THE ATLANTIC SPECIES OF RHIZOPHORA

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1. INTRODUCTION

The Atlanctic species of *Rhizophora* have been subject of several publications recently and it seems currently accepted that three species ought to be distinguished for the Atlantic area: *R. mangle* L., *R. racemosa* G. F. W. Meyer, and *R. harrisonii* Leechman.

R. mangle was first described being based on a Jamaica specimen. *R. racemosa* and *R. harrisonii* were based on material from Guiana when first described. KEAY (1953) proved after studying West African *Rhizophora* that the 3 species occur on both sides of the Atlantic, on the American coast as well as on the western coast of Africa.

The specific delimitation was based on morphological characters, correlated with ecological data (KEAY 1953; SAVORY 1953). JONKER (1959) made field observations in Suriname and supported Keay's and Savory's conclusions. HOU (1960) made a review of the whole of the genus *Rhizophora* and united the Pacific species of America with the Atlantic ones.

When carrying out field work in the mangrove areas of Venezuela and Colombia, I arrived at some doubt about the delimitation of the Atlantic species of *Rhizophora*, especially as regards the taxonomic position of *R. harrisonii*.

The present paper is a result of these field studies carried out in America, to which field-observations in Africa are added while the study was completed by an investigation of herbarium material and various other data.

2. TAXONOMY

The morphological characters to be applied when differentiating the Atlantic *Rhizophora* species are found in the inflorescence, the pedicel, the flower bud, and the hypocotyl. These characters (mainly of quantitative nature) are listed below.

When it is realized that the tabulated characters are the generally accepted characteristics in delimiting the species, it can be said that the table shows that in *R. harrisonii* characters of either *R. mangle* or *R. racemosa* or of both these species are present. By its morphology it might be suspected of a hybrid origin.

R. harrisonii has the much-branched, many-flowered inflorescence of *R. racemosa*, but the bud shape, the lax branching and the longer pedicels of *R. mangle*. The inflorescence of the latter species is often tri- or even tetrachasially branched. Such a basal branching can often be observed in inflorescences of *R. harrisonii* but never in those of *R. racemosa*.

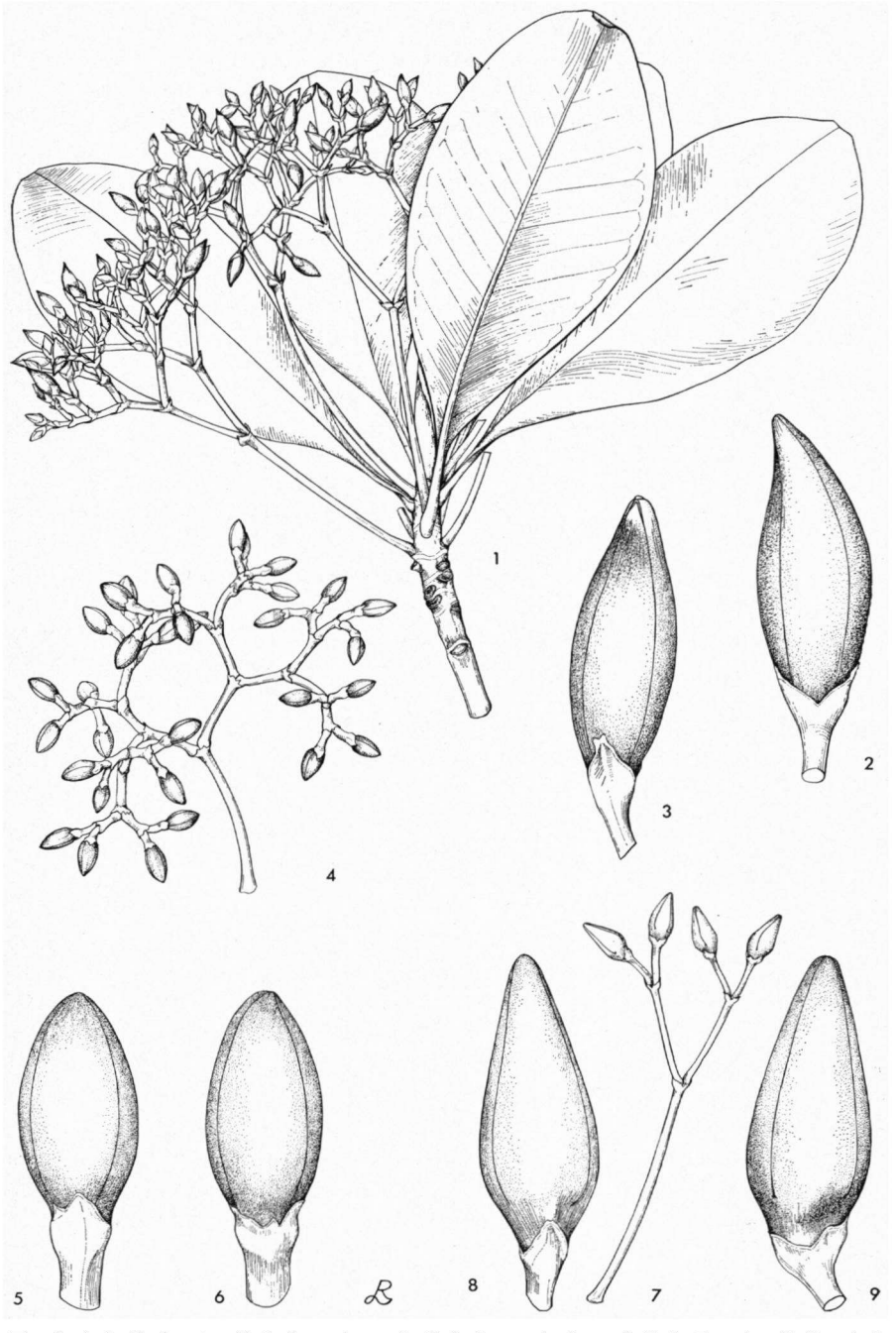

Fig. 1. 1–3. *R. harrisonii*: 1. branch, × ½; 2–3. flower bud, × 3 (1–3. Breteler 5168); 4–6. *R. racemosa*: 4. inflorescence, × ½; 5–6. flower bud, × 3 (4–6. Breteler 5164); 7–9. *R. mangle*: 7. inflorescence, × ½; 8–9. flower bud, × 3 (7. de Bruijn 1268; 8–9. Breteler 5173).

The bracteolar cup, and also the cup formed by the bracts, is closed in the beginning, when the bud is young. The bracteoles are then almost completely united; only the thin, apical part is free and hood-like (see *fig. 2: 1–3)*. When the enclosed flower bud or branches of the inflorescence develop *(fig. 2: 4)* the cup must split downwards. The cup is rather thin in *R. mangle* and thick in *R. racemosa*. In *R. harrisonii* the cup is intermediate in thickness. For this reason a splitting into two "lips" results in this species as in *R. mangle*. I was unable to confirm that the bracts and bracteoles are "acute" as KEAY (1953) noted for *R. harrisonii*, but found them always truncate-emarginate. However, the thin, apical part sometimes is deciduous and the persistent part then becomes more or less acute.

The bud of *R. racemosa* sometimes is obtuse at top, especially when young, but mostly acutish or even acute. This is, to some extent, contrary to KEAY (1953) who described the bud as obtuse at top, but the picture illustrating this description shows, in my appreciation, an acute or, at least, acutish bud. STEARN (1958) described the *R. racemosa* bud as 'blunt at tip'.

HOU (1960) used as a key-character that the calyx lobes are unequal in length in *R. mangle* and equal in *R. racemosa* and *R. harrisonii*. The calyx lobes, however, are unequal in all the Atlantic species, although, sometimes only slightly so.

A useful field character to distinguish *R. racemosa* from *R. mangle* and *R. harrisonii* was found in the colouring of stipules, and midrib and petiole on the lower surface. In *R. racemosa* these parts are mostly red, in *R. harrisonii* sometimes with a pinkish tinge, but mostly green as in *R. mangle*. KEAY (1953), however, described the midribs of *R. harrisonii* as 'reddish', which could not be confirmed by JONKER (1959) or by my own observations in Venezuela and Gabon.

3. ECOLOGY AND DISTRIBUTION

The three Atlantic species were studied ecologically in Nigeria by SAVORY (1953) and in Suriname by JONKER (1959). My own field observations were at the Atlantic coast of Venezuela in 1965–1966 and at the coast of Gabon in 1968. LEECHMAN (1918) when describing *R. harrisonii* from Guiana gave information about the ecology of the three species.

The most salt-tolerant species is *R. mangle*, which may occur even in somewhat marshy localities on generally dry sandy shores. *R. racemosa* is the least salt-tolerant species occurring often in only slightly brackish localities (or even in fresh water). The zoning in the *Rhizophora* habitat, although not clearly demarcated, can be observed in river estuaries and upstream river as far the tide may reach. JONKER (1959) made observations regarding this zoning in several rivers of Suriname.

I did so in the San Juan River in Venezuela. There the first scattered *R. racemosa* trees of a fair size appear where the salt water penetrates in the dry season. Going downstream the number and height of *R. racemosa* trees increase

	R. mangle	*R. harrisonii*	*R. racemosa*
Inflorescence	1–4-flowered	many flowered	many flowered
length	4–9(13) cm	5–12 cm	4–8(12) cm
length of peduncle	1.7–6(10) cm	2.0–5.5(8) cm	1.5–4.8(7) cm
branching	not, or at most twice branched; lax, at narrow angles	(2)4–5(6) times branched; lax, mostly at narrow angles	5–6 times branched; stiff; stout; at large angles
Pedicel	(5)7–20(25) mm	3–11 mm	(2)3–5(7) mm
Bracteolar cup	thin becoming 2-lipped	intermediate, mostly becoming 2-lipped	thick, mostly irregular lacerate-dentate
Flower bud	ovate in general outline; top acute	ovate to slightly elliptic in general outline; top acute	mostly elliptic in general outline; top acutish or acute, sometimes obtuse
Radicle length (Hypocotyl)	15–20(34) cm	11–25 cm	up to 50 cm

and *R. racemosa* is a more and more important part of the bank vegetation. Further downstream both the other species appear and the three together form a homogenous mixed stand of 25–35 m tall trees. Still closer to the sea the number and size of *R. racemosa* trees decrease, but the presence of the latter species could still be demonstrated in *Rhizophora* forests facing the open sea. This growing locality, however, has large amounts of brackish water in the rainy season. Here *R. mangle* and *R. harrisonii* are the dominant species in a tall mixed forest.

Although the salt-tolerance of the species is different, they appear to find their optimum environment in the same area, where the 3 species grow as tall trees in a mixed forest. Ecological separation thus proves to be clearly marked only where conditions (salt percentage) are extreme.

The ecological demands of *R. harrisonii* are exactly in between those of *R. mangle* and *R. racemosa*. It avoids the extremes in the growing conditions, but occurs, as a rule, accompanied by either *R. mangle* or *R. racemosa*, or by both.

The geographical distribution of *R. harrisonii* appears to be closely linked to the distribution of *R. mangle* and *R. racemosa*. The localities from which *R. harrisonii* was recorded often appear to be identical for both the other species or at least are connected by tidal influences or otherwise. From several localities in Africa (*fide* KEAY 1953) all the three species are known to occur, but in some localities only *R. harrisonii* was collected, and there is no record for the occurrence of the other species. To prove that in those localities *R. mangle* and *R. racemosa* are, nevertheless, also present or that a locality with *R. harrisonii* only is connected with the habitats of these two species, a fieldtrip to that area is needed.

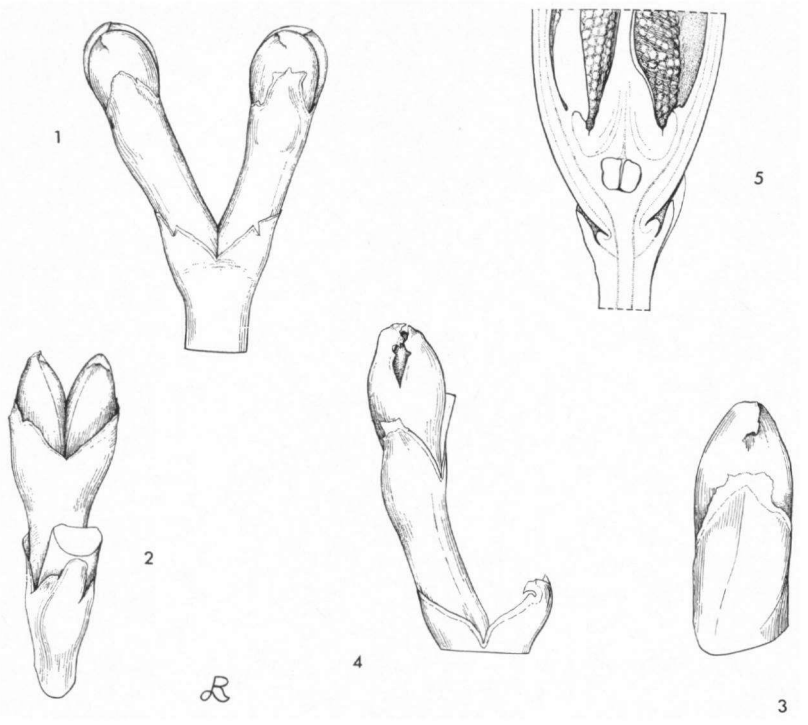

Fig. 2. *R. harrisonii*: 1. detail of inflorescence, each branch with two buds at top, × 4; 2. cupula with two closed buds, × 5; 3. detail of closed cupula, × 10; 4. cupula partly open, × 5; 5. length cut of flower part with cupular swellings, × 6 (1. Breteler 5166; 2–5. Breteler 5168).

Field studies dealing with the local distribution of these three species are mostly restricted to certain small areas or one country, like SAVORY's (1953) to Nigeria, JONKER's (1959) to Suriname, and JACQUES-FELIX's (1957) to Guinea. In all these areas, and in Venezuela and Gabon, where I was able to study the habitats, it could be shown that the presence of *R. harrisonii* was accompanied by the occurrence of both *R. mangle* and *R. racemosa.*

4. PHENOLOGY

The *Rhizophora* species are evergreen trees with no special flowering season. In poor habitats the trees soon reach their mature size and flower mostly profuse and all the year round. Where the species grow as tall forest trees the mature stage is reached later and flowering is mostly less profuse. From notes of different field observers and others (LEECHMAN 1918, KEAY 1953, JONKER 1959) and from my own experience it is known that *R. harrisonii* is a taxon which flowers often profusely but bears few fruits. This is also demonstrated by the fact that

a small percentage of herbarium specimens of *R. harrisonii* is in fruit. Herbarium of *R. mangle* and *R. racemosa* is significantly much richer in fruiting specimens. It is to be noted that only a few intermediate specimens are found between *R. harrisonii* and the other two Atlantic species.

5. CONCLUSIONS

The position of *R. harrisonii* is morphologically and ecologically intermediate between *R. mangle* and *R. racemosa*. Its distribution is closely linked with both these species. The fruiting of *R. harrisonii* is poor although it flowers profusely.

These three points lead to suspect that *R. harrisonii* must be considered to be of hybrid nature, *R. mangle* and *R. racemosa* being its parents. When this view had been arrived at, I looked for further data.

Mr. J. Muller (Leiden, Rijksherbarium) investigated the pollen of the 3 species of *Rhizophora* at my request. Mr. Muller studied samples of 9 *R. mangle* specimens, of 8 *R. racemosa* specimens, and of 7 *R. harrisonii* specimens, originating from both sides of the Atlantic. He was able to show that *R. harrisonii* has always a strongly reduced pollen fertility (ca. 20–60% fertile), whilst the pollen of *R. racemosa* and *R. mangle* is mostly for 97–100% fertile.

In a few specimens, identified either as *R. mangle* or as *R. racemosa*, also a reduced pollen fertility was observed. These specimens, however, all originate from localities where the three taxa occur together, and it may be noted that these specimens, although morphologically resembling *R. mangle* or *R. racemosa*, most probably belong to the F2, F3, etc. generation of hybrids between those two species, or may be of another hybrid nature. I wish to thank Mr. Muller for his very valuable help which strengthens considerably the conclusion that *R. harrisonii* is the hybrid between *R. mangle* and *R. racemosa*.

As regards the wood anatomy in Atlantic *Rhizophora*, it is stated that no clear anatomical difference can be established among the taxa, partly perhaps, because the anatomical characters appear to vary rather widely according to growing conditions. Nevertheless, Mr. Chr. Versteegh (wood anatomist in the Laboratory for General Botany of the University for Agriculture at Wageningen) kindly informed me that judging from his preliminary research, a possible means of distinguishing between the woods when growing under similar conditions might be found.

There is need for morphological research on the Pacific species of the genus. I hope to report on these species later.

SPECIMENS EXAMINED

AFRICA

R. harrisonii. Gabon: Cape Lopez, near Port Gentil, Breteler 5542 (WAG), 5552 (WAG), 5554 (WAG).

R. mangle, Sierra Leone: Near Freetown, Morton SL 630 (WAG).
Liberia: Monrovia, Kunkel 537 (WAG), 551 (WAG).
Gabon: Cape Lopez, near Port Gentil, Breteler 5549 (WAG), 5550 (WAG), 5551 (WAG), 5555 (WAG).

R. racemosa. Sierra Leone: near Freetown, Morton SL 608 (WAG); ibid. Morton et Gledhill SL 617 (WAG).
Liberia: Monrovia, Breteler 5452 (WAG); ibid., H. C. D. de Wit 9129 (WAG); ibid., Kunkel 9 (WAG), 536 (WAG); Paynesville, Voorhoeve 99 (WAG).
Ivory Coast: Fresco, Breteler 5351 (WAG), 5352 (WAG); near Port Bouet, Leeuwenberg 2715 (WAG); ibid., Oldeman 430 (WAG); Grand Bassam, Breteler 5332 (WAG); ibid. J. J. F. E. de Wilde 482 (WAG), 1026 (WAG); ibid., Oldeman 942 (WAG).
Nigeria: Lagos, Bels 16 (U); Nun R., Mann 492 (U).
Gabon: Cape Lopez, near Port Gentil, Breteler 5553 (WAG), 5556 (WAG).

AMERICA

R. harrisonii. Venezuela: Monagas, San Juan R., Breteler 4683 (U; WAG), 4686 (WAG) 4687 (U; WAG), 5166 (U; WAG), 5167 (WAG), 5168 (U; WAG); Peninsula Paria, near Yaguaraparo, Breteler 5171 (U; WAG). Note: The specimens Breteler 4683 and 4686 are intermediate between *R. harrisonii* and *R. racemosa*, but closer to *R. harrisonii*.
Guiana: Coastal region near Georgetown, Leechman s.n. (U).
Suriname: Nickerie R., Tulleken 583 (U); Lower Saramaca R., Jonker 600 (U); Suriname R., near Liberté, J. et P. A. Florschütz 910 (U); Suriname R., S. E. of Braamspunt, Kramer et Hekking 2096 (U); Suriname R., Pauluskreek, Mennega 191 (U); Commewijne R., Jonker et Jonker-Verhoef 570 (U), 571 (U), 573 (U); Marowijne R., near Galibi, Lanjouw 544 (U); s.l., Suriname Forest Service V 64 (U).

R. mangle. (only South American specimens are cited). Venezuela: Lake Maracaibo, de Bruijn 1268 (WAG), 1299 (WAG), 1300 (WAG), 1310 (WAG), 1313 (WAG); Peninsula Paraguana, Breteler 4343 (U; WAG); near Tucacas, Raets s.n. (U; WAG); between Puerto La Cruz and Cumana, Breteler 5175 (WAG), 5176 (U; WAG); Peninsula de Paria, near Yaguaraparo, Breteler 5172 (U; WAG); 5173 (U; WAG); Monagas, San Juan R., Breteler 4682 (U; WAG), 4684 (U; WAG).
Guiana: near Georgetown, Harrison, Graham & van der Hammen 1699 (U); ibid., Leechman s.n. (U).
Suriname: lower Saramaca R., Jonker 602 (U); Suriname R., Leonsberg, Suriname Forest Service 138 (U); ibid., Helstone 13 (U; WAG); Suriname R., plantage Purmerend, Jonker 514 (U); Suriname R., Soeprata 20 F (U); ibid., S. E. of Braamspunt, Kramer et Hekking 2095 (U); Cultuurtuin, Dalger 6215 (U); lower Commewijne R., Kronenburg, Jonker et Jonker-Verhoef 574 (U).
Brazil: Maranhao, Maracassumé R. region, Froes 1762 (U); near Rio de Janeiro, Barra de Tijuca, Pulle-Lutz 1093 (U); Rio de Janeiro, Lino Tatto 37 (U).

R. racemosa. Venezuela: Peninsula de Paria, near Yaguaraparo, Breteler 4452 (WAG); Sucre, San Juan R., Breteler 4674 (U; WAG), 4675 (WAG), 4679 (U; WAG), 4681 (U; WAG); Monagas, San Juan R., Breteler 4685 (WAG), 5162 (U; WAG), 5163 (U; WAG), 5169 (WAG); Monagas, Guarapiche For. Res., Breteler 5151 (WAG), 5152 (U; WAG); Monagas, Guarapiche R., Breteler 5164 (U; WAG); Delta Amacuro, ca. 62°15'W, 9°55'N, Breteler 3555 (U; WAG).
Guiana: Essequibo R., Meyer 226 (GOET, holotype).
Suriname: Nickerie R., Wageningen, Jonker & Jonker-Verhoef 596 (U), 597 (U), 598 (U); Saramaca R., Huwelijkszorg, Jonker 599 (U), 601 (U); ibid., Carel Francois, Stahel 108 (U); Suriname R., Focke 679 (U); Commewijne R., near Slootwijk, Soeprata 47 J (U); lower Commewijne R., Jonker & Jonker-Verhoef 572 (U), 575 (U); Marowijne R., Albina, Lanjouw et Lindeman 325 (U).

Note. *Fig.* 2: 5 shows cupular swellings as have been observed in several specimens of *R. harrisonii*. These two swellings alternate with the bracteoles. In *R. racemosa* and *R. mangle* these swellings are wanting or sometimes very slightly developed unilaterally. In the latter species colleters are mostly present in the cupula, but rarely in *R. racemosa* and *R. harrisonii*.

ACKNOWLEDGEMENTS

The author is much indebted to MR. J. MULLER from the Rijksherbarium, Leiden, for his research on the pollen of the Atlantic *Rhizophora* species and to MR. CHR. VERSTEEGH from the Laboratory for General Botany, Wageningen, for his preliminary anatomical investigation. He expresses his gratitude to the director of the Systematisch-Geobotanisches Institut, Göttingen, for sending on loan the type of *R. racemosa*, to the curator of the Utrecht herbarium for facilities when visiting this herbarium, and to MISS L. VAN DER RIET for her fine drawings.

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