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ORIGINAL ARTICLE

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Effects of flooding on wood and bark anatomy of four species in a mangrove forest community

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Abstract Variation in the wood and bark anatomy of the dominant species of a mangrove forest community in Mexico was evaluated in relation to some environmental factors, and their physiological adaptations to salinity and flooding period are discussed. The forest is characterized by three zones according to the presence of dominant tree species and flooding periodicity. Vessel arrangement and wood and bark ray height are strongly associated with flooding zones where trees are growing. Variance analyses revealed significant differences among zones for these anatomical characteristics. Soil texture and water salinity were the most useful parameters for the prediction of values of anatomical characteristics. More abundant vessels in radial multiples in a shorter flooding period suggest a functional advantage of multiple vessel groups. Taller wood and bark rays in response to prolonged flooding period can be attributed to anoxic conditions. Among zones, significant differences in the vulnerability index of the species were detected, but not with respect to relative conductivity. Significant differences among zones exist for wood and bark characteristics involved in vertical and horizontal water transport, photosynthates and gas exchange.

Keywords Mangrove · Flooding · Wood anatomy · Bark anatomy · Mexico

Introduction

Ecological interpretations of secondary xylem and phloem are based on correlations among anatomical characteristics and environmental factors (Baas 1982). Well-known trends have been established for species, genera, families and regional floras (Baas 1986; Carlquist 1988; Zhang et al. 1992). However, few studies have been carried out on mangrove species, especially in which their wood structure is correlated with physiological features which allow plants to tolerate or avoid flooding and salinity (Panshin 1932; Jansonnius 1950; Van Vliet 1976; Tomlinson 1986; Carreras 1988). Moreover, only a few studies have examined bark in this community (Karstedt and Parameswaran 1976; Roth 1981).

In Mexico, the mangrove forest community is dominated by a few species; its floristic and structural composition varies depending on its localization regarding the seashore (Flores et al. 1971). The studies conducted by Lopez-Portillo and Ezcurra (1989) and Valdez (1994) showed that a floristic and structural gradient is defined by the geomorphological and hydrological local conditions. However, studies that correlate wood and bark structure with environmental factors have not been carried out.

In this study we evaluate the variation in the wood and bark anatomy of the dominant species of a mangrove forest community in relation to some environmental factors, and we discuss their physiological adaptations to salinity and flooding periodicity.

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Materials and methods

The study area is located in the estuarine river El Conchal in the state of Nayarit, Mexico (21°31′00″–21°36′19″N; 105°11′26″–105°16′46″W). The area has a mean annual temperature of 25°C and 1436 mm annual rainfall, with a dry season of 8 months (October–May) and a rainy season of 4 months (June–September). This forest is mainly composed of *Rhizophora mangle* L., *Laguncularia racemosa* (L.) Gaertn.f., *Avicennia germinans* (L.) Stearn, and *Annona glabra* L. which is replacing *R. mangle* in some estuarine channels. This mangrove forest was subdivided into three zones according to flooding periodicity (Valdez 1994). *R. mangle* and *A. glabra* have the highest importance value in sites where flooding periodicity is >8 months, *L. racemosa* in sites with 8 months of flooding, and *A. germinans* in sites with the lower flooding periodicity (Table 1). We selected two sites per zone (flooding periodicity) and in each site we sampled three–five trees of the dominant and associated species (Table 1). The samples were obtained from those trees which had the largest diameter and

Table 1 Distribution of dominant and associated species in sampled sites and some site features in El Conchal estuary, Nayarit, Mexico. *d* dry season, *r* rainy season

Flooding periodicity	Sampled sites	EC (mmhos cm^{-1})	pH	Sand (%)	Silt (%)	Clay (%)	Species	Importance value	Sampled trees	Diameter (cm)	Height (m)
FZ4 (4 months)	2	10.6–12.9	5.9–6.5	30–65	9–29	26–41	*Avicenia germinans*	59.2	6	14.2±1.4	10.6±0.9
		(d) 13–21					*Laguncularia racemosa*	29.6	6	20.5±2.2	14.8±1.3
		(r) 12–15					*Annona glabra*	15.0	5	23.8±3.3	11.2±0.6
FZ8 (8 months)	2	12.5–15.0	6.4–6.5	17–30	13–14	57–69	*L. racemosa*	76.1	6	21.8±2.2	16.0±1.9
		(d) 16–18					*Rhizophora mangle*	21.5	6	19.1±3.2	11.3±0.6
		(r) 16–17					*A. germinans*	11.8	6	14.0±1.9	11.8±1.0
FZ>8 (>8 months)	2	3.3–14.4	6.4–6.9	17–54	5–22	24–76	*R. mangle*	54.3	6	16.8±1.4	12.7±2.7
		(d) 5–20					*L. racemosa*	45.7	6	23.8±2.3	14.7±2.7
		(r) 2–16					*A. glabra*	60.1	5	23.0±1.1	7.0±0.4

were the tallest in each site for each species during January (Table 1), when the flooding level was at its lowest. The samples were cut with a machete at a height nearly 1.30 m above ground level and with a north orientation. Each sample included bark, vascular cambium and wood. All the samples were immediately fixed in formalin-ethanol-glacial acetic acid. Two days later the samples were washed with tap water and stored in glycerin-ethanol-water (1:1:1) until sectioning.

Transverse, radial and tangential sections including wood, vascular cambium and bark were obtained with a sliding microtome. Additional tangential serial sections from noncollapsed phloem to rhytidome were cut. Section thickness depended on the species characteristics and varied from 40 µm in *A. germinans* to 70 µm in *R. mangle*. For each sample unbleached and bleached sections were stained with safranin-fast green (Johansen 1940) and mounted in synthetic resin. Macerations were prepared using Jeffrey's solution (Berlyn and Miksche 1976). Temporary slides were prepared to gather data on vessel elements and fibre lengths.

Thirteen quantitative wood characteristics and four bark characteristics were evaluated (Table 2). Twenty-five linear measurements per sample were carried out for eight wood characteristics and three bark ones. Number of vessels, percentage of solitary vessels and percentage of vessels in radial rows or clusters were calculated in 25 fields of 1 mm^2, and number of rays in wood and bark in 25 intercepted lines of 1 mm. All measurements and counts were carried out with the image analyser Image-Pro Plus version 3.1 (Media Cybernetics 1997).

Sieve tube element length was not measured, as it is considered that vessel elements and sieve tube elements have a common origin in the cambial initial cells (Esau 1985) and it has been proven that they are similar in length (Terrazas 1995; Orduño and Terrazas 1998).

The influence of environmental conditions on characteristics (vessel diameter and vessel number) associated with water conduction was evaluated through relative conductivity (Zimmermann 1983) and the vulnerability index (Carlquist 1977). The relative conductivity (RC) was calculated from a unit of secondary xylem using a Hagen-Poiseuille modified equation (Fahn et al. 1986): RC=r^4FRE; where: r=vessel radius and FRE=vessel frequency. The vulnerability index (V) was calculated to estimate susceptibility to damage during water conduction of wood, as proposed by Carlquist (1977): V=VAT/FRE; where: VAT=vessel diameter and FRE=vessel frequency (numerous and narrow vessels give the plant protection against cavitation, especially in stress environments, while fewer and wider vessels are more susceptible to cavitation).

The possible effects of flooding on wood and bark anatomical characteristics were evaluated by several site variables. For each site, data on flooding period (months), flooding level (centimetres; mean annual, dry and rainy seasons), pH of interstitial water, electrical conductivity (mmohs cm^{-1}) as an indicator of salinity (mean annual, dry and rainy seasons) and soil texture (sand, silt and clay particles percentage) were gathered (Table 1). Flooding period and flooding level were observed directly in the field. The pH was measured with a pH meter, model ATC PICCOLO (Hanna Instruments) and the electrical conductivity was read on a portable digital meter model TPS LC84. Soil texture was determined by standard laboratory techniques. Valdez (unpublished data) provided soil and interstitial water data for the entire year, and mean values per each sampled site are given in Table 1.

Data were natural logarithm or square-root transformed to carry out the statistical analyses. A canonical discriminant analysis (CANDISC) was applied to all species, including anatomical characteristics common to all species and site variables. This analysis allowed us to identify a subset of characteristics that separate zones to the maximum and identify the relative contribution of each characteristic to their separation. The ray characteristics related with their width (microns and number of cells) and height (number of cells) were excluded, because they are inherent in each species and are not comparable (Yañez-Espinosa 1999). Total fiber diameter and vessel tangential diameter were also excluded be-

Table 2 Anatomical characteristics and site variables used in canonical discriminant analysis (CANDISC) and their partial contribution to the functions expressed by standardized coefficients of discriminant functions

Characters	Function coefficients	
	Function 1	Function 2
Wood		
Fibre lumen diameter (µm)	0.9775	0.3330
Fibre wall thickness (µm)	–0.0202	0.4792
Vessel lumen diameter (µm)	1.0180	0.0044
Vessel wall thickness (µm)	0.1554	–0.3115
Vessel number per mm^2	0.0833	–0.3009
Solitary vessels (%)	–5.9328[a]	–0.0129
Radial multiple vessels (%)	–5.5413[a]	0.7264
Clustered vessels (%)	–1.8093	0.0677
Pit diameter (µm)	0.3005	0.2764
Ray height (µm)	–2.3551	3.7078[a]
Ray number per mm	0.4842	0.0990
Fibre length (µm)	–0.7884	1.3235
Vessel element length (µm)	2.2723	–1.0949
Bark		
Sieve tube diameter (µm)	–0.9341	0.4529
Phloem ray height (µm)	2.2654	–2.5984[a]
Phloem ray number per mm	0.2232	1.1525
Periderm thickness (µm)	1.1820	–0.4291
Site variables		
pH	1.9427	0.4739
EC (mmhos cm^{-1})	1.2769	0.9833
Flooding level (cm)	1.3867	0.4373

[a] Characteristics with a high contribution to centroid separation among zones

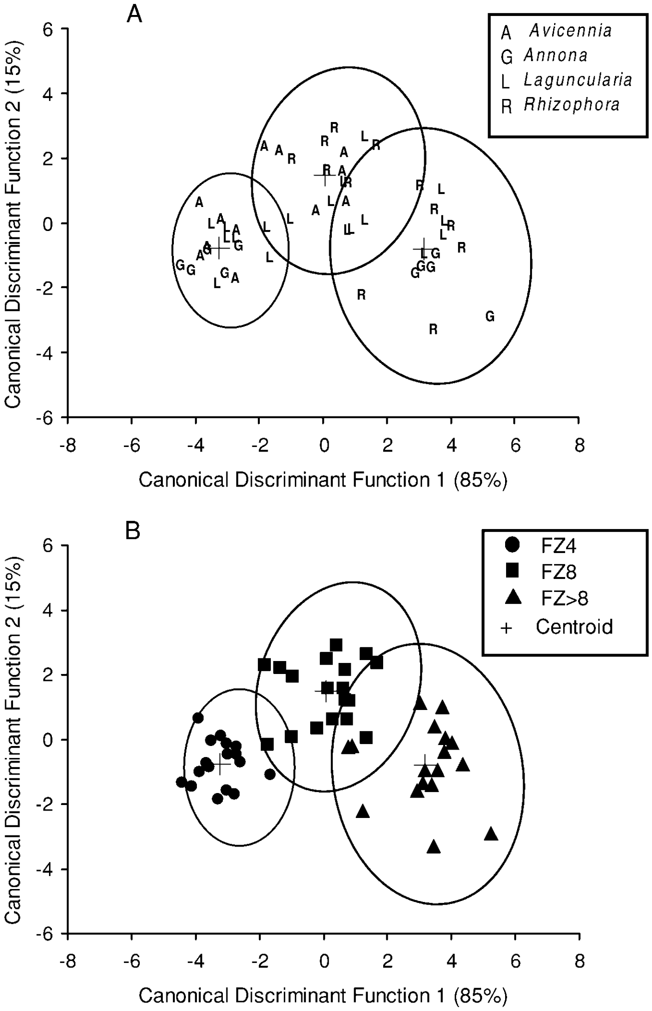

Fig. 1A, B Ordination of individual trees in the three flooding zones using two canonical discriminant analysis functions. **A** Species identity, **B** flooding zones

cause they tend to be similar among species, nevertheless, lumen percentage and wall thickness were included for both vessels and fibers, because they differ among species and were more sensitive to the zone parameters studied (Yañez-Espinosa 1999). A discriminant classificatory analysis (DISCRIM) was applied to verify the zones determined.

Significant differences among means of those anatomical characters identified by CANDISC were evaluated by variance analyses using the model II of aleatory effects for nested sampling (Snedecor and Cochran 1970). Differences among means were compared and segregated by Duncan's test (P<0.05). The same analyses were also applied to each species to identify its contribution to the opposing differences for the characteristics in each zone. Stepwise multiple lineal regression analyses were performed between site variables and those anatomical characteristics identified by CANDISC. All statistical analyses were performed with SAS software (SAS 1989).

Results

Discriminant analysis

The CANDISC analysis showed that two discriminant functions explained 100% of the total variation, contributing significantly to the separation among mangrove zones for the four species (Wilks' λ: P<0.0001, n=52). The first function (eigenvalue of 7.1376) explained 85.26% of the total variation and the second (eigenvalue of 1.2341) explained all the remaining variation. Also, DISCRIM analysis showed that the centroids of each zone were significantly different (P<0.0001) and 100% of the FZ4, 94% of FZ8, and 88% of FZ>8 observations were correctly classified (Fig. 1). Anatomical characters that contributed significantly to the separation of zone centroids were percentage of solitary vessels, percentage of vessels in radial multiples, and wood and bark ray height (Table 2) and their mean values for species per zone are given in Table 3.

Table 3 Multiple comparison of species' means (±SE) of wood and bark characteristics selected through CANDISC analysis

Species/variables	FZ4	FZ8	FZ>8
L. racemosa			
Solitary vessels (%)	68±4	69±4	66±5
Radial multiple vessels (%)	28±2	29±3	28±4
Wood ray height (μm)	270±9	284±21	253±14
Bark ray height (μm)	223±15	203±13	229±15
A. germinans			
Solitary vessels (%)	31±4	25±4	
Radial multiple vessels (%)	66±4	74±4	
Wood ray height (μm)	371±45	343±23	
Bark ray height (μm)	370±45	343±23	
R. mangle			
Solitary vessels (%)		78±2	66±7
Radial multiple vessels (%)		18±2	24±3
Wood ray height (μm)		1088±34*	869±92
Bark ray height (μm)		811±29	757±56
A. glabra			
Solitary vessels (%)	37±4*		58±3
Radial multiple vessels (%)	45±6*		26±3
Wood ray height (μm)	298±23*		344±9
Bark ray height (μm)	308±15		335±21

* P<0.05, Duncan's test

Analysis of variance

ANOVA revealed significant differences for percentage of solitary vessels among zones (F=12.97 df=2, P<0.0001, n=52) and percentage of vessels in radial multiples among zones (F=25.01 df=2, P<0.0001, n=52). Duncan's multiple comparison analysis corroborated the finding that statistically significant differences exist (P<0.05) among zones for both anatomical characters (Table 4). When applying the analyses to each species, only *Annona glabra* showed statistically significant differences among zones for percentage of solitary vessels (F=17.65 df=1, P<0.0030, n=10) and percentage of vessels in radial multiples (F=7.37 df=1, P<0.0265, n=10). Vessels are 33–41% solitary and 39–51% grouped in radial multiples in FZ4, whereas 55–61% solitary and 23–29% in radial multiples in FZ>8 (Table 3). Also, the analysis revealed significant differences for wood ray

Table 4 Multiple comparison of means (±SE) of wood and bark characteristics selected through CANDISC analysis

Characters	FZ4	FZ8	FZ>8
Solitary vessels (%)	46±5*	57±6	64±3
Radial multiple vessels (%)	46±5	40±6	26±2*
Wood ray height (μm)	314±20*	572±90*	497±76*
Bark ray height (μm)	300±22*	452±64	447±62

* P<0.05, Duncan's test

Table 5 Stepwise multiple regressions among anatomical characteristics and the variables measured. B Partial regression coefficient, R^2 determination coefficient

Variables	Regression estimators	
	B	R^2
Solitary vessels (%)		0.90
Clay (%)	0.80****	0.84
Rainy season flooding level (cm)	1.42****	0.06
Radial multiple vessels (%)		0.79
Dry season electrical conductivity (mmhos cm^{-1})	1.59****	0.76
Silt (%)	0.80*	0.03
Wood ray height (μm)		0.74
Clay (%)	7.58****	0.73
Sand (%)	2.15 n.s.	0.01
Bark ray height (μm)		0.78
Clay (%)	6.10****	0.75
Sand (%)	2.52*	0.03

* P<0.05, ****P<0.0001; *n.s.* non significant

height among zones (F=33.01 df=2, P<0.0001, n=52), and for phloem ray height (F=24.48 df=2, n=52, P<0.0001, n=52). Duncan's multiple comparison analysis corroborated the finding that statistically significant differences exist (P<0.05) among zones for both characters (Table 4). When applying the analyses to each species, *A. glabra* showed statistically significant differences for wood ray height (F=8.55 df=1, P<0.0038, n=10), between FZ4 and FZ>8 (Table 3). *Rhizophora mangle* also showed statistically significant differences (F=5.38 df=1, P<0.0489, n=12) for ray height between FZ8 and FZ>8 (Table 3). However, no species showed statistically significant differences for bark ray height among zones, though for *A. glabra* and *R. mangle* it presented the same tendency as wood ray height (Table 3).

Multiple regression

Water pH was the only variable significantly associated with the flooding period (r_s=0.61, P<0.05), indicating that, the higher the pH of interstitial water the longer the flooding period.

Clay percentage was the site variable which contributed most to the prediction of the percentage of solitary vessels, as indicated by R^2 (Table 5). Moreover, silt percentage and interstitial water salinity in the dry season contributed most to the prediction of the percentage of vessels in radial multiples. Clay and sand percentages contributed most to the prediction of wood and bark ray height, as indicated by R^2 values (Table 5).

Table 6 Multiple comparison of means (±SE) of relative conductivity (RC) (μm^4×10^{-6}) and vulnerability index (VI)

Species/Variables	FZ4	FZ8	FZ>8
Total RC	61±9	77±8	67±12
Total VI	8±1*	6±1*	12±2
L. racemosa			
Vessel diameter	98±2	102±5	108±6
Vessel number	12±2	9±1	12±1
RC	70±16	63±13	112±20
VI	10±2	12±2	9±1
A. germinans			
Vessel diameter	73±3	74±3	
Vessel number	36±3	34±2	
RC	69±14	66±9	
VI	2±0.1	3±0.2	
R. mangle			
Vessel diameter		89±3*	76±1
Vessel number		25±2	31±7
RC		103±15	63±13
VI		4±0.2	3±1
A. glabra			
Vessel diameter	93±7		94±4
Vessel number	7±1*		4±1
RC	39±10*		18±4
VI	14±1*		27±3

* P<0.05, Duncan's test

Table 7 Stepwise multiple regressions with relative conductivity and vulnerability index as response variables and environmental variables as predictors. For abbreviations, see Table 5

Variables	Regression estimators	
	B	R^2
Relative conductivity (μm^4×10^{-6})		0.80
Rainy season electrical conductivity (mmhos cm^{-1})	4.82****	0.80
Vulnerability index		0.82
Rainy season flooding level (cm)	0.97****	0.81
Dry season flooding level (cm)	0.18*	0.01

*P<0.05, ****P<0.0001

Relative conductivity and vulnerability index

The ANOVA did not show significant differences for relative conductivity of the species among zones (Table 6; F=0.44 df=2, P>0.69, n=52). However, when applying the analyses to each species, *A. glabra* was the only one that showed significant differences (F=17.80 df=1, P<0.0020, n=10) for relative conductivity between FZ4 and FZ>8 (Table 6). On the other hand, the ANOVA revealed significant differences for vulnerability index of the species among zones (Table 6; F=20.99 df=2, P<0.0001, n=52). When applying analyses to each species, *A. glabra* presented significant differences for vulnerability index (F=20.14 df=1, P<0.0020, n=10) between FZ4 and FZ>8 (Table 6), and no differences were detected for the other species.

Multiple regression analysis showed that interstitial water salinity during the rainy season is the site variable which contributes most to the prediction of relative conductivity as indicated by R^2 (Table 7). Whereas flooding level during the rainy season is the variable which contributes most to the prediction of the vulnerability index (Table 7).

Discussion

Vessel grouping and wood ray height are strongly associated with the flooded zones where trees are growing. For bark, only ray height, which is associated with water conduction, gas and humidity exchange, showed a major relationship with flooded zones. Rays have been correlated with site variables such as soil water availability and flooding period (Jansonnius 1950; Kozlowski 1984; LevYadun and Aloni 1995).

DISCRIM showed that all observations were correctly classified in FZ4, but in FZ8 and FZ>8 a wide variation in the characteristics exists. Characteristics tend to present wider variation with increasing flooding period. This suggests an ample response of the species growing in zones with a prolonged flooding period, that depends on salinity and aeration; not on the physical presence of water in this case.

There is a tendency in FZ4 for few solitary vessels and more abundant vessels in radial multiples, suggesting a functional advantage of the multiple vessel groups. When species present more vessels which are in contact with each other, there are more available alternative routes for water flow, avoiding the cavitated vessels in the groups (Baas 1983; Zimmermann 1983). A direct relationship among solitary vessels percentage, flooded level during the rainy season and clay particle percentage in soil could be explained in terms of water security, because in the study area silt soil retains more water (Pritchett 1986; Valdez 1994). So, if the flooding level during the rainy season is higher, more water will be available during the dry season, especially in FZ8 and FZ>8 zones.

Although soils with fine particles are more humid, they retain more saline water, leaving a higher salt concentration when evaporating. Therefore, the salt concentration during the dry period is considerably higher than during the humid period (FitzPatrick 1984). In such cases, soils with a higher silt percentage increase their salinity during the dry season. This may cause a more drastic physiological drought, as probably occurs in FZ4 and FZ>8. According to Waisel (1972) and Carreras (1988) although water availability in mangroves is abundant, high salinity concentration diminishes water availability for the plant, causing physiological drought. *Avicennia germinans*, *L. racemosa* and *R. mangle* do not show statistically significant differences among zones for solitary vessels and radial multiple percentages, neither for vessel number nor vessel diameter, which could be attributed to their halophytic preference (Tomlinson 1986; Lin and Sternberg 1993). *Avicennia germinans* shows successive cambia development (Zamski 1979) and Culp (1986) suggested that successive cambia and conjunctive tissue may increase the plant's negative water potential by accumulating salts, thus attracting water from vessels. However, *Annona glabra* is considered a glycophyte that tolerates salinity in low concentrations and produces numerous adventitious roots in response to flooding periods (Lin and Sternberg 1993; Zotz et al. 1997). The response of *A. glabra* to flooding variation is more significant.

Species tend to have lower wood and bark rays in FZ4 than in FZ>8 and FZ8. In this case, differences in wood and bark ray height can be attributed to anoxic conditions favoured by prolonged flooding, because silt soils retain more water. Kozlowski et al. (1991) mention that increments in wood rays are related with flooding because larger cells could mobilize a higher oxygen volume and more photosynthates, and also increase the efficiency of horizontal flow. Carlquist (1988) also mentions that the intercellular space system of ray tissue is essential, because ray cells have indefinite viability and require gas exchange for metabolic activity. The similar function of wood and bark ray height suggests that horizontal communication exists between them through the vascular cambium (Catesson 1990).

Statistically significant differences exist for wood ray height among zones for *R. mangle* and *A. glabra*. In the case of *A. glabra* the tallest rays are present in FZ>8. Considering that *A. glabra* tolerates prolonged flooding periods by developing numerous adventitious roots (Zotz et al. 1997), this could be related with radial transport of oxygen. However, *R. mangle* shows an inverse tendency, and shorter rays occur in FZ>8. In this species rays are not related with adventitious roots because it develops stilt roots. Nevertheless, there are no differences for wood ray height expressed in cells number in FZ8 and FZ>8 or bark ray height in FZ8 and FZ>8. In this case, reduction in ray size could be associated with the effect of prolonged flooding that is similar to that of drought (Lambers et al. 1998).

Relative conductivity is not significantly affected by flooding period. However, a direct relationship exists between relative conductivity and interstitial water salinity during the rainy season. Interstitial water salinity diminishes notably during the rainy season in the three zones. Relative conductivity values are comparable with those of hydraulic conductivity reported by Lambers et al. (1998) for deciduous trees with diffuse porosity, although the species studied by us are evergreen. Lambers et al. (1998) mention that vessels with narrow diameters have the disadvantage of a low hydraulic conductivity, which could be the case in the species studied. However, vessels with wider diameters randomly distributed in xylem compensate for narrow ones in the trees with diffuse porosity.

Annona glabra is the only species in which statistically significant differences exist between relative conductivity and zones, showing lower relative conductivity when flooding period increases and salinity diminishes. Lambers et al. (1998) showed that hydraulic conductivity diminishes with flooding, whereas López-Portillo and Ezcurra (1989) found that in mangrove species the hydraulic conductivity is lower when salinity diminishes. It is remarkable that a non-mangrove species shows similar behaviour related to water salinity as mangrove species. This may imply that glycophyte species growing in brackish water with a prolonged flooding period follow similar strategies to mangrove halophyte species.

The vulnerability index is lower in FZ8 than in FZ4 and FZ>8. The values are higher than the 4.5 reported by Carreras (1988) for the same species growing in Cuba. Besides differences in vessel diameter and vessel frequency, regression analysis indicated that a direct relationship exists between vulnerability index and flooding level during the rainy and dry seasons. In the studied area flooding level rises during the rainy season, but sandy soils cause the water level to drop quickly when the dry season begins (Rico-Gray and Palacio-Ríos 1996). The difference in the flooding level during the rainy and dry seasons is about 28 cm in FZ4, 14 cm in FZ>8 and only 10 cm in FZ8. This would cause higher vulnerability in FZ>8 if a sporadic drought occurs, because an increase in salt concentration in the soil during the dry season will then occur. In *A. glabra* there is a tendency for its vulnerability to increase in FZ>8. This tendency can be associated with water availability during the whole year and lower salinity (dry season=5 mmhos cm^{-1}, rainy season=2 mmhos cm^{-1}).

According to Panshin (1932) and Carreras (1988) some anatomical characteristics of mangrove species can be interpreted as adaptations to habitat, while others should be attributed to genetic factors. It is remarkable that significant differences among zones exist for wood and bark characteristics involved in vertical and horizontal water transport, transport of photosynthates and gas exchange. This fact suggests a response to zones with different flooding periodicity and specifically to water availability, salinity and oxygen supply.

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