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ORIGINAL

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Wood variation in *Laguncularia racemosa* and its effect on fibre quality

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Abstract *Laguncularia racemosa* wood is commonly used in north-western Mexico and harvested without the knowledge of whether environmental conditions affect wood quality. *Laguncularia racemosa* anatomy variation was evaluated to identify which cell features, mainly fibre features, are related to an environmental gradient and how this variation affects wood quality. Trees were sampled in six sites along the river where different flooding periods and levels occur. Analyses revealed that in sites with high salinity and flooding levels, there are more abundant vessels and axial parenchyma although the fibres and vessel elements are shorter, suggesting a water stress effect. Correlation analysis confirmed that the higher the percentage of gelatinous fibres, the longer the fibres. This occurred in *L. racemosa* trees growing in those sites with a high sand particle percentage and a lower flooding level. Anova (analysis of variance) revealed non-significant differences among sites for flexibility, rigidity and Peteri coefficients as well as for Runkel ratio, however the rigidity coefficient is affected by occurrence of gelatinous fibres. *L. racemosa* wood harvesting should avoid those sites with high flooding level, high sand particle percentage and high salinity that may modify wood quality.

Introduction

Laguncularia racemosa (L) Gaertn. f. is a common component of mangrove forests along the Pacific and Atlantic coasts of Mexico (Flores et al. 1971; Rzedowski 1978; Pennington and Sarukhán 1998). The species grows under a wide variety of conditions. It is commonly restricted to elevated soils on the landward fringe of the mangrove forests where tidal inundation is less frequent and less intense, but it also grows in the basin mangrove forests where tidal flushing is limited, and it colonizes disturbed sites where it can form pure stands (Tomlinson 1986). In these areas, *L.racemosa* is generally found associated with

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Avicennia germinans (L.) Stearn. Along rivers or estuarine channels with a high influence of freshwater runoff and frequent tidal inundation, *L.racemosa* grows in low swales or point bar deposits frequently associated with *Rhizophora mangle L.* (Jimenez 1985; Valdez 1994).

In Mexico, the wood of *L. racemosa* does not have industrial uses (Pennington and Sarukhán 1998). It is used for local house construction, poles, fences, sticks for fish trapping, tool handles, carpentry, boat framing, as well as for fuel (Niembro 1986). In north-western Mexico, poles are sold to build wooden frames for drying tobacco leaves and to be incorporated as tutors for horticultural crops such as tomatoes (Valdez 2001).

The anatomy of mangrove woods has been studied extensively because of their economic importance and to correlate structure with physiological specialisation towards the mangrove habitat (Tomlinson 1986). Moreover, few studies have been carried out on mangrove species in which their wood structure is correlated with environmental factors (Panshin 1932; Jansonnius 1950; van Vliet 1976, 1979; Carreras 1988; Yáñez-Espinosa and Terrazas 2001). Wood and bark anatomy variation in four species growing in a mangrove forest has been evaluated in relation to flooding periodicity (Yáñez-Espinosa et al. 2001). These authors did not detect significant differences for *L. racemosa* wood and bark characters related to flooding periodicity; nevertheless, this species is the only one growing under a wide range of environmental conditions in the estuarine river El Conchal which experiences more than eight months of flooding and salinity conditions that only *R. mangle* tolerates. In this study we evaluated *L. racemosa* wood anatomy variation in terms of environmental gradients (salinity, flooding level and soil characteristics) to identify which cell features are related to them, and how such variation affects wood quality in terms of fibre features.

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 in annual rainfall with a rainy season of four months (June-September) and a dry season of eight months (October-May). This forest is mainly composed of *L. racemosa*, *Rhizophora mangle*, and *Avicennia germinans*. Generally, *L. racemosa* is located across the intertidal zone, along the estuary and landward, and its natural regeneration is abundant (Valdez 2001). We selected six sites along the river and in each site three trees of *L. racemosa* were sampled. Mean height and diameter of trees in each site along with other site variables are presented in Table 1.

The samples were obtained from the tallest trees with the largest diameter in each site during January, when the flooding level was at its lowest. The samples were cut with a machete at a height nearly 1.30 m above floor level and with a northward orientation. Wood samples were immediately fixed in formalin-ethanol-glacial acetic acid. Two days later, they were washed with tap water and stored in glycerin-ethanol-water (1:1:1) until sectioning. Transverse, tangential and radial wood sections 30 μm thick were obtained with a sliding microtome. For each sample, unbleached and bleached sections were stained with safranin-fast green and mounted with synthetic resin. Macerations were prepared using

Table 1 Trees (mean ± SE) and site features in El Conchal estuary, Nayarit, Mexico

Site	Trees		Flooding		Soil			
	Diameter (cm)	Height (m)	Periodicity (days)	Level (cm)	EC (mmhos cm^{-1})	Sand (%)	Silt (%)	Clay (%)
1	16.1 ± 1.3	12.7 ± 1.5	124	−12.9	10.6	30.0	41.0	29.0
2	24.9 ± 1.8	17.0 ± 1.5	124	4.8	12.9	65.0	26.0	9.0
3	19.6 ± 1.4	12.7 ± 2.2	242	4.8	15.0	17.0	69.0	14.0
4	23.9 ± 4.3	19.3 ± 1.8	242	−4.6	12.5	30.0	57.0	13.0
5	26.7 ± 1.8	19.3 ± 2.3	336	2.5	13.4	17.0	69.0	14.0
6	20.9 ± 3.7	10.0 ± 2.9	336	3.6	14.4	19.0	76.0	5.0

Jeffrey's solution (Berlyn and Miksche 1976). Temporary slides were prepared to gather data on vessel element and fibre lengths.

Sixteen quantitative wood characters were evaluated. Twenty-five linear measurements were carried out for nine characters. Number of vessels, percentage of solitary vessels, and percentage of gelatinous fibres were calculated in 25 fields of 1 mm^2, and number of rays in 25 intercepted lines of 1 mm. Measurements and counts were carried out with the image analyser Image-Pro Plus v.3.1 (Media Cybernetics 1997).

Axial parenchyma was classified as paratracheal vasicentric, aliform or confluent. Each type was classified with ordinal numbers and evaluated in 25 fields of 1 mm^2. Indexes, which evaluate wood quality in terms of fibre characteristics, were estimated (Tamolang and Wangaard 1961; Dinwoodie 1965; Ogbonnaya et al. 1992) and include: the flexibility coefficient which is a measure of strength properties of paper (lumen diameter/fibre diameter), the coefficient of rigidity which is a measure of tensile strength of fibre (2×fibre wall thickness/fibre diameter), Runkel ratio, which is a measure of the suitability of fibre for paper production (2×fibre wall thickness/lumen diameter), and the Peteri coefficient which is a measure of the tear property of pulp in paper production (fibre length/fibre diameter).

The site variables evaluated included data on the flooding period (days), mean annual flooding level (cm), mean annual electrical conductivity (EC, mmhos/cm) as an indicator of salinity, and soil texture (sand, silt and clay particles percentage). Flooding period and flooding level were observed directly in the field. The electrical conductivity was read on a portable digital meter model TPS LC84. Soil texture and pH were determined by standard laboratory techniques. Valdez (2001) provided soil and interstitial water data for the entire year (Table 1).

Continuous data were logarithm transformed and discrete data were square root transformed to carry out the statistical analyses. A canonical discriminant analysis (candisc) was applied to identify a subset of characters that maximally separate sites and to identify the relative contribution from each characteristic to their separation. A discriminant classificatory analysis (discrim) was applied to verify site variation for each sample.

Significant differences among means of the anatomical characters identified by candisc, as well for fibre indexes, were evaluated by analysis of variance (anova). Differences among means were compared and segregated by Tukey test ($P < 0.05$). We used Pearson correlation analysis to evaluate association among quantitative anatomical characteristics and Spearman rank correlation to evaluate association between quantitative and qualitative anatomical characteristics. Stepwise multiple regression analyses (reg) were performed between trees and 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 revealed that three canonical functions accounted for 88% of the total variation, contributing significantly to the separation among sites (Wilks' λ, $p < 0.0001$, $n = 450$). The first function (eigenvalue of 0.835) explained 38.6% of the total variation, the second function (eigenvalue of 0.734) 34.0% of the remaining variation, and the third (eigenvalue of 0.332) explained 15.4% of the remaining variation. Anatomical characters that contributed significantly in the separation of site centroids were gelatinous fibre percentage, fibre length, fibre wall thickness, ray number per mm, number of vessels per mm^2 and vessel element length (Table 2). Discriminant analysis showed that the centroids of each site were significantly different ($p < 0.0001$) and 100% of samples in sites 1, 2, and 5 were correctly classified, as compared to 67% of sites 4 and 6, and 33% of site 3. Additionally, we observed a change in cross sections from paratracheal vasicentric parenchyma to aliform and confluent in relation to sites (Fig. 1 a–c), as well as a change in the proportion of gelatinous fibres (Fig. 1d, e).

Table 2 Anatomical characters used in canonical discriminant analysis (candisc) and their partial contribution to the functions expressed by coefficients of discriminant functions

Characters	Function coefficients		
	Function 1	Function 2	Function 3
Fibre lumen diameter (μm)	0.3659	−0.1421	−0.5431
Fibre wall thickness (μm)	−0.8435**	−0.2994	−0.3053
Fibre total diameter (μm)	−0.1791	−0.3968	−0.5432
Fibre length (μm)	0.8794**	−0.3840	0.2594
Gelatinous fibre (%)	0.9871**	0.1187	0.0742
Vessel lumen diameter (μm)	−0.4579	−0.1552	0.8431
Vessel wall thickness (μm)	−0.6133	−0.7312	0.1317
Vessel total diameter (μm)	−0.5262	−0.2724	0.7682
Vessel element length (μm)	0.1079	−0.2709	0.9503**
Vessel number per mm^2	−0.5278	0.8299**	0.0785
Solitary vessels (%)	−0.5490	0.7807	0.2795
Pit diameter (μm)	−0.0177	−0.4358	−0.0021
Ray height (μm)	0.6769	−0.0928	0.4497
Ray width (μm)	0.1730	0.6581	−0.6240
Ray height (cell number)	0.5222	0.0250	0.6473
Ray number per mm	0.3046	−0.8375**	0.4158

** Characters with high contribution to centroid separation among sites

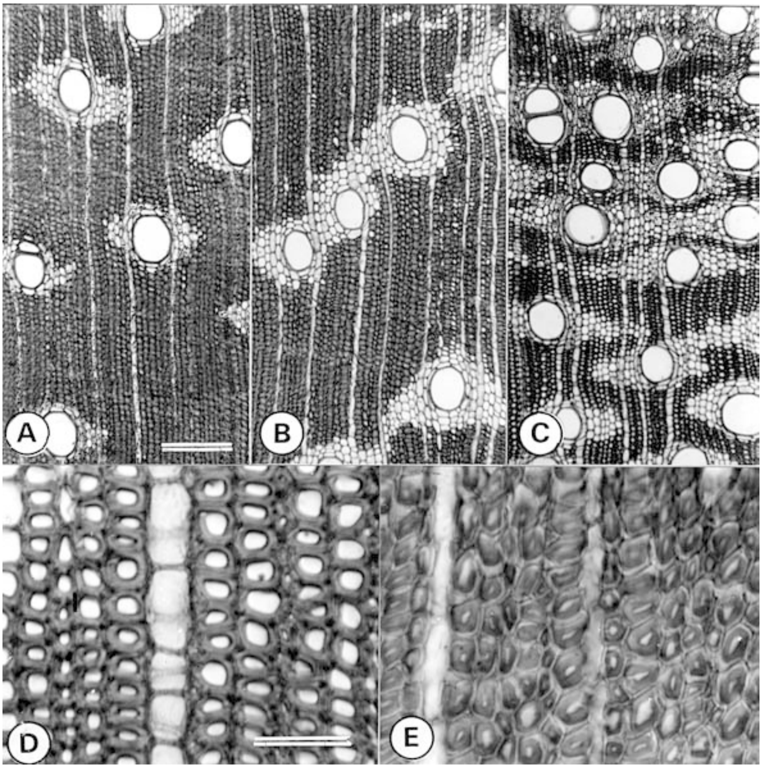

Fig. 1A–E Variation of *L. racemosa* axial parenchyma and fibres among sites. **A** Vasicentric parenchyma in sites 1 and 4. **B** Aliform parenchyma in site 3. **C** Confluent parenchyma in sites 2, 5 and 6. **D** Normal fibres. **E** Gelatinous fibres. Scale bar = 200 μm in **A**–**C**, 50 μm in **D**, **E**

Analysis of variance

With the exception of number of vessels per mm^2 ($F = 3.98$ $df = 5$, $p < 0.0232$, $n = 18$), the anova revealed non-significant differences among sites for percentage of gelatinous fibre ($F = 1.94$ $df = 5$, $p < 0.1611$, $n = 18$), fibre length ($F = 1.46$ $df = 5$, $p < 0.2721$, $n = 18$), fibre wall thickness ($F = 0.91$ $df = 5$, $p < 0.5064$, $n = 18$), ray number per mm ($F = 0.19$ $df = 5$, $p < 0.9593$, $n = 18$) and vessel element length ($F = 2.20$ $df = 5$, $p < 0.1223$, $n = 18$) (Table 3). In addition, the anova showed non-significant differences among sites for flexibility coefficient ($F = 0.58$ $df = 5$, $p < 0.7118$, $n = 18$), coefficient of rigidity ($F = 0.53$ $df = 5$, $p < 0.7498$, $n = 18$), Runkel ratio ($F = 0.54$ $df = 5$, $p < 0.7431$, $n = 18$), and Peteri coefficient ($F = 1.53$ $df = 5$, $p < 0.2525$, $n = 18$) (Fig. 2).

Correlation analysis

Correlation analysis revealed a negative association between gelatinous fibre percentage and normal fibre wall thickness (–0.69, $p < 0.002$, $n = 18$) but positive with fibre length (0.62, $p < 0.006$, $n = 18$). Gelatinous fibre percentage was negatively correlated with vessel number per mm^2 (-0.52, $p < 0.03$, $n = 18$).

Table 3 Multiple comparison of means (±SE) of wood characters selected through candisc analysis

	Sites					
Characters	1	2	3	4	5	6
Gelatinous fibre (%)	72 ± 4	61 ± 5	29 ± 5	65 ± 5	0 ± 0	11 ± 2
Fibre length (μm)	1015 ± 26	894 ± 19	894 ± 23	1043 ± 15	837 ± 17	872 ± 20
Fibre wall thickness (μm)	4 ± 0.2	4 ± 0.1	5 ± 0.2	4 ± 0.2	5 ± 0.1	5 ± 0.1
Ray number per mm	14 ± 1	13 ± 1	13 ± 1	15 ± 1	14 ± 1	14 ± 1
Vessel number per mm^2	7 ± 1**b**	16 ± 1**a**	11 ± 1**ab**	8 ± 1**b**	11 ± 1**ab**	13 ± 1**a**
Vessel element length (μm)	419 ± 14	433 ± 12	400 ± 16	513 ± 15	460 ± 15	428 ± 14

Means with different letters are significantly different at $p < 0.05$, Tukey test

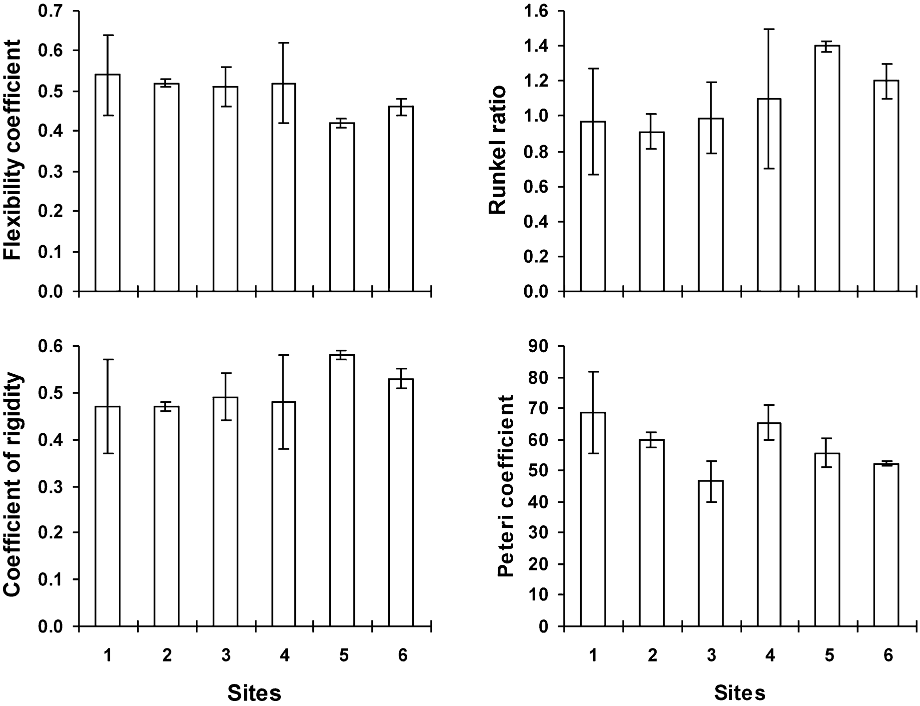

Fig. 2 Frequency distributions of mean and standard error values of fibre indexes of *L. racemosa*. Vertical lines are the ±SE

Axial parenchyma type and vessel number per mm^2 were positively associated ($0.78, p < 0.0001$, $n = 18$).

Multiple regression

Salinity (EC) and flooding level were the site variables with a higher contribution to predict most wood characters as indicated by R^2. Sand percentage in soil also contributed to predict gelatinous fibre percentage in addition to flooding level (Table 4).

Table 4 Stepwise multiple regressions among anatomical characters and the variables measured. *B* = partial regression coefficient; R^2 = determination coefficient; * = $p < 0.0001$; n.s. = nonsignificant

Anatomical variables	Regression estimators *B* (environmental variables)	R^2
Gelatinous fibre	14.81 (in flooding level)* −1.39 (in sand) n.s.	0.60
Fibre length	70.33 (salinity)* −23.63 (flooding level)*	0.98
Fibre wall thickness	0.31 (salinity)*	0.97
Ray number per mm	1.03 (salinity)* −0.25 (flooding level)*	0.98
Vessel number per mm^2	0.85 (salinity)* 0.21 (flooding level) n.s.	0.92
Vessel length	33.35 (salinity)* −7.51 (flooding level)*	0.98

Discussion

High plasticity allows a genotype to maintain dominance in spatially or temporally variable environments by facilitating continuous exploration of new territory that has not been exhausted, thus maintaining resource capture and fitness. Greater plasticity is associated with competitive ability in a particular environment (Lambers et al. 1998). According to Valdez (1994), in the forest area studied, *L. racemosa* shows the highest importance value (61.6%) followed by *R. mangle* (32%) and *A. germinans*(5.9%). This suggests that plasticity of wood anatomical characters, particularly those related to water conduction and mechanical strength, allows *L. racemosa* to grow under a wide variety of conditions.

In sites with higher salinity and flooding level, more vessels per mm^2 are present. Numerous vessels favour protection against cavitation in stressed environments. It seems that in mangrove species more cavitation damage exists when flooding level is higher, because a sporadic drought could occur (Yáñez-Espinosa et al. 2001). Moreover, some studies have found that vessel number per mm^2 in tension wood is lower than in normal wood (Jourez et al. 2001); this was confirmed by the negative correlation between gelatinous fibre percentage and vessel number per mm^2 for *L. racemosa*.

According to Levitt (1980) many plants exposed simultaneously to both a salt stress and an evaporative water stress, e.g. mangrove species whose roots are submerged in saline water, must possess both tolerance to this osmotic water stress and to specific ion stress in order to survive. Influence of salinity and flooding level on vessel element length could be related to the water stress effect because this kind of stress causes cell size reduction (Tyree and Jarvis 1982). Although water availability in mangroves is abundant, high salinity diminishes water availability for the plant causing physiological drought, as seen with *L. racemosa* (Carreras 1988). Influence of salinity on fibre length and wall thickness could be related to the water stress effect as is vessel element length. A reduction in all fibre features (length, diameter, lumen diameter, and wall thickness) has been also found in *Gmelina arborea* Roxb. seedlings growing under water stress (Ogbonnaya et al. 1992).

Kozlowski et al. (1991) and Yáñez-Espinosa and Terrazas (2001) found that increments of the xylem ray number are related to flooding because differentiation of ray cells could be an alternative to uptake more oxygen by increasing intracellular spaces. This is not applicable to *L. racemosa* because its rays are quite similar among sites. However, observations suggest that in this species there was a trade-off between maintaining ray number and increasing axial parenchyma. As mentioned, axial parenchyma is vasicentric in sites with lower flooding level and salinity and confluent in sites with higher flooding level and salinity (Fig. 1). Positive correlation between vessel number per mm^2 and axial parenchyma type suggests that a continuous system of parenchyma cells arises and guarantees photosynthates, water, and gas conduction (Roth 1981; Carlquist 1988), similar to the parenchyma netlike pattern of *Annona glabra* (Yáñez-Espinosa and Terrazas 2001).

Presence of gelatinous fibres revealed the existence of tension wood in trees of most sites. Apart from the development of a gelatinous layer, various fibre modifications are associated with the development of tension wood (Panshin and Zeeuw 1980). Correlation analysis confirms that the higher the percentage of gelatinous fibres the longer the fibres, a common modification associated with tension wood (Jourez et al. 2001; Carlquist 1988). Tension wood is weaker than normal wood in the green condition because, in a moisture condition, the gelatinous layer is not well bonded to the secondary wall and contributes little to tensile strength. As wood dries, the gelatinous layer bonds to the remainder of the secondary wall and can contribute to the tensile strength of tension wood (Panshin and Zeeuw 1980). Furthermore, normal fibre walls are thinner when the percentage of gelatinous fibres is greater, as correlation analysis confirmed. However, other modifications associated with tension wood, like longer vessel elements or more rays per mm (Jourez et al. 2001) were not found in *L. racemosa.*

The highest percentage of gelatinous fibres is present in sites with high sand particle percentage and low flooding level. Carlquist (1988) mentioned that tension wood develops as a mechanism to correct lean in stems.*L. racemosa* is highly susceptible to leaning or wind throw because its root system is shallow with large, spreading, horizontal roots (Jimenez 1985). This could especially occur in sandy sites where trees have less stability. However, the great variation of gelatinous fibre percentage observed and the low R value in the model suggest that there are other environmental and tree variables involved in the development of tension wood which may include light availability or hormone content (Kollmann and Côté 1968; Angeles 1994).

Fibre characteristics are very important in relation to paper pulp. The Runkel ratio showed that fibres of *L. racemosa* have a regular quality for paper production (1.10), with higher values than *Ceiba pentandra* (L.) Gaertn. (0.55), *Gmelina arborea* (0.55), and *Persea americana* Mill. (0.23) (Tamolang and Wangaard 1961; Ogbonnaya et al. 1992; Tamarit-Urias 1996). The rigidity coefficient is affected by occurrence of gelatinous fibres, because higher values for this coefficient occur in sites with a lower percentage of gelatinous fibres; however, no clear tendency was detected for the flexibility coefficient. Higher Peteri coefficient values are present in sites with a higher percentage of gelatinous fibres. Results suggest that *L. racemosa* wood harvesting should come from sites with low flooding level and low sand particle percentage in soil to avoid a higher percentage of gelatinous fibres, as well as from sites with low salinity to avoid abundant parenchyma that may modify wood quality.

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