
FIRST REPORT OF *Rhizophora racemosa* MEYER (RHIZOPHORACEAE) IN THE MANGROVE FORESTS OF THE VENEZUELAN CARIBBEAN COAST

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SUMMARY

Rhizophora racemosa G.F.W. Meyer is reported for the first time in mangrove forests of the Venezuelan Caribbean Coast. The specimens were collected in the Cariaco River and the Gulf of Santa Fe, on the western coast of Sucre State. The

diagnostic character used to distinguish the species is the order of the number of bifurcations in the inflorescence. Description of the habitat of this species is included.

PRIMER REPORTE DE *Rhizophora racemosa* MEYER (RHIZOPHORACEAE) EN LOS MANGLARES DE LA COSTA CARIBE DE VENEZUELA

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RESUMEN

Se reporta por primera vez la presencia de la especie *Rhizophora racemosa* G.F.W. Meyer en los manglares de la costa Caribe de Venezuela. Los ejemplares fueron recolectados en el río Cariaco y el golfo de Santa Fe, en la costa occidental del

estado Sucre. El carácter diagnóstico empleado para diferenciar la especie fue el orden en el número de bifurcaciones de la inflorescencia. También se mencionan algunas observaciones del hábitat de *R. racemosa*.

PRIMEIRO RELATÓRIO DE *Rhizophora racemosa* MEYER (RHIZOPHORACEAE) NOS MANGUES DA COSTA DO CARIBE DA VENEZUELA

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RESUMO

Relata-se por primeira vez a presença da espécie *Rhizophora racemosa* G.F.W. Meyer nos mangues da costa do Caribe da Venezuela. Os exemplares foram recolhidos no rio Cariaco e no golfo de Santa Fe, na costa ocidental do estado

Sucre. O carácter diagnóstico empregado para diferenciar a espécie foi a ordem no número de bifurcações da inflorescência. Também se mencionam algumas observações do hábitat de *R. racemosa*.

Introduction

Mangroves are intertidal ecosystems present in tropical and subtropical coastlines, exposed to variable hydrological conditions as a result of tidal flushing and freshwater sources, and characterized by being hypoxic or anoxic, having organic and mineral substrates, textures ranging from clay-like to sandy, and vari-

able salinity. They are generally restricted to areas where the average air temperature during the coldest months exceeds 20°C and the seasonal variation in temperature does not exceed 10°C (Walsh, 1974; Chapman, 1977; Tomlinson, 1994).

The genus *Rhizophora* is the most common of the three genera found in woodland habitats that dominate these

ecosystems (Duke *et al.*, 1998). Ten *Rhizophora* taxa have been recognized worldwide in two bio-geographical regions: the Indo-West-Pacific (IWP) and the Atlantic-Caribbean-Eastern-Pacific (ACEP; Duke, 1992; Duke *et al.*, 2002; Nettel and Dodd, 2007). The latter includes the tropical and subtropical coasts of America, the Caribbean islands and western Africa (Figure 1).

In the ACEP region, three species of the genus *Rhizophora* have been recognized: *R. mangle* (L.), *R. harrisonii* Leechman and Leechman, and *R. racemosa* G.F.W. Meyer (Leechman, 1918; Salvoza, 1936; Keay, 1953; Prance *et al.*, 1975; Jiménez, 1987). Some authors indicate that *R. harrisonii* is a hybrid of the other two species (Breteler, 1969; Tom-

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linson, 1994; Dodd *et al.*, 1995). Cerón-Souza *et al.* (2010) maintain that *R. harrisonii* possibly represents a morphotype resulting from the backcrossing and introgressive hybridization between *R. mangle* and *R. racemosa*.

R. mangle, which has a wider distribution, is spread throughout the wetlands and dry coasts of America. The other two species, *R. racemosa* and *R. harrisonii*, are restricted to more humid climates in areas that have lower salinity and regular fresh water flows (Afzal-Rafii *et al.*, 1999; Duke *et al.*, 2002; Duke and Allen, 2006; Figure 1; Table I). *R. racemosa* is found on the Pacific coast of America, from Puerto Lobos, Mexico, to Punta Malpelo, Tumbes River, Peru. On the eastern coast of America it is distributed from Yaguaraparo, Gulf of Paria, Venezuela, to Maranhense Gulf, Brazil, and in the Caroní River estuary located on the western coast of Trinidad (Bacon, 1993).

R. mangle, the dominating taxon in the mangroves of Venezuela, has been reported throughout continental and insular coasts that have dry to humid climates. The distribution of *R. racemosa*, however, had been confined to the estuaries of the drainage basins of the Atlantic in Venezuela, including the Orinoco River Delta, the San Juan River and the coastal mud plains of the Gulf of Paria (Breteler, 1969; MARNR, 1986; Medina and Francisco, 1997; Vegas-Vilarrúbia and López, 2008).

In his revision of the Atlantic species of *Rhizophora*, Breteler (1969) recognized among the samples collected in Venezuela specimens of *R. racemosa* in Yaguaraparo, Paria Peninsula, Sucre State; the San Juan and Guarapiche rivers, Monagas State; and Pedernales, Delta Amacuro State.

The presence of *R. racemosa* in the Cariaco Riv-

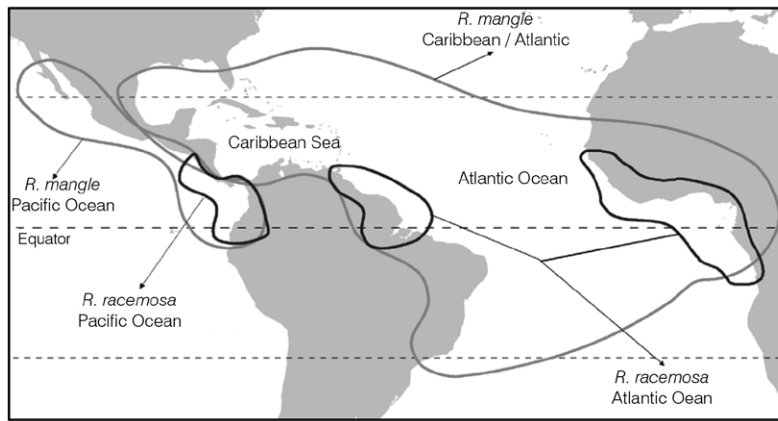


Figure 1. Distribution of the taxa *Rhizophora* throughout the Atlantic-Caribbean-Eastern-Pacific (ACEP) biogeographical region.

TABLE I
LATITUDINAL BOUNDARIES FOR THE DISTRIBUTION OF THE THREE SPECIES
OF THE GENUS *Rhizophora* IN AMERICA

Species	Atlantic Ocean		Pacific Ocean	
	North	South	North	South
<i>Rhizophora mangle</i> L.	Bermuda (32°20')	Praia do Sonho, Brazil (27°53')	Puerto Lobos, Mexico (30°15')	Tumbes River, Peru (3°40')
<i>R. harrisonii</i> Leechman	Yaguaraparo River, Venezuela (10°30')	Preguiças River, Brazil (2°40')	Chantuto, Mexico, 15° 15'	Guayas River, Ecuador (2°30')
<i>R. racemosa</i> G.F.W. Meyer	Yaguaraparo River, Venezuela (10°30')	Maranhense Gulf, Brazil (2°45')	Lempa River, El Salvador (13°17')	Guayas River, Ecuador (2°20')

Sources: Salvoza (1936), Jiménez (1985), Santos (1986), Lacerda *et al.* (2001).

er and the Gulf of Santa Fe reported here represents a new finding for the Venezuelan Caribbean coast and broadens the distribution of the species in the ACEP region.

Sampling Areas

R. racemosa specimens were collected in (Figure 2):

1- The mangrove forests bordering the whole length of the Cariaco River, all the way to its estuary in the Gulf of Cariaco (10°29'42"-10°29'34"N, 63°38'33"-63°37'55"W), in the external part of the mangrove strip, in the low intertidal zone.

2- Near the road that runs parallel to the La Bodega Lagoon (10°16'43"N, 64°23'59"W), in the internal part of the man-

grove strip, 65m from the lagoon's edge, west of the Nurucual River and east of the Santa Fe River.

3- The flood zone in the village of Santa Fe (10°16'46"N, 64°25'46"W), which is fed by a nameless drainage running more or less parallel to the Santa Fe River 1.3km to the east. Here a relict mangrove of what was possibly a wetland located in the Santa Fe River flood plain, before entering the Gulf of Santa Fe, was observed.

At each site, samples of interstitial water were collected at a depth of 20cm around the trunks of trees identified as *R. racemosa*, and salinity was measured with a refractometer calibrated for seawater (Atago). Units are expressed in parts per thousand (ppth).

We examined the exsiccatae deposited as *Rhizophora* at the National Herbarium of Venezuela (VEN) and the Isidro Rafael Bermúdez Rodríguez Herbarium (IRBR) (Cumaná, Universidad de Oriente), the available literature, and several on-line databases regarding this genus. No previous record of *R. racemosa* was found for the Venezuelan Caribbean basin or the Gulf of Mexico.

Results and Discussion

The genus *Rhizophora*, present in woodland habitats, is characterized by having aerial prop roots, opposite,



Figure 2. Sites on the Cariaco River and in the Gulf of Santa Fe where the observations were made and the specimens collected. The distribution of *R. racemosa* along the Venezuelan Atlantic coast is shown.

TABLE II
INFLORESCENCE CHARACTERISTICS USED TO
DISTINGUISH THE *Rhizophora* SPECIES
(ADAPTED FROM CERÓN-SOUZA *ET AL.*, 2010).

Species	Order of the number of bifurcations in the inflorescence	Number of flowers
<i>R. mangle</i>	1, 2	2, 3, 4, 5
<i>R. harrisonii</i>	3, 4, 5	8, 16, 32
<i>R. racemosa</i>	5, 6, 7	32, 64, 128



Figure 3. *Rhizophora racemosa* Meyer. Inflorescence of a specimen collected in the mangrove forests of the Gulf of Santa Fe. The order of the bifurcations is indicated.

simple, whole, deciduous leaves, each pair associated with a pair of lanceolate stipules that leave an annular scar. The inflorescences are axillary with perfect flowers. The seeds start to germinate even when the fruit is still attached to the plant; hence the propagules have extended hypocotyls (Salvoza, 1936). These viviparous plants are dispersed by water to great distances, and they can remain viable for over one year (Rabinowitz, 1978).

The morphological characteristics used to distinguish the three species of *Rhizophora* are ramification; number of flowers and length of inflorescence; peduncle length; form and type of flower bud apex; and length of the hypocotyl (Keay, 1953; Hou, 1960; Breteler, 1969; Jiménez, 1987).

In a study on hybridization and introgression of the genus *Rhizophora* in the Neotropics, Cerón-Souza *et al.* (2010) distinguish the species based on the characteristics of the inflorescence. The diagnostic

character chosen was the number of sequential bifurcations in the inflorescence. The number of bifurcations (b) in *R. racemosa* varies from 5 to 7, and the number of flowers (n) is related to the number of bifurcations ($n = 2^b$; Table II). Prance *et al.* (1975), in their description of the three species of *Rhizophora* in the Neotropics, also consider bifurcation in the inflorescence as a diagnostic character. The authors indicate that the inflorescence is axillary, in a dichotomous panicle, with 5 to 6 successive bifurcations in *R. racemosa* and 3 to 5 in *R. harrisonii*.

The number of sequential bifurcations in the inflorescence was the diagnostic character used to determine the species in the samples examined in the present study, both those deposited in the herbariums and those collected in the Gulf of Santa Fe and the Cariaco River, which had inflorescences with 6 to 9 bifurcations. The number of flowers per inflorescence

counted *in situ* was 47 to 100 (Figure 3).

The trunks of the specimens observed in the Cariaco River varied in diameter from 10 to 30cm and the height of the trees varied from 7 to 15m. The average interstitial salinity of the samples collected at a depth of 20cm was 2.3ppt.

Sewage water from the villages surrounding the Santa Fe flood plains and the La Bodega Lagoon drain directly into the mangroves. At this site *R. racemosa* grows in monospecific patches near *R. mangle* stands. *R. racemosa* trees measured on average 11m (8-14m) in height and 10-36cm in stem diameter. The soils are more clayey than those of the Cariaco River, and the average interstitial salinity at a depth of 20cm was 20ppt.

Savory (1953) studied the ecology of the genus *Rhizophora* in Nigeria and found that when the three taxa occur in sympatry, *R. racemosa* grows upstream bordering the tributaries in very wet soils. The distribution and spatial segregation of the three species of *Rhizophora* have been attributed to a differential tolerance to salinity (Jonker, 1959; Savory, 1953). Ukpong (2000) found that in Nigerian mangroves growing in habitats with varying physiological aspects, such as topography and morphometry, *R. racemosa* was the dominating species in topographically lower areas, always bordering the tributary canals, a fact the author ascribed to a higher tolerance to flooding.

In the San Juan River in Venezuela, the three species

of *Rhizophora* form mixed stands with trees growing 25-35m high. Environmental conditions allow the three species to coexist in mixed stands with a high degree of structural development (Breteler, 1969; Medina *et al.*, 2008). Breteler adds that ecological separation is possible only where salinity conditions are extreme.

The restricted distribution of *R. racemosa* along the more humid areas of the Pacific coast from El Salvador to Ecuador and along South America's eastern coast from Brazil to Venezuela (Gulf of Santa Fe) can be explained by the reduction of its range during the Miocene-Pliocene, and more recently during the last glacial period. During the Plio-Pleistocene glaciations, variations in sea levels produced significant changes in the extension of mangrove forests: when sea levels were high, distribution expanded; when they were low, it contracted (Van der Hammen, 1974). It is possible that *R. racemosa* had a wider range of distribution in the ACEP region and that changes in climate (drops in temperature and humidity) and sea levels during the Late Quaternary reduced its population, caused local extinctions and ultimately led to a reduced range of distribution along the American Caribbean coast (Jiménez, 1984). Climate conditions during the Quaternary glaciation limited colonization or led to extinction, and, consequently, to the species' reduced distribution range in the Caribbean and the Gulf of Mexico. Duke *et al.* (1998) point out that the absence of *R. racemosa* along

the Central American Atlantic coast can be explained by extinction processes that took place when conditions were unfavorable for the species.

After a long period of contraction in their range of distribution, mangroves have expanded along coastal areas since the last ice age (Duke *et al.*, 1998; Saenger, 1998; Dodd *et al.*, 2002). The drainage and outflow of rivers in more humid areas may have created refuges for mangroves. The species that survived in these refuge areas may have dispersed to surrounding regions via step-by-step colonization once favorable conditions returned.

Long-distance dispersal (LDD) seems to have played an important part in the sporadic colonization events in the recent history of *Rhizophora* in the Neotropics (Cerón-Souza *et al.*, 2010). Evidence of LDD has also been obtained for *A. germinans* (Nettel and Dodd, 2007) and the mangrove-associated species *Hibiscus pernambucensis* (Takayama *et al.*, 2006).

Two possible pathways can be postulated for the recent dispersal and colonization of *R. racemosa* throughout Venezuela's eastern Caribbean coast. First, through an ancient channel connecting the gulfs of Paria and Cariaco, and, second, by migration and dispersal along the northern coast of the Paria and Araya Peninsulas.

Macsoy (2005) has proposed a so-called Humboldt channel, a shallow marine corridor connecting the gulfs of Paria and Cariaco, dating from the Early Pleistocene (1.8-1.54Ma), running 240km from east to west, and fed by masses of water influenced by the currents of the Guyanas. However, the two gulfs may have been connected more recently, ~120,000 years, ago when the sea level was higher than it is today (Van Daele *et al.*, 2011). This connection between the gulfs of Paria and Cariaco may have allowed for the dispersal of *R.*

racemosa, its establishment in the Gulf of Cariaco and its later expansion and dispersal to the Gulf of Santa Fe.

The last connection of the Gulf of Cariaco to the Caribbean Sea was ~11,500 years ago (Van Daele *et al.*, 2011). In the present, only a few rivers and streams drain directly into the Gulf of Cariaco. Of these, the Cariaco River, which drains into the gulf's eastern extremity, is the largest and has the most significant output. During part of the Quaternary, the Manzanares and Casanay rivers, two important rivers with relatively large drainage basins and significant sediment loads, flowed into the Gulf of Cariaco.

It could also be proposed that populations of *R. racemosa* in the Gulf of Santa Fe acted as areas of refuge, and dispersed by LDD to the Gulf of Cariaco at the end of the Quaternary, once the Caribbean Sea was reconnected to the Gulf. This colonization, however, may have occurred more recently due to the step-by-step process of LDD from the Atlantic coasts of southern Venezuela (Orinoco River), Guyana, Surinam and Brazil to the Gulf of Paria, Trinidad and the gulfs of Cariaco and Santa Fe, as a result of the North Brazil Current, which carries masses of water with sediments from the Orinoco and Amazon rivers into the Caribbean Sea (Chérubin and Richardson, 2007). In the northern part of the Gulf of Paria 7000-year old mangroves have been documented at 9.2m beneath the current sea level. These are the oldest Quaternary mangroves registered in Venezuela (Rull and Vegas-Vilarrúbia, 1999; Vegas-Vilarrúbia and Rull, 2002).

In the ACEP region, in addition to the Central American Isthmus (CAI) that acts as a land barrier, there is evidence, based on the cpDNA of *A. germinans*, of a restricted gene flow from the western Atlantic coast to the Caribbean region and throughout

the Atlantic coast of Central America (Nettel and Dodd, 2007). The restricted gene flow in the Caribbean region provides evidence that hydrological factors, such as currents (intensity and direction), and terrestrial factors, such as the existence of insular or continental barriers, configuration of the continental shelf, coastal geomorphology or climate, may be restricting the range of distribution of *R. racemosa* throughout the Caribbean region.

Research into the genetic variability of *R. racemosa*, with the purpose of assessing if colonization or re-colonization processes originated in the populations located along the Atlantic coast, and determining the direction of colonization on the South American Atlantic coast, will allow to answer some of the questions regarding the diversification and dispersal of *R. racemosa*, and to establish if extinction processes can account for the current disjunction in parts of the Caribbean region and the western Atlantic.

Material Examined

VENEZUELA: Delta Amacuro State: Manamo Creek, Orinoco River, 01/31/1964 (9°55'N, 62°15'W), F. Breteler 3555 (VEN); Araguabisi Creek, 10/15/1977 (9°10'N, 61°06'W), J. Steyermark 114660 (VEN); Monagas State: Colorado Creek, San Juan River, 05/8/1966, F. Breteler 5152 (VEN); Francés Creek, San Juan River, 05/9/1966, F. Breteler 5162 (VEN); San Juan River, 05/10/1966, F. Breteler 5169 (VEN); San Juan River, 05/9/1966, F. Breteler 5163 (VEN); Francés Creek, San Juan River, 05/22/1967, J. Wessels 1802 (VEN); San Juan River, 05/9/1966, F. Breteler 5163 (VEN); Sucre State: San Juan River, w/o date, M. Sanabria, w/o number (IRBR).

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