in the rhytidome, phelloderm, and phloem parenchyma, which suggests a greater volume for aeration, particularly in the immersed portion of the stem. *Laguncularia racemosa* and *Conocarpus erectus* (Combretaceae) axial and radial parenchyma cells in the collapsed phloem region dilate slightly close to periderm, but develop abundant aerenchyma in the rhytidome. *Avicennia germinans* only develops rhytidome in the immersed portion of the stem and presents an aerenchymatous cork that may be the path connecting the aerial atmosphere with the immersed tissues (Fig. 7).
Even though aerenchyma and hypertrophy are the most common events related to flooding, each type of tissue responded differently, depending on the species. The mangrove and mangrove associate species respond to different flooding periods and then cohabit on a wide environmental gradient, suggesting that accelerated sea-level rise caused by global warming, would affect distribution of the species according to their particular tolerance.

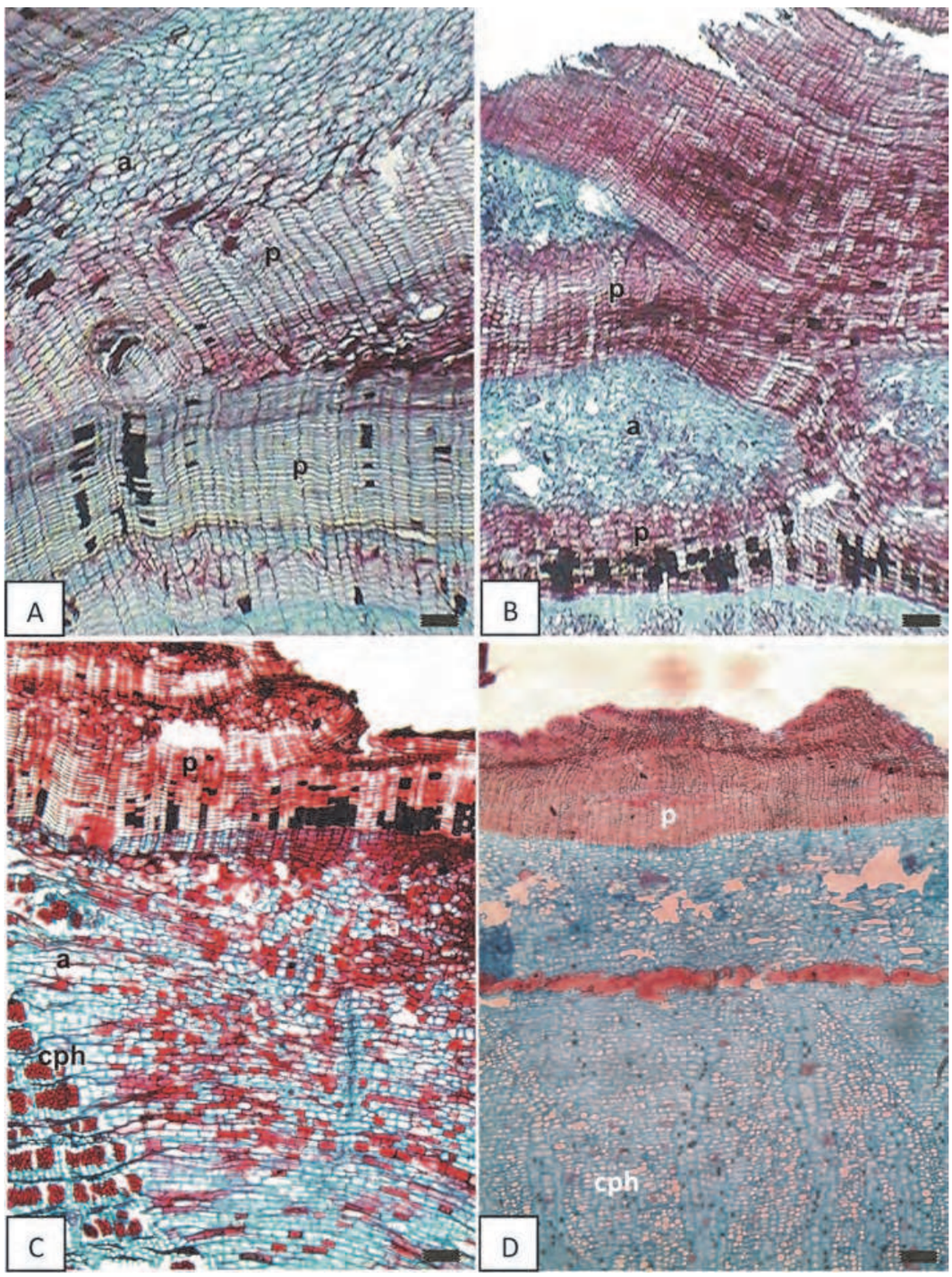


Fig. 7. *Annona glabra* aerenchyma in rhytidome of immersed portion of the stem (A), *Avicennia germinans* aerenchyma in rhytidome of immersed portion of the stem (B), bar = 200 µm; *Hibiscus tiliaceus* axial and radial parenchyma dilatation close to periderm (C), *Rhizophora mangle* aerenchyma close to periderm and dilatation of axial and radial parenchyma in collapsed phloem region (D). Light microscope micrograph. Transverse section. a = aerenchyma; p = periderm; cph = collapsed phloem; bar = 100 µm.

5. Modifications of leaf structure in response to environmental factors

Mangroves show many xerophytic adaptations that are evident in their leaves. Leaves are dorsiventral (Fig. 8), excepting *Lumnitzera racemosa*, where they are isobilateral and amphistomatic; the cells of the lower epidermis are larger than those of the upper surface, and water storage tissue is present in all the species, except *Aegialitis rotundifolia* (Seshavatharam & Srivalli, 1989; Tomlinson, 1986).

Experimental studies point to mangrove species-specific responses to increases in atmospheric CO_2 concentration. Increase in atmospheric CO_2 can be expected to improve mangrove tree growth, *i.e.* leaf area ratio increased with a decrease in humidity when *R. stylosa* was grown under elevated CO_2 (700 cm^3 m^{-3}) (Ball et al. 1997). However, elevated CO_2 (until 700 $\mu l l^{-1}$) did not affect leaf area of *Rhizophora mangle* seedlings (Farnsworth *et al.* 1996). In addition, increased CO_2 until 700 cm^3 m^{-3} did not affect leaf area of *Rhizophora apiculata* limited by high salinity, but did enhance leaf area when the plants were limited by humidity (Ball et al. 1997).

Responses of mangrove to sea-levels rise depend on reactions of individual plants, and some evidence exists on modifications of leaf structure in response to increasing flooding or waterlogging. *Bruguiera gymnorrhiza* and *Rhizophora stylosa* seedlings decreased leaf area intensely with decreasing tidal elevation (from 30-40 cm) in Yingluo Bay, a core zone within the Shankou Mangrove Reserve of Guangxi, China. Inversely, *Aegiceras corniculatum* and *Avicennia marina* seedlings increased leaf area with decreasing tidal elevation, at 10, 0, and - 30 cm (He et al. 2007).

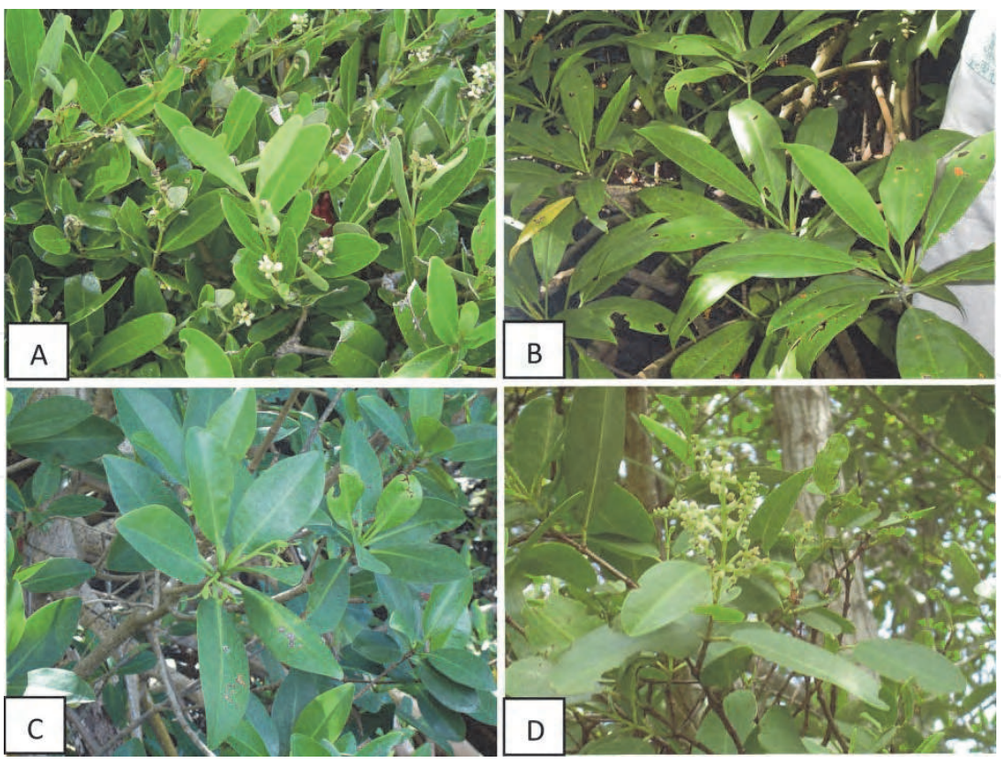


Fig. 8. Leaves with xerophytic adaptations of *Avicennia germinans* (A), *Bruguiera* sp. (B), *Rhizophora mangle* (C), *Laguncularia racemosa* (D).

In addition, leaf area of adult individuals from *Laguncularia racemosa*, *Rhizophora mangle*, *R. racemosa*, *R. harrisonii*, and *Avicennia germinans* was generally significantly larger for species growing in wet (dry season lesser than 1 month) than in dry sites (dry season of seven months) in the Caribbean coast of Venezuela (Medina & Francisco, 1997). Similarly, *Rhizophora mangle* seedlings in Belize decreased leaf area in plants under water (Ellison & Farnsworth, 1997). However, there are some species with leaf area unaffected by tidal flooding, like *Xylocarpus granatum* seedlings in the Federated States of Micronesia (Allen et al. 2003), as well as *Aegiceras corniculatum* and *Avicenia marina* seedlings in Yingluo Bay, China (He et al. 2007), and *Annona glabra* after 56 days of flooding showed no symptoms of stress, and there were no changes in total leaf area (2.20 m^2) (Mielke et al., 2005).
Mangrove leaf anatomy is very uniform matched by a suite of features common to most mangrove species, including the colorless "water storage" tissue, the short tracheids terminating vein endings, the marked absence of sclerotic vein sheaths, presence of sclereids, thickened outer epidermal wall strongly cutinized, thick mesophyll including the adaxial hypodermis layers, palisade parenchyma layers and spongy parenchyma (Tomlinson, 1986) (Fig. 9).

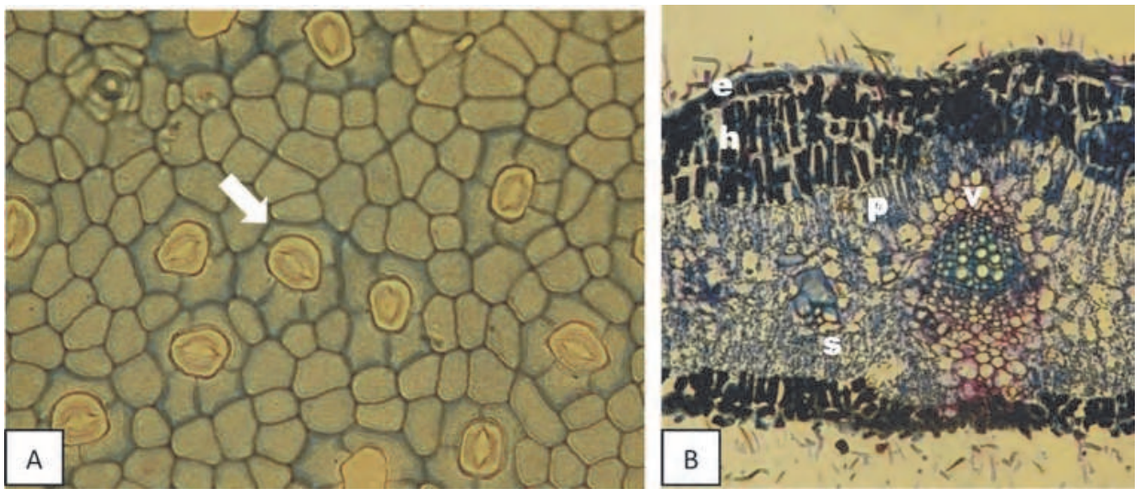


Fig. 9. *Conocarpus erectus L. (Combretaceae)* leaf epidermis showing stomata (arrow) (A), and showing dorsiventral structure: epidermis, adaxial hypodermis with two distinct layers, assimilating tissue below, and a vascular bundle. Light microscope micrograph .Paradermal (A) and transverse (B) section, by Guillermo Angeles. e = epidermis; h = hypodermis; p = palisade parenchyma; s = spongy parenchyma; v = vascular bundle.

Nevertheless, studies of modifications on leaf anatomical features under experimental conditions are scarce. Changes of *Avicennia marina* seedlings under experimental conditions were expressed in the progressive increase of upper and lower epidermis thickness to leaf thickness ratio and mesophyll to leaf thickness ratio with prolonged waterlogging duration, but prolonged waterlogging duration have negative effects on hypodermis thickness, leaf thickness, mesophyll thickness, palisade parenchyma thickness, palisade–spongy ratio, tangential vessel diameter and vessel wall thickness in leaf tissue (Xiao et al., 2009), contrary to *Bruguiera gymnorrhiza* seedlings grown under experimental conditions of simulated semidiurnal tides with salinities of 15‰, after 12 h treatments, that showed declination in leaf thickness, palisade parenchyma thickness, spongy parenchyma thickness, xylem length

of the vascular system and number of vessels and vessel lines, up to 67.1%, compared with the 0 h treatments. However, the upper and lower epidermis and stomatal density of 12 h treatments showed increases of up to 104.3% over the 0 h treatments. The cuticle and percentage of intercellular spaces in spongy tissue decreased significantly with waterlogging duration at first and then increased. These results suggest that modifications in the anatomical features of *B. gymnorrhiza* as a result of periods of immersion longer than 2 h, would result in a reduction of photosynthesis and water transport (Wang et al., 2007). However, anatomical characters of *Rhizophora mangle* leaves did not differ when Ellison & Farnsworth (1997) simulated a 16 cm decrease and increase of sea-level.

There are many studies indicating the importance of salinity for mangrove species as well as evidence that various mangroves may have different tolerances and optimal salinity (Ball et al., 1997; Ball, 2002). The physiology of their ability to survive in saline environment may shed light on the evolution of mangroves from terrestrial species (Parani et al. 1998).

Leaf structure traits reflect the long-term adaptive strategy successfully (Cunningham et al., 1999; Wang et al,. 2003; Wright et al., 2004). Salinity affects ion accumulation in leaves, thereby membrane permeability and chlorophyll synthesis (Cram et al., 2002). In addition, with increase in salinity, carbon allocation to roots increases at the expense of leaf area (Ball 1988). Leaf area decreased at higher salinity concentrations (47-92‰) for *Laguncularia racemosa* in the Sontecomapan lagoon in Veracruz, Mexico (Medina et al., 1995), and for *Sonneratia alba* at 100‰ sea water and *S. lanceolata* seedlings at 50‰ sea water, in northern Australia (Ball & Pidsley 1995). The average leaf area of *Rhizophora apiculata* and *R. stylosa* propagules in the Northern Territory of Australia decreased with an increase in salinity from 125 to 350 mol m^{-3} NaCl, with *R. apiculata* being the more sensitive (Ball et al. 1997). For *Bruguiera parviflora* in Bhitarakanika mangrove forest, Orissa, India, leaf area was significantly less at 400 mM NaCl as compared to 0 mM NaCl (Parida et al., 2004), for *Laguncularia racemosa* in Sepetiba Bay, Rio de Janeiro, Brazil, which showed significant lower leaf area in salt marsh plants with high soil salinity and low nutrient input, than in riverside plants with daily tidal fluxes and consequently high nutrient input, that can be associated with environmental restrictions of their habitat (Lira-Medeiros et al., 2010), and for *Rhizophora mucronata* seedlings in the 45 PSU in South Africa (Hoppe-Speer et al., 2011).

In some species, leaf area is unaffected by salinity concentrations, *i.e. Rhizophora mangle*, which had similar leaf area in plants from El Real (at 47-92 ‰) and from La Boca (at 0-22 ‰) in the Sontecomapan lagoon in Veracruz, Mexico (Medina et al., 1995), and *Xylocarpus granatum* seedlings at 0.5 and 23 ‰ salinity in the Federated States of Micronesia (Allen et al,. 2003).

Increasing flood level and salinity due to sea-level rise, may result in mangrove leaves morphology and anatomy modifications, considering that extant studies show perceptible modifications, although not all species are affected (i.e. *Rhizophora* and *Xylocarpus).* Modifications include increasing stomatal density, reduction of leaf area and thickness, palisade parenchyma thickness, number of vessels and vessel diameter in leaf tissue, whose may generate the reduction of transpiration, photosynthesis and water transport.

6. Modifications of root structure in response to environmental factors

The anatomy of mangrove roots has been extensively studied in relation to development and function (Tomlinson, 1986). Prolonged flooding alters soil physical and chemical properties, as well as bacterial composition, directly affecting species roots (Rajaniemia &

Allison, 2009). Root vascular system affects stem vascular system and leaves structure of mangrove species, even when there are present modified roots like pneumatophores, cable, knee and stilt roots (Visser & Pierik, 2007).

Pneumatophores arise vertically from cable roots and have evolved independently in at least five mangrove families and genera: *Laguncularia* (Combretaceae), *Avicennia* (Avicenniaceae), *Bruguiera* (Rhizophoraceae), *Xylocarpus* (Meliaceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson 1986). They have abundant lenticels, and aerenchyma may account for up to 70% of root volume (Hogarth, 1999) (Fig. 10).

The normal pneumatophores of *Sonneratia* and *Avicennia* are slender and cone shaped, standing erect and aligned on the cable root, of 1-20 m or more in length, which spread horizontally in the soil. *Sonneratia alba* trees in Ranong and Phang-nga Bay, Thailand, produce pneumatophores 25-35 cm long, 4–6 cm thick at the base, with a regular conical shape. However, pneumatophores of *S. caseolaris* may become 1.2 m tall and 12 cm thick at the base. The cable roots morphology and length are more related to soil structure and tidal regime than tree variables, as well as pneumatophores that may be deformed due to massive waves, sediments deposition, and other environmental changes (Nakamura et al., 2004).

Avicennia marina in Kenya has the ability to adapt its pneumatophores to micro-topographical irregularities in the regularly sloping intertidal zone. Significantly higher pneumatophore densities and total pneumatophore lengths are present in the center of the landward depression, and significantly lower lengths in the center of the seaward depression (Dahdouh-Guebas et al., 2007), suggesting that cable roots and pneumatophores morphology, density and length may be affected by sea-level rise. *Rhizophhora mangle* underground roots are in permanently hypoxic or anoxic environment, and then vertical roots have the role of supplying oxygen to underground roots, reaching adequate gas exchange at low tide. Air passes through aerenchyma tissue, constituted by air spaces running longitudinally the root axis (Hogarth, 1999) (Fig. 10).

Experiments with *Avicennia marina* have demonstrated that oxygen concentrations decrease from 16 to less than 2% within one hour after exposure to hypoxic conditions. The roots increased then the capacity for alcoholic fermentation, although ethanol concentration was low in intact and hypoxic roots, but may have diffused from the roots into the surrounding substrate (McKee & Mendelssohn, 1987). *Avicennia germinans* roots, commonly found in anaerobic substrate, create oxidized rhizospheres substantially larger, but when air cannot enter the root system through the pneumatophores, the rhizospheres become as reduced as nearby non-vegetated soil. *Rhizophora mangle* have no effect on the oxidation state of surrounding anaerobic soils (Thibodeau & Nickerson, 1986).

Studies realized in *Laguncularia racemosa* cable roots and pneumatophores showed that cable roots are very efficient for water transport, and that this occurs mainly through the external vessels of the secondary xylem (Angeles et al., 2002). The development of a massive root system under soil flooding conditions in *Annona glabra* can be a mechanism to compensate for the high resistance to water flow in the roots (Mielke et al., 2005). However, more studies on mangrove root water transport are necessary to understand hydraulic properties of the whole plant system.

Sea-level rise caused by global warming may affect mangrove roots in different ways, depending of different functional root types (McLeod & Salm, 2006). Lenticels in the aerial roots have the role of supplying oxygen to underground roots, then if a rapid increment of sea-level occurs, pneumatophores of *Sonneratia* and *Avicennia* may have not the capacity of

increase pneumatophore density and length fast enough to avoid oxygen concentration decrease, producing death of the plant. However, *Rhizophora* aerial roots could not be affected, because lenticels would remain above sea-level.

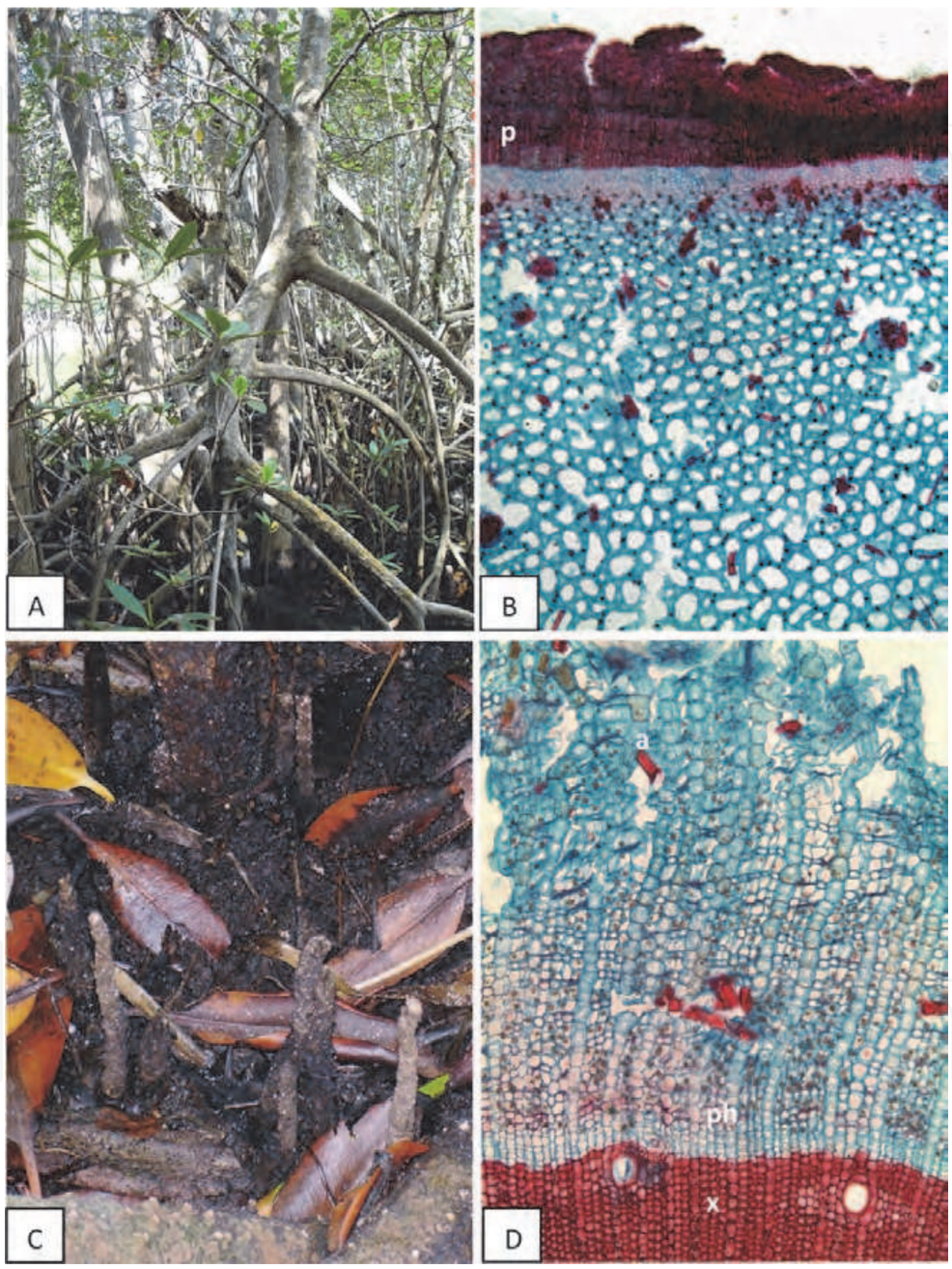


Fig. 10. *Rhizophora mangle* stilt roots (A); Light microscope micrograph of aerenchyma tissue close to periderm in a *R. mangle* aerial root (B); *Avicennia germinans* pneumatophores (C); Light microscope micrograph of dilated parenchyma tissue in *Laguncularia racemosa* pneumatophore (D). p = periderm; a = aerenchyma; x =secondary xylem; ph = secondary phloem; bar = 100 μm.

7. Modifications of growth in response to environmental factors

Growth of a plant is the increment in dry mass, volume, area or length as a result of division, expansion and differentiation of cells, determined by the interaction of photosynthesis, long-distance transport, respiration, water relations, and mineral nutrition (Lambers et al., 1998). Total above-ground biomass varies widely being highest at low latitude and declining northward and southwards from the equator. Undisturbed *Rhizophora* forests in northern Australia may reach up to 700 t ha^{-1} dry weight, but in old mangrove forests of South-east Asia range from 500 to 550 t ha^{-1} dry weight (Hogarth, 1999). However, the growth rate of mangroves is critically related to the availability of water to the trees and this is reflected in the soil water content and soil salinity (Field, 1995).

7.1 Biomass

The relative growth rate of *Bruguiera gymnorrhiza* decreased significantly with waterlogged time, with the highest value found for drained plants and the lowest in plants less than 12 weeks waterlogging. On the contrary, no significant difference was found between waterlogged and drained *Kandelia candel* plants. The shoot to root biomass ratio of *K. candel* increased when subjected to 8 or 12 weeks waterlogging but little change was recorded in *B. gymnorrhiza*, indicating a shift in biomass allocation from roots to shoots in *K. candel* under prolonged waterlogging but not in *B. gymnorrhiza*. Chlorophyll contents of *K. candel* increased more rapidly in response to waterlogging than *B. gymnorrhiza*. These physiological indicators supported the hypothesis that *K. candel* is more tolerant to waterlogging than *B. gymnorrhiza (*Ye et al., 2003*).* In mangrove associate *Annona glabra* seedlings, the high survival and growth rates are directly related to the capacity to develop a massive root system and maintain a high stomatal conductance and net photosynthesis under soil flooding. In most flood-tolerant species the initial decrease in stomatal conductance is followed by recovery, like in *A. glabra* seedlings under flooding treatment, where stomatal conductance was reduced to 65% of control levels with four days of flooding, but reached 152% at day 56. Significant increases in root, stem and total plant biomass and in collar diameter were observed. These results suggest that *A. glabra* is highly adapted to both periodic and permanent flooding (Mielke et al., 2005).

The effect of salinity on the growth of *Avicennia germinans* propagules collected in Cuman´a, Venezuela, was experimentally determined comparing the relative growth rates (RGR) after 27 weeks, reaching a maximum 10.4 mg g^{-1} d^{-1} in 170 mol m^{-3} NaCl, followed by the 0 and 430 mol m^{-3} NaCl treatments (8.4 and 7.9 mg g^{-1} d^{-1} respectively). At the same period the RGR of plants grown in 680 and 940 mol m^{-3} NaCl were 47 and 44% lower than that of plants grown in 170 mol m^{-3} NaCl. Higher salt tolerance of *A. germinans* in relation to other mangrove species might be due to low relative growth rates and high water-use efficiency over a wide salinity range. The decline in RGR with increasing salinity was clearly associated with a decrease in net assimilation rate (Suárez & Medina, 2005).

Also nutrient deficiency is relevant, when comparing dwarf and taller fringing tree forms of *Rhizophora mangle* in Belize, allow identifying trait plasticity in hydraulic properties of trees as more plastic than those of leaf structural and physiological characteristics, implying that hydraulic properties are significant in controlling growth in mangroves. Improvement of P deficiency reduced the structural and functional distinctions between dwarf and taller fringing tree forms, releasing trees from hydraulic limitations (Lovelock et al., 2006b).

Topography would be relevant if tidal effect would change. In one experiment, seven mangrove species *Rhizophora mucronata, R. apiculata*, *Bruguiera cylindrica*, *Ceriops tagal*, *Sonneratia alba*, *Avicennia officinalis* and *Xylocarpus granatum*, were planted at various topographic sites in an intertidal zone of Phang Nga, Thailand. The experimental plots were on a slope and showed a maximal elevation difference of 1.8 m, submerged with 2-3% saline water twice a day. Survival and growth performance of seedlings were measured differing and showing increasing tolerance to higher tidal inundations in the order: *R. mucronata, S. alba, R. apiculata, A. officinalis, C. tagal, B. cylindrica* and *X. granatum* (Kitaya et al., 2002).

7.2 Growth rings

Secondary growth, or secondary tissues added lateral to stems and roots increasing their thickness, are produced by the vascular cambium. In secondary xylem or wood, growth rings may be produced during one season, and usually they are delimited by growth boundaries (Beck, 2010) (Fig. 11). In mangroves, the highly dynamic intertidal environment and the overriding ecological drivers difficult the existence of growth rings. Nevertheless, climatic conditions that result in a range of soil water salinity experienced over the year are a prerequisite for the formation of growth ring (Robert et al., 2011).

Recently, annual growth rings were discovered in *Rhizophora mucronata* in Kenya, but the ring boundaries are indistinct and growth ring consists of a low vessel density earlywood, produced during the rainy seasons, and a high vessel density latewood, produced during the dry season. Intra-annual differences in the vessel features revealed a trade-off between hydraulic efficiency (large vessels) during the rainy season and hydraulic safety (small vessels) during the dry season (Verheyden et al., 2005).

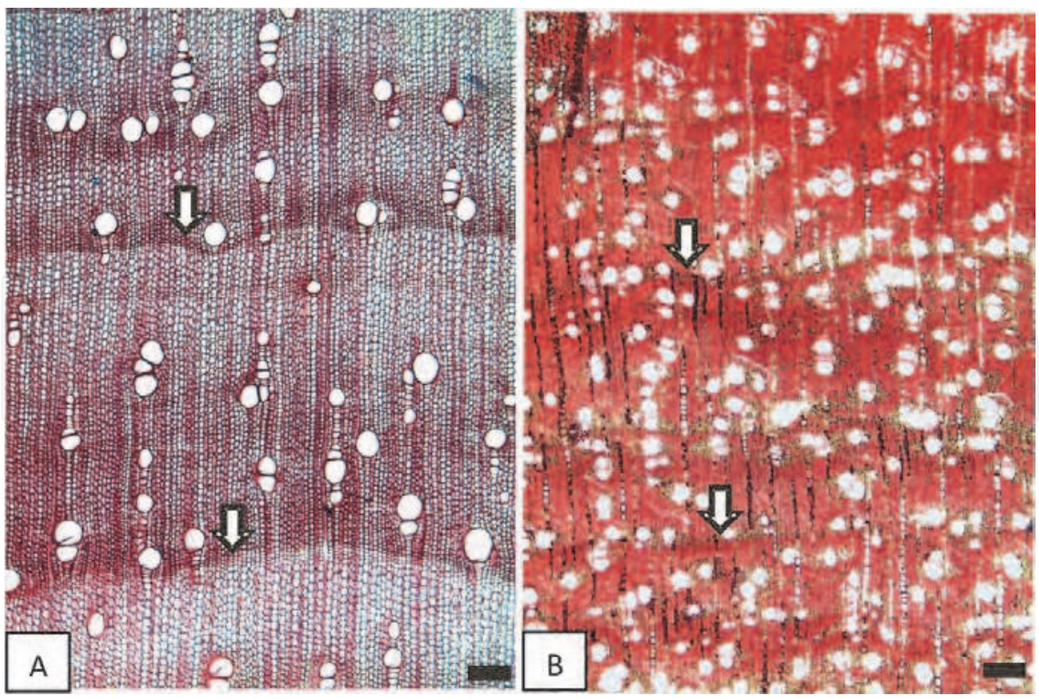


Fig. 11. Light microscope micrograph growth boundaries (arrows) distinct in *Pachira aquatica* (A), slightly defined in *Conocarpus erectus* (B). bar = 100 µm.

Laguncularia racemosa from Rio de Janeiro, Brazil, also present distinguishable growth rings macroscopically, with alternating early wood formed between spring and autumn and consists of layers with abundant paratracheal axial parenchyma, while late wood is formed in winter and consists of narrower dark layers which are basically fibrous zones with scarce paratracheal axial parenchyma. The occurrence of a dry season in winter could be the seasonal factor determining the formation of annual rings (Duque Estrada et al., 2008). These results are relevant because a factor that may be important for the future of mangrove ecosystems is any change in precipitation (Field, 1995).

Sea-level rise might reduce survival and growth performance of mangroves seedlings, expressed as biomass decrement due to variation in flooding and salinity. However, initial decrease is followed by recovery, suggesting that mangrove species are adapted to both periodic and permanent flooding, and high salinity levels. Secondary growth apparently is determined by seasonal precipitation, expressed by the formation of growth rings. Considering that precipitation rates are predicted to increase by about 25% by 2050 in response to global warming (McLeod & Salm, 2006), changes in precipitation patterns may affects at local scale the patterns of freshwater inflow, diminishing salinity concentration in consequence, and affecting mangroves growth and their distribution.

8. Conclusions

Modification of anatomical and morphological patterns of wood, bark, leaf and root of mangrove and mangrove associate species are predictable as result of sea-level rise caused by global warming. Sea-level rise will alter environmental conditions, increasing salinity, flooding level, and altering the rate of deposition of sediment. These species show a wide plasticity in structural and physiological patterns, allowing them to survive and prosper in this ecosystem exposed to a dynamic environment, and occasionally subjected to extreme events, like hurricanes and massive waves. General tendencies suggest a strong association between structure patterns and environmental gradient (salinity, flooding level and periodicity, and soil structure). Cell and organ size decrease while salinity and flooding or waterlogging increases.

Nevertheless, each species has its specific tolerance range, allowing to success along different zones of the mangrove ecosystem with particular geomorphology and environmental conditions, causing a change in forest species composition and dominance, allowing expanding distribution of more tolerant species and limiting or suppressing those less tolerant, particularly in places where sedimentation rates are low. Some studies suggest that mangroves can adapt to sea-level rise if it occurs slowly, there are sufficient space for distribution expansion, and the other environmental factors are tolerable. They may adapt growing inland on more elevated areas, probably increasing their distribution, but if these not occur fast, mangroves adaptation to stressing factors will result in smaller trees until disappearing.

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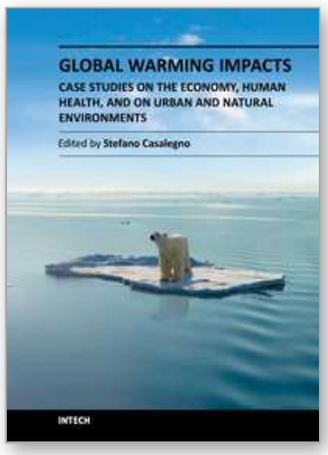
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This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic. The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that this book will stimulate further developments in relation to the impacts of changes in the global climate.

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