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AMERICA'S PACIFIC SPECIES OF RHIZOPHORA

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1. INTRODUCTION

When studying the Atlantic species of *Rhizophora* (BRETELER 1969), I came to the conclusion that of the three species occurring within the area, *R. harrisonii* Leechm. had to be considered as a hybrid between the other two species, i.e. *R. mangle* L. and *R. racemosa* G. F. W. Mey. This conclusion was based on morphological, ecological, and phenological grounds and was supported by the results of pollen investigations by J. Muller. The Pacific species of the American continent were not discussed in the first paper, but a later publication was announced, dealing with these.

HOU (1960) reduced the two Pacific species of America, *R. brevistyla* Salvoza and *R. samoensis* (Hochr.) Salvoza, into synonymy of *R. harrisonii* and *R. mangle* respectively. At that time the available material did not show the presence of *R. racemosa* on America's Pacific coast. At present this situation has not changed, although PRANCE et al. (1975) report two collections of *R. racemosa* from the coast of Ecuador. The possible presence of *R. racemosa* on the Pacific coast will be discussed more detailed below.

If *R. brevistyla* is synonymous with *R. harrisonii*, the hybrid between *R. mangle* and *R. racemosa*, the question arises how its presence can be explained in absence of one of its parents, namely *R. racemosa*.

2. THE ABSENCE OF R. RACEMOSA IN THE PACIFIC AREA

Fieldstudies in the Atlantic area have revealed that the Atlantic *Rhizophora* species differ in salt tolerance (SAVORY 1953; JONKER 1959; BRETELER 1969). The least salt tolerant species is *R. racemosa*, while *R. mangle* is the most salt tolerant one. *R. harrisonii* is intermediate. Under favourable topographical conditions both extremes i.e. *R. mangle* and *R. racemosa* may occur together. Such is the case in long river estuaries with a slight fall of the river and thus with a deep penetration of tidal influence. In such estuaries the sea water penetrates far inland until it is counterbalanced by the fresh water running downstream. This amount of fresh water, however, varies with the season, at least when in the catchment area distinct dry and rainy seasons occur. In the dry season the smaller amount of fresh water running downstream allows the salt water to penetrate very far inland. Maximum salt water penetration is reached at the end of the dry season. This limit of tidal influence constitutes at the same

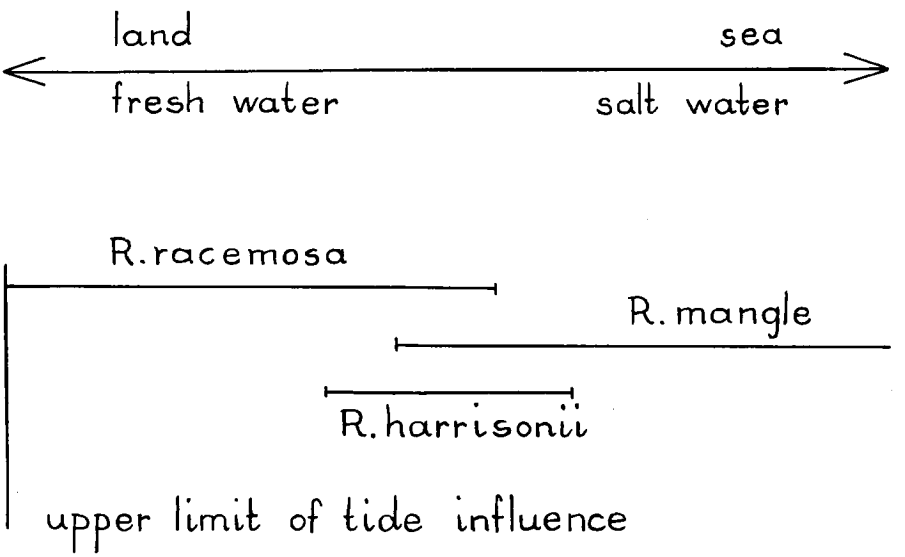
time the inland boundary of the *Rhizophora* distributional area, as the dispersal of *Rhizophora* species is effected by water. In such estuaries the zone occupied by *Rhizophora* may extend over 50 km or even more. Under such conditions *R. racemosa* is invariably found on the fresh water side (see *fig.*) i.e. in the fresh or slightly brackish water area.

Situations as described above are found in several river estuaries on the Atlantic coast of South America, e.g. in Venezuela, Guyana, Surinam, and Brazil.

At the Pacific coast of the American continent, however, such conditions are not present. Most rivers there are small, have a rather strong fall with a more constant and comparatively large output of fresh water, as a dry season is absent or at least less pronounced. As a result the transition zone between fresh and salt water is rather narrow and the brackish zone between fresh and salt water, the suitable habitat for *R. racemosa*, is very small or absent.

WEST's (1956) description of the mangrove of Colombia's Pacific coast shows that the zone occupied by mangrove is rather narrow, usually not more than one-half to three miles wide. That *R. racemosa* has not been found so far in the Pacific mangroves of America is most probably due to the fact that these mangroves lack a suitable habitat for this species. Contrary to HOU (1960: 627, 628), I feel that it is unlikely that future fieldwork will reveal its presence on America's Pacific coast.

The two specimens of *R. racemosa* reported from Ecuador's coast by PRANCE et al. (1975) most likely will prove to be *R. harrisonii* (see also section 3).



Schematic representation of the distribution of *Rhizophora* species in a long river estuary as occurring on the Atlantic coast of America.

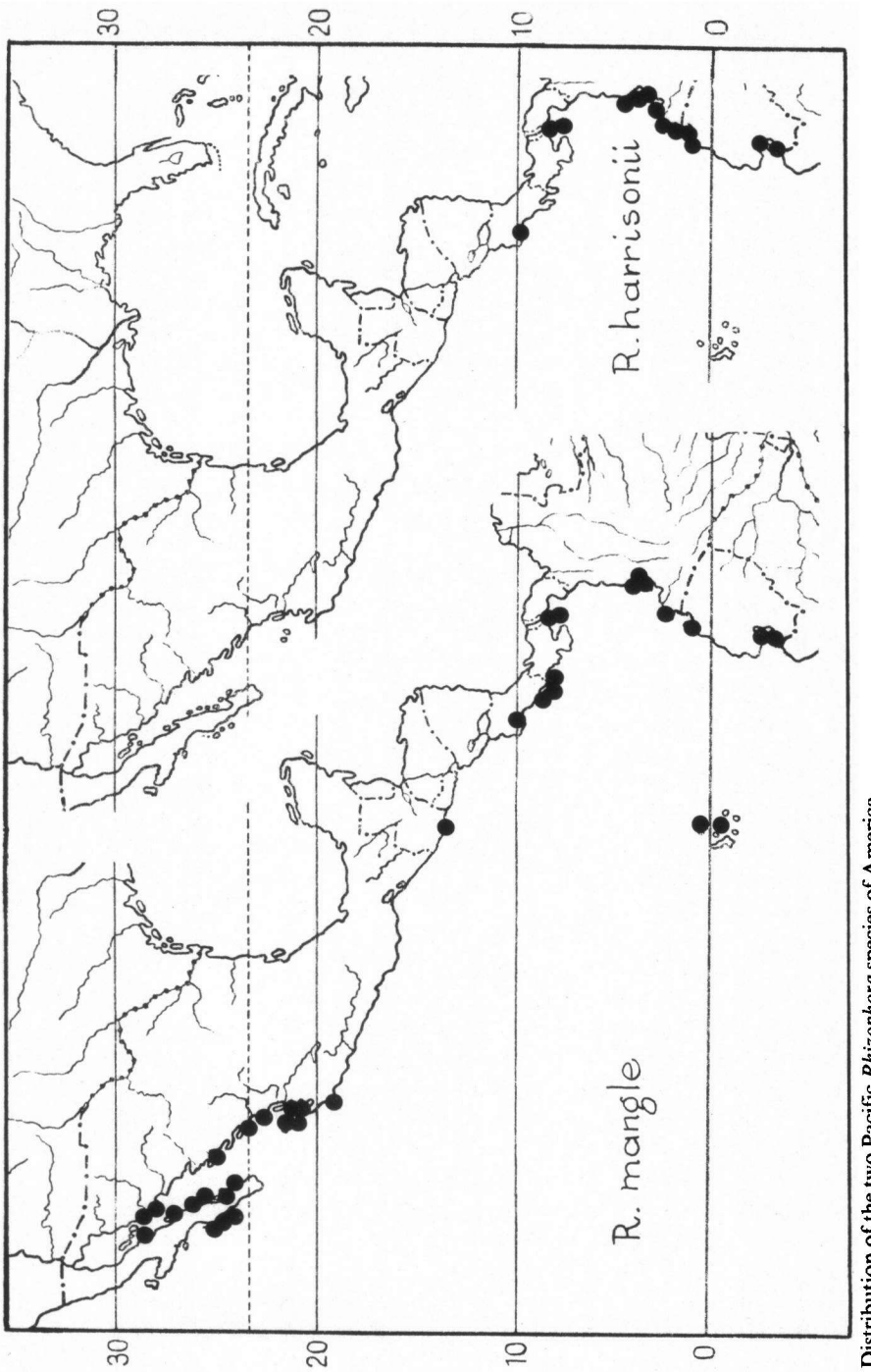
3. THE IDENTITY OF R. BREVISTYLA

In 1960 Hou reduced *R. brevistyla* to a synonym of *R. harrisonii*. The small differences mentioned by Salvoza to distinguish between his species and *R. harrisonii* do not justify its segregation. The same holds for the segregation of *R. samoensis* and *R. mangle*. Here also small differences of quantitative nature were used to distinguish between them. That the mangrove vegetations of both sides of the American continent are closely related as regards their specific composition, is not only demonstrated by sharing common *Rhizophora* species, but also by having common species associated with them, e.g. *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.f.) Gaertn., *Acrostichum aureum* L. Moreover, in geological terms, both mangrove areas have been separated only recently by the isthmus of Panama.

It is most likely that even before separation of the two areas the hybrid *R. harrisonii* was already present on the West coast of South America, together with one parent, namely *R. mangle*. The other parent, *R. racemosa*, may have been present as well, at least contact with *R. mangle* must have been possible in order to create the hybrid *R. harrisonii*. After separation of the two mangrove areas or even earlier, conditions for *R. racemosa* on the Pacific side must have changed considerably, either causing the complete extinction of this species or its complete isolation, i.e. by the formation of the isthmus. Remaining were *R. mangle* and, within its boundaries (see map) and often occurring in mixed stands, the hybrid *R. harrisonii*. Continuous interbreeding between the hybrid and *R. mangle* caused introgression i.e. genes of the disappeared *R. racemosa* slipping into *R. mangle*. This resulted in the often smaller flowers seen in this species, a character used by SALVOZA (1936) to create *R. samoensis* (see also GREGORY 1958). Another indication of the hybrid influence in *R. mangle* is seen in the often reduced pollen fertility in specimens which are morphologically pure *R. mangle*, ranging from 44% in a specimen from Guayaquil, Ecuador (Asplund 16590) to 95 % in a specimen from Nariño, Colombia (Idrobo & Weber 1432A).

On the other hand, backcrossing between *R. mangle* and *R. harrisonii* resulted in a higher pollen fertility in the latter as could be observed in several specimens (e.g. Erlanson 13: 74%; Cuatrecasas 15919: 68%; Killip & Cuatrecasas 38654: 78%; Romero-Castañeda 3203: 87%). It may be stated that in the area where both taxa occur, a leveling took place as regards their pollen fertility. The morphological differences between the two taxa, which are rather clear cut in the Atlantic area, are also affected. This resulted in a less homogenous *R. harrisonii* when compared with the Atlantic material of this hybrid, ranging from almost pure *R. racemosa* types with multiflowered widely branched inflorescences (Breteler 5185) to almost pure *R. mangle* specimens. In all the material investigated a morphologically pure *R. racemosa* was never met with.

A more or less similar situation has been observed in a small *Rhizophora* population on Cape Lopez (Gabon), where *R. mangle* and the hybrid occurred in a mixed stand, rather isolated from *R. racemosa*. Here again smaller flowers



Distribution of the two Pacific *Rhizophora* species of America.

in *R. mangle* with lower pollen fertility (e.g. Breteler 5550: 65%; Breteler 5555: 15%) could be observed while a greater difficulty to distinguish between *R. mangle* and the hybrid *R. harrisonii* was experienced.

4. CONCLUSIONS

The Pacific *Rhizophora* species of America are *R. mangle* and the hybrid *R. harrisonii* (*R. mangle* × *R. racemosa*). The small differences with the Atlantic material do not justify their separate status and *R. samoensis* and *R. brevistyla* should be reduced into synonymy. The small differences of quantitative nature are due to introgression.

R. racemosa does not occur on the Pacific coast of America. The mangroves there do not provide a suitable habitat for this, least salt tolerant, species.

SPECIMENS EXAMINED

The cited material has been identified with certainty. Much more specimens, either sterile or with fragmented inflorescences have been examined. These, however, could not be identified as belonging to either *R. harrisonii* or *R. mangle*, and are not cited.

R. harrisonii

COSTA RICA. Puntarenas, between Caldera and Matalimon, Lems 5025 (NY).
PANAMA. Canal Zone, Allen 1276 (A); Bella Vista, Salvoza 1007 (A); San José I., Erlanson 13 (US); Harlow 33 (A, US); Johnston 1357 (A); Mireya & Correa 100 (A, MO); Taboga I., Miller 1763 (MO, US); Porto Rosado, Williams 616 (NY, US).
COLOMBIA. Valle del Cauca. S. of Buenaventura, Ria Raposo, Breteler 5185 (WAG); Rio Yurumangui, Cuatrecasas 15919 (COL); Quebrada de Aguadulce, Cuatrecasas 20001 (COL); Punta Arenas, Killip & Cuatrecasas 38654 (US); Bahia de Buenaventura, Perez Arbelaez s.n. (COL). Cauca. Rio Bubuey, Romero-Castañeda 5456 (COL). Nariño. Tumaco, Espinosa 3012 (NY); Romero-Castañeda 3203 (COL); S. of Tumaco, Romero-Castañeda 5370 (COL).
ECUADOR. Esmeraldas. Near La Tolita, Jativa & Epling 1172 (US); 3 km S.W. of San Lorenzo, Little 6282 (US); 6285 (NY, US). Guayas. Rio Guayas, Asplund 7706 (NY).

R. mangle

MEXICO. Baja California, East Coast. Los Angeles Bay, I.L. & D. B. Wiggins 14883 (US); Johnston 3492 (A, UC); Las Animas Bay, Johnston 3492 (A, MO); Mulege, Johnston 3657 (A, NY, UC); 16 miles S. of Mulege, Ferris 8679 (US); Conception Bay, I.L. & D. B. Wiggins 18052 (US); I.L. Wiggins 5453 (A, NY, UC, US); Rose 16949 (US); Carter & Kellog 2826 (A, US); Carmen I., Johnston 3822 (A, UC); near La Paz, I.L. Wiggins 15611 (A); Nelson & Goldman 7530 (US); Carter 2739 (US). Baja California, West Coast. Magdalena I., Orcutt 19 (NY, US); Pichilinque I., Rose 16525 (US); Magdalena Bay, Brandegee s.n. (UC); Mason 1914 (A); Estero Salinas, I.L. Wiggins 11493 (A, UC, US); Porter 467 (A, UC). Sonora. Rio de Sonora, Drouet & Richards 3543 (A); N. of Guayamas, Straw & Gregory 1273 (NY, UC); Guayamas, Coville 1667 (US); Palmer 342 (A, NY, US). Sinaloa. Near Tobolobampo, Rose, Standley & Russell 1333 (A, NY, US); Mazatlan, Ortega 6524 (US); Escuinapa, Ortega 5179 (US). Nyarit. Mexcaltitlan, Mexia 1003 (A, MO, NY, UC, US); San Blas, Alava & Cook 1598 (UC); Detling 8174 (US); Fer-

ris 5398 (A). Colima. Manzanillo, Gregory & Eiten 332 (NY). Oaxaca. Chacalina Bay, Conzatti 4468 (US); Elmore 24 (A, NY, UC, US).
GUATEMALA. San José, Donnell Smith 2512 (US); Maxon & Hay 3661 (US); Las Fianzas, Salas 373 (US).
COSTA RICA. Playas El Coco, W. of Liberia, Lems s.n. (NY); Puntarenas, Lems 5024 (NY); Lems s.n. (NY); West 3590 (UC); Golfito, Burger & Matta 4739 (NY); S. Domingo de Golfo Dulce, Tonduz in herb.nat. Cost. 10059 (A, MO, NY, US).
PANAMA. Burica Peninsula, near S. Bartlomé, Woodson & Shery 934 (MO, US); Bella Vista, Salvoza 1006 (A); Canal Zone, near Tarfan, Stern & Chambers 149 (A, MO, NY, US); San José I., Johnston 253 (A).
COLOMBIA. Valle del Cauca. Buenaventura Bay, Breteler 5179 (WAG); 5180 (WAG); 5182 (WAG); Core 1568 (NY, US); Duque-Jaramillo 4390A (COL); Killip & Cuatrecasas 38817 (US). Nariño. Tumaco, Romero-Castañeda 5308 (COL); Choco, Delta del Atrato, West 14 (COL); Rio Mira, Dryander 2614 (US); 2616 (US).
ECUADOR. Guayaquil, Asplund 15248 (NY); Puna I., Gilmartin 151 (MO); Puerto Bolivar, Espinosa 2413 (NY); 2451 (NY); between Machala and Puerto Bolivar, Hitchcock 21100 (US). Galapagos Islands. Tower I., Svenson 284 (NY; UC): Indefatigable I., Conway Bay, Conway 1116 (NY); Indefatigable I., S.E. side, Stewart 3022 (US).

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A – Cambridge, U.S.A.: Arnold Arboretum.
COL – Bogota, Colombia: Instituto de Ciencias Naturales de la Universidad Nacional.
MO – Saint Louis, U.S.A.: Herbarium of the Missouri Botanical Garden.
NY – New York, U.S.A.: Herbarium of the New York Botanical Garden.
UC – Berkeley, U.S.A.: Herbarium of the University of California.
US – Washington, U.S.A.: United States National Herbarium.

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