

## SONNERATIACEAE (concluded)

### SONNERATIACEAE AND OTHER MANGROVE-SWAMP FAMILIES, ANATOMICAL STRUCTURE AND WATER RELATIONS

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The question whether tidal and non-tidal members of a family have a separate wood anatomical structure would be examined best in such genera as embrace both types. The sequel to this examination, whether any such differences are connected with peculiarities in the water relations of the plants, should be examined in the same way. There are, however, few genera that comprise both littoral and inland species. In some of these genera, *Excoecaria*, *Ixora* and *Dolichandrone*, wood anatomical data can be compared but water relations among the species have not been examined nor are comparative data from the nearest relatives available.

According to MOLL & JANSSONIUS the mangrove-swamp species possess more vessels per mm<sup>2</sup> with a larger total area on cross section and the pores are mostly distinctly smaller than in the nearest related inland species. However, data on area JANSSONIUS did not record.

*Excoecaria agallocha* L. has 7–14 vessels per mm<sup>2</sup> of cross section with a diameter up to 80 μ, whereas these data in *E. virgata* Zoll. & Mor. are 3–6 per mm<sup>2</sup> and 40–150 μ. The total area occupied in the tidal species by the water conductive tissue is said to be larger than in the non-tidal *E. virgata*. The same relations are found among *Ixora paludosa* Boerl. [KOORDERS & VALETON 8 (1902) 156] and the other Javanese *Ixora* species (MOLL & JANSSONIUS, JANSSONIUS, PANSHIN, PEARSON & BROWN). As regards *Dolichandrone spathacea* (L. f.) K. Schum. and inland species from India, the tidal species *D. spathacea* has 4–6 vessels per mm<sup>2</sup> with a diameter of 40–150 μ (MOLL & JANSSONIUS, JANSSONIUS) or 9–12 per mm<sup>2</sup> and 120–130 μ (PANSHIN). In the inland species [*D. atrovirens* Sprague (= *D. crispa* Seem.), *D. falcata* Seem., *D. arcuata* C. B. Clarke] the vessel number is scanty to rather scanty and the diameter has been classified as small (GAMBLE) which data do not differ appreciably from those found in the tidal species.

With regard to the tidal and non-tidal genera in the same families, JANSSONIUS found the said tendency. The data e.g. for the tidal genus *Sonneratia* and the inland genus *Duabanga* are 35–40 against 4–5 per mm<sup>2</sup> and the diameter is 35–175 μ against 130–400 μ respectively. JANSSONIUS also found these relations among genera of the *Combretaceae* (cf. PANSHIN) and the *Meliaceae* but less conspicuously in the latter family. Vessels are extremely numerous in *Aegiceras* with 200 per mm<sup>2</sup> and less so in the other *Myrsinaceae* where 100 or less and 140 at the utmost have been found. An exception is formed by *Heritiera littoralis* Dry. which species with 5,1 vessels/mm<sup>2</sup> and a pore diameter of 100–175 μ (CHATTAWAY, DEN BERGER) does not differ markedly from the other genera of the *Sterculiaceae*.

As regards the *Rhizophoraceae* JANSSONIUS's data seem to point to vessels being more numerous and smaller in the tidal tribe but the data have not been quite confirmed by MARCO.

The tidal species in which the vessel number per cross section is less than 15 per mm<sup>2</sup> with the exception of *Heritiera* are characterized by thinner-walled libriform fibers with wider lumina (PANSHIN).

The same differences have been recorded between two tidal species of *Sonneratia* of which *Sonneratia apetala* Ham. in the Delta forests of Bengal at a river mouth grows in less salty localities than *Sonneratia griffithii* Kurz. *Sonneratia apetala* has 18–32 vessels per mm<sup>2</sup> with a diameter of 135–150 μ against the data 34–50 and 85–100 μ in *Sonneratia griffithii* Kurz (PEARSON & BROWN). JANSSONIUS, however, did not find these facts in *Sonneratia alba* J. E. Smith from the outer fringe and *Sonneratia caseolaris* (L.) Engl. from the inner zone of the mangrove swamp formation (Fl. Mal. I, 4, p. 280; TROLL & DRAGENDORFF) in Java, both species showing the same vessel number.

However, in the non-tidal genus *Markhamia* (*M. platycalyx* (Bak.) Sprague; *M. stipulata* Seem. = *Dolichandrone stipulata* Benth. in PEARSON & BROWN) even more vessels have been reported than in the tidal genus *Dolichandrone* (PEARSON & BROWN, HARRIS & EGGELING).

Discrepancy among data such as in the *Bignoniaceae* and in the *Rhizophoraceae* can be attributed to variations due to the place of taking samples in the tree. This statement is supported by the following example. In *Bruguiera gymnorrhiza* Lamk. PEARSON & BROWN report 40–62 vessels per mm<sup>2</sup> with a maximum tg diameter of 115–135  $\mu$  whereas JANSSONIUS found 25 vessels and a maximum diameter of 115  $\mu$ . These facts may mean that the latter author did not examine mature wood. Consequently, future investigators would do well to eliminate the influence of different age and of different height in the tree.

Summarizing the data it may be concluded that there is in the tidal species a tendency towards increase of the number of vessels and the total area of water conductive tissue in the cross section and a tendency towards decrease of the vessel diameter. Not justified seems to be JANSSONIUS's suggestion that the variation in number of vessels per unit area in 3 species of *Bruguiera* might be correlated with the different number of every month inundations (DE HAAN). Cf. PANSHIN for data on *Bruguieras*.

The anatomy of leaf and stem shows structural features that are called xeromorphic by MULLAN and non-xeromorphic by SHMUELI. WALTER & STEINER avoid using the terms.

*Succulent leaves* are a common feature and induced by the presence of a distinct hypodermal aqueous tissue which in *Sonneratia* even forms an inner layer of many cells [WALTER & STEINER, MULLAN (a, c, d)]. In leaves that are immersed during high tide the layer is 3–5 times as thick as at a higher level in the tree and it is almost absent in plants grown in fresh water in botanical gardens. Succulency appears to be a response to the presence of chloride in the medium (WALTER & STEINER, VAN EYK, see also review by UPHOF).

Under mesophytic conditions the salt excreting *glandular hairs* developed feebly [MULLAN (b)] and salt incrustations failed to appear on the leaves of the plant studied (*Acanthus ilicifolius* L.).

As regards water relations: *transpiration*, *osmotic pressure* and *suction force* have been studied.

*Transpiration* in mangroves and in halophytes in general appears to be low (WALTER & STEINER, WALTER (b), ADRIANI, SHMUELI) as it was once supposed to be by SCHIMPER, and by no means considerable (see WALTER & STEINER, footnote p. 106) as VON FABER's data seemed to suggest (VON FABER, UPHOF). Transpiration in *Sonneratia* and other typical mangrove trees if expressed in mg/g fresh weight or in mg/unit leaf area (WALTER & STEINER) is equal to or even lower than the water loss in glycophytic tropical trees (STOCKER) or in the mesophytes studied by PISEK & CARTELLIERI (a). Comparative data from the nearest relatives are not available. In recent ecological work in other plant associations transpiration per m<sup>2</sup> of soil area is studied [PISEK & CARTELLIERI (b)].

Although not being as high as it was originally thought, the *osmotic value* in the cells of the leaves is always higher than in the soil or in the sea water. WALTER & STEINER with the kryoskopik method found that *Sonneratia alba* J. E. Smith has an osmotic value of about 32 atms whereas in the soil and in the sea water this value fluctuates between 20 and 25 atms. Similar data have been recorded for other tidal genera. BLUM using the plasmolytic method found ca 50 atms in the same (? : "*albida*") species. SEN GUPTA (a) with the kryoskopik method found the osmotic values in *Rhizophora* and other mangrove trees in India to be somewhere between those of WALTER & STEINER and of BLUM. No data are available about the osmotic pressure of related non-tidal species or genera but it is a well known fact that the glycophytes (except some xerophytes) do not show such high values. Such tidal species as are not obligate halophytic (cf. BENECKE & ARNOLD) show lower osmotic values if they are grown artificially in glycophytic conditions (Bogor Botanical Gardens). BLUM in the upper epidermis of the leaf of *Sonneratia caseolaris* (L.) Engl. (*S. acida*) calculated the pressure to be 22 atms whereas in the natural habitat this value was 27 atms. The same conditions prevail in connection with the salinity of the natural habitat, the higher value being found in the seaward zone. WALTER & STEINER found the osmotic pressure in *Avicennia marina* (Forsk.) Vierh. var. *typica* Bakh. ranging from 35–46 atms. SEN GUPTA (a) is confirming this statement for all species studied by him with the only exception of *Excoecaria agallocha*. In this species the higher value of 43 atms has been found in the brackish

water with the lower osmotic value, whereas in a more salty habitat 26 atms were calculated. No explanation has been presented for this apparently exceptional case.

SEN GUPTA (b) studied the annual variation of osmotic values and found low values at the time of flowering and fruiting.

It seems now well agreed that VON FABER's data of 60–160 atms are overrated and due to methodic errors.

COOPER & PASHA and BLUM are bringing data on the *suction pressure* values of mangrove swamp plants [see also WALTER (a)]. In the lower littoral zone where the sea water always covers the ground suction pressure did not vary with the tides and in *Rhizophora conjugata* was found to be 33 atms. In plants growing in brackish water in the vicinity of river mouths e.g. in *Sonneratia caseolaris* (*S. acida*), there is a difference of about 5 atms, the higher value (27 atms) being found during high tide against 23 atms at low tide. Contrarily, in plants from more saline localities, as in *Sonneratia alba* (*S. albida*), the higher value of 40 atms has been found during low tide and the lower one of 34 atms at high tide. The difference between suction pressure at a level of 8 m in the tree and substratum was found by BLUM to be *ca* 20 atms. BLUM for purposes of comparison studied suction pressure in trees of the rain-forest and found values of 15.1 atms and 0.3 atms in leaf and soil. Only one tree species has been mentioned by name: *Excoecaria agallocha* which species is not an inland species but a mangrove plant and as such is not the right example to illustrate differences in suction pressure in the rain-forest soil.

COOPER & PASHA found high osmotic values and suction force values with little difference between the two figures. An increase was found from July to October [60–80 atms].

Summarizing physiological and anatomical data we may conclude that succulency, formation of glandular hairs, osmotic pressure and suction force values are to a certain extent depending on environmental conditions. Further research about the water balance especially about the saturation deficit of mangrove tree species and related inland species will have to be awaited (*cf.* ROUSCHAL; CRAFTS *et al.*). The smaller diameter of the pores in the mangrove tree might be advantageous as in such narrow vessels the rupture of the water column may be hampered. Whether the larger area of water conductive tissue in the tidal species would be advantageous also, depends on physical properties that cannot be discussed here. The anatomical data, however, will have to be verified in connection with the variations resulting from wood samples taken in different annual rings and at different heights in the tree.

*References*:—ADRIANI (a), Proc. Kon. Ned. Ak. Wet. Amsterdam 40 (1937) 524; (b), Comm. 88, Sigma, Montpellier (1945); BACKER & VAN STEENIS, Fl. Mal. I, 4 (1951) 280; BECKING *et al.*, Tectona 15 (1922) 561; DEN BERGER, Handel. N. I. Natuurwet. Congr. 4 (1927) 397; BENECKE & ARNOLD, Planta 14 (1931) 471; BLUM, Ber. Schweiz. Bot. Ges. 51 (1941) 401; CHATTAWAY, Phil. Trans. Roy. Soc. London 228 (1937) 313; COOPER & PASHA, J. Indian Bot. Soc. 14 (1935) 109; CRAFTS *et al.*, Water in the Physiology of Plants (1949); VAN EYK, Rec. Trav. Bot. Néerl. 36 (1939) 559; VON FABER in SCHIMPER—VON FABER, Pflanzengeographie 1 (1935) 35; GAMBLE, Man. Indian Timb. (1922) 511; DE HAAN, Tectona 24 (1931) 39; HARRIS & EGGELING in CHALK *et al.*, For. Trees & Timb. Brit. Emp. 4 (1939) 21; JANSSONIUS, Blumea 6 (1950) 465; KOORDERS & VALETON 8 (1902) 156; MARCO, Trop. Woods 44 (1935) 1; MOLL & JANSSONIUS, Mikr. Holzes 1–6 (1906–1936); MULLAN (a), J. Indian Bot. Soc. 10 (1931) 126; (b), *ibid.* 10 (1931) 184; (c), *ibid.* 11 (1932) 103 and 285; (d), *ibid.* 12 (1933) 165 and 235; PANSHIN, Philip. J. Sc. 48 (1932) 143; PEARSON & BROWN, Commercial Timb. India 1 & 2 (1932); PISEK & CARTELLIERI (a), Jahrb. Wiss. Bot. 79 (1934) 131; (b), *ibid.* 90 (1941) 255; ROUSCHAL, Jahrb. Wiss. Bot. 87 (1939) 436; SEN GUPTA (a), Ber. D. B. G. 56 (1938) 474; (b), J. Indian Bot. Soc. 26 (1947) 157; SHMUELI, Palest. J. Bot. Jerus. ser. 4 (1948) 117; STOCKER, Jahrb. Wiss. Bot. 81 (1935) 464; TROLL & DRAGENDORFF, Planta 13 (1931) 311; UPHOF, Bot. Review 7 (1941) 1; WALTER (a), Zeitschr. Bot. 23 (1930) 74; (b), Ber. Schweiz. Bot. Ges. 46 (1936) 217; WALTER & STEINER, Zeitschr. Bot. 30 (1936) 65.