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Root System of Tropical Trees 5. The Peg-roots and the Pneumathodes of *Laguncularia racemosa* GAERTN.

**Kořenový systém tropických dřevin 5.
Kolíkovité pneumatofóry a pneumatódy u *Laguncularia racemosa* GAERTN.**

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Abstract — In an attempt to explain the uncertain origin and development of aerial roots of *Laguncularia racemosa* GAERTN. (*Combretaceae*), excavations were carried out in the mangrove woodlands of Nigeria and Ghana, West Africa. The formation of the root system in this tree proceeds in a different way from that in *Avicennia germinans* (LINN.) LINN., a species commonly compared with *Laguncularia racemosa*. In the latter tree, only young root-tips and slender distal rootlets spontaneously penetrate above the ground, where they are readily modified into the pneumathodes. The pneumathodes of *Laguncularia racemosa* are upright or creeping organs 2 to 4 mm in diameter, and 1 to 2 cm in length; closely behind the apex the cortex is transformed into white, mealy-like tissue composed of loose, rod-like cells. Remaining alive for a short period only, the decaying pneumathodes are successively substituted by new crops of aerial rootlets arising on the top of a subterranean peg-root which has the function of a pneumatophore. The thicker peg-roots possess secondary anatomical structure which is distinguished by large intercellular spaces developed in the secondary phloem. The tips of older peg-roots show a club-shaped swelling formed by decaying bases of the pneumathodes, and by wound-healing callus. Owing to erosion on the seaward side and on the banks of the channels draining the tidal waters, the subterranean peg-roots become secondarily exposed, and together with their parent horizontal roots appear above the ground. At this stage of exposure, however, the peg-roots cease creating new terminal pneumathodes, and gradually die off.

Introduction

Laguncularia racemosa GAERTN. (*Combretaceae*) is a short shrubby tree growing in the mangrove woodlands of the New World and on the shores of West Africa. Both in botanical literature and in actual investigations the aerial roots of this species remain a puzzling feature.

Starting with a paper by SCHENCK (1889), the roots of this species are repeatedly compared with the pneumatophores of *Avicennia germinans* (LINN.) LINN. which frequently grows in association with *Laguncularia racemosa*. SCHENCK (op. c., p. 84—85) did not mention any morphological difference between the aerotropic roots of the two species, however, he has recognized several anatomical peculiarities differentiating these organs. Later on, the pneumatophores of *Laguncularia racemosa* remained to be quoted in connection with *Avicennia* roots, e.g. SCHIMPER (1898, p. 431), OGURA (1940, p. 404), TROLL (1941—1942, p. 2431—2434), TAYLOR (1960, p. 23), etc. IRVINE (1930) and LÖTSCHERT (1969, p. 126) published photographs suggesting a far reaching similarity of *Laguncularia* pneumatophores with respective organs of *Avicennia germinans*. In a classification of "abnormal" roots in mangroves and freshwater swamps, OGURA (l.c.) puts aerial roots of *Laguncularia racemosa* in the same category of "erect roots" with *Avicennia* and *Sonneratia* roots. In a summarizing work on the roots of plants, TROLL (l.c.) treats *Laguncularia* and *Avicennia* in a joint chapter, noting more frequent branching of the former species as the substantial difference in the aerotropic roots.

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During the Cambridge University expedition to Jamaica, CHAPMAN (1944, p. 429 et p. 440) realized that the horizontal roots of *Laguncularia racemosa* produced tuberous pneumatophores under certain conditions "which are not yet known", and that in sand mangroves the pneumatophores were entirely missing. Taking into account the detailed knowledge of this author of aerotropic roots in the mangroves, we can accept his statement as a challenge for a new attempt to clarify the morphogenesis of *Laguncularia* roots.

In the course of our ecological work in tropical West Africa, we have repeatedly encountered numerous peg-roots in the mangrove woodlands. In single-dominant stands of *Avicennia germinans* these roots were always present in "thick" growths and they could be easily identified as organs of the dominant tree. In mixed stands with *Avicennia germinans* and *Laguncularia racemosa*, only one kind of conspicuous peg-roots could be distinguished, and the nature of the *Laguncularia* pneumatophores remained doubtful. In the tangle of the surface roots in the mangrove forests, physical connection of roots with a particular tree is difficult to ascertain. Single-dominant stands of *Laguncularia racemosa* are very rare in tropical West Africa.

Finally, club-shaped aerial roots were observed by J. B. HALL in the Elmina Lagoon, Ghana, and safely identified as organs of *Laguncularia racemosa*. Following his suggestion we have undertaken root studies in this area. In 1966 we made some diggings in the Volta Estuary; Mr. C. W. AGYAKWA is gratefully acknowledged for his cooperation. In the same year, we used the opportunity of studying the root ecology of *Laguncularia racemosa* in the Niger Delta. Thanks are due to the University of Ghana, Legon, Ghana, for transport and necessary grants.

Sites of the observations

S-1: The Elmina Lagoon, Ghana, near the bridge 10 km westward of the Cape Coast. Single trees of *Laguncularia racemosa* on elevated ground flooded during the spring tides. The soil surface shows no signs of erosion or accretion. Within the reaches of the trees, bunches of little upright pneumathodes protrude above the soil surface (see Plate VII., Photo 1). Excavation reveals that these pneumathodes arise as adventitious roots on swollen tips of larger underground peg-roots.

S-2: The Elmina Lagoon, Ghana, eastern margin of the mangrove woodlands, northward of the motorway Cape Coast — Takoradi. An old tree of *Laguncularia racemosa* on the margin of a small channel draining the tidal waters regularly flooding the area. Soil is successively washed out of the steeper banks of the channel. Both *Avicennia* and *Laguncularia* subterranean roots get exposed. Club-shaped peg-roots, at places together with their parent horizontal roots become exposed and can easily be identified as organs of *Laguncularia racemosa*. The majority of peg-roots resemble dead stumps without further branching on their tip. Epiphytic algae and mosses cover some of these roots. Plate VII., Photo 2 gives a close-up picture of these aerial roots.

S-3: The Volta Estuary, Ghana, in the vicinity of Ada. A group of young shrubby trees of *Laguncularia racemosa* growing in a depression not far from the river bank. Flooded by spring tides only, the soil surface seems to be stabilized. White pneumathodes capped with brown apices protrude 1 to 2 cm above the ground. On excavation, all pneumathodes proved to be borne by thicker subterranean peg-roots which were the negatively geotropic laterals of larger horizontal roots radiating from the stems. Adventitious roots, both geotropic and negatively geotropic, could be observed on the lower part of the stem.

S-4: The Niger Delta, Nigeria-Biafra, 3 km southward of Port Harcourt. Flat ground in the interior of vast mangrove woodlands visited during the low tide. A mixed stand of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora racemosa*. Around the *Laguncularia* trees the soil surface without any aerial peg-roots. Soil accretion very probable. Detailed searching showed slender white pneumathodes creeping on the mud surface. The digging showed that most of the pneumathodes represented distal ends of normal root branches, few of them were borne by underground peg-roots.

S-5: The Niger Delta, Nigeria-Biafra, 1 km southward of Port Harcourt. Single trees of *Laguncularia racemosa* on the margin of a large river arm serving as ship-canal connecting Port Harcourt with the sea. Streaming waters and the wave action caused by floating ships affect the process of erosion on the bank. Previously underground roots of *Laguncularia racemosa* get exposed. At places radiating rows of club-shaped peg-roots on larger horizontal roots. No living pneumathodes on the tips of the peg-roots. Similar exposure of roots observed in *Avicennia germinans*.

The morphogenesis

The short account of sites and observations made in West African mangrove woodlands shows that the root forms and root development in *Laguncularia racemosa* vary according to age of the tree and environmental setting.

In the absence of any long-term observations and cultivation experiments we must attempt to piece together a coherent picture of the morphogenesis from the full range of root forms observed on various sites. We shall use the abbreviations of the sites as references to the material actually observed.

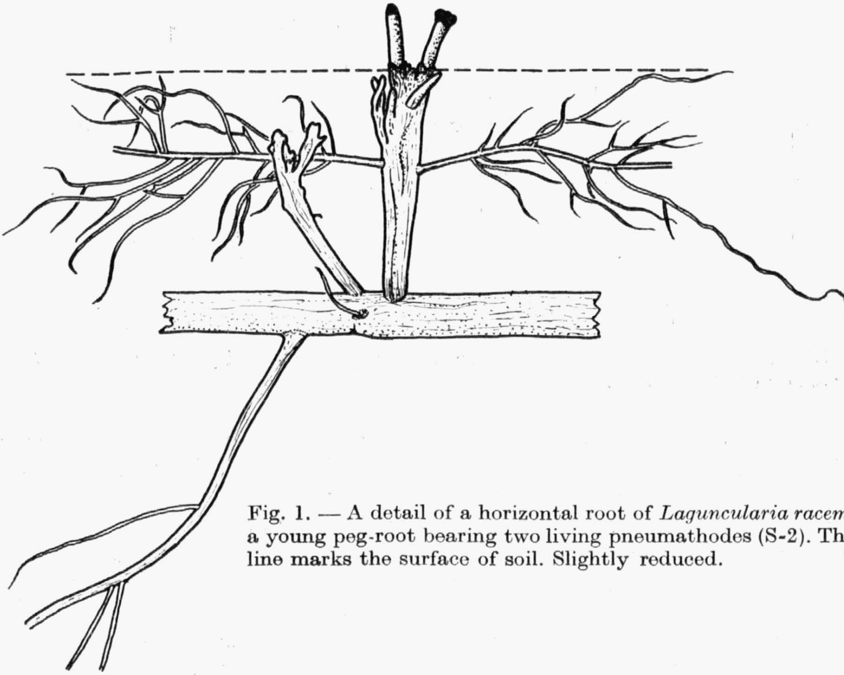

Fig. 1. — A detail of a horizontal root of *Laguncularia racemosa* with a young peg-root bearing two living pneumathodes (S-2). The broken line marks the surface of soil. Slightly reduced.

Young shrubby trees develop a set of vertical and oblique sinkers under the ground; a set of horizontal roots radiates from the stems in a depth of about 10 to 20 cm (**S-3**). While in the stage of primary anatomical structure these horizontal roots form lateral branches growing both positively and negatively geotropically. The more abundant negatively geotropic laterals grow towards the ground surface and, even, several centimetres above the surface (**S-3**; **S-5**). The aboveground portion of these roots undergoes anatomical modifications: the rhizodermis is ruptured by a loose, mealy-like tissue derived from the cortex; the root cap and the apical meristems remain as a brown peel at the end of the modified root; very slender rootlets of this kind do not keep upright growth and creep on the surface of the mud (**S-4**). According to Yampolsky (1924), these aerial organs can be called — as a whole — the pneumathodes.

The life-span of the pneumathodes can be estimated as a few months only. After this period which can be affected by the tidal range in the course of the year, the pneumathodes die off and decay. However, they are substituted by new terminal roots (pneumathodes) arising on the top of the subterranean portion of the vertical root. On young roots the pneumathodes arise singly, on older underground peg-roots they originate in groups (see Fig. 1). The new crop of pneumathodes behaves in the same manner as the primary aerial branches: they remain in the stage of primary anatomical structure and successively die off.

In the course of the multiple decay and regeneration of the pneumathodes, the subterranean portion of the vertical root radially thickens and develops as a 1 to 2 cm thick peg-root with secondary anatomical structure. In view of its formation of pneumathodes, and large intercellular spaces in the secondary phloem, this underground peg-root can be regarded as true "pneumatophore", i.e. organ bearing ventilating organs and tissues, in *Laguncularia racemosa*. The tip of the subterranean peg-root frequently develops a characteristic terminal swelling caused by spherical extension of the secondary xylem and wound-healing callus surrounding the decaying bases of the pneumathodes (**S-1**; **S-2**; **S-5**). New aerial pneumathodes originate as adventitious roots on the surface of this spherical tip. A diagram of the morphogenesis proceeding to the formation of a club-shaped underground peg-root is presented on Fig. 2.

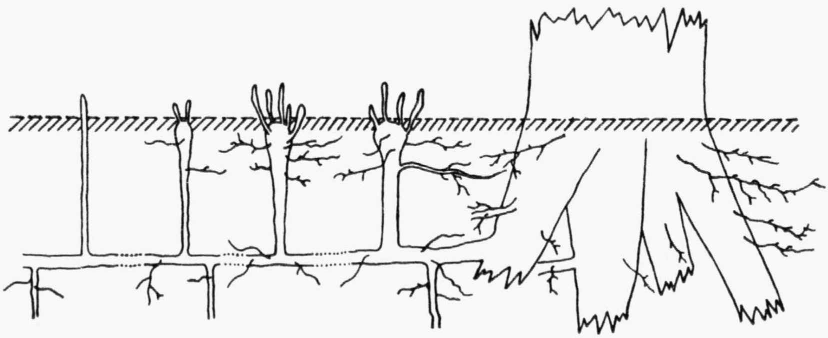

Fig. 2. — Diagram of four stages in the development of the peg-roots and pneumathodes of *Laguncularia racemosa* (S-4) in stabilized soil.

In mangrove woodlands with stabilized soil surface or with depositing mud, the perennial peg-roots never occur above the ground (**S-1**; **S-3**; **S-4**). However, on sites which are affected by wave action and erosion by streaming water, the peg-roots get secondarily exposed (**S-2**; **S-5**). In the first stage of their exposure, they still bear occasional pneumathodes and keep thickening by the activity of the vascular cambium; even their spherical

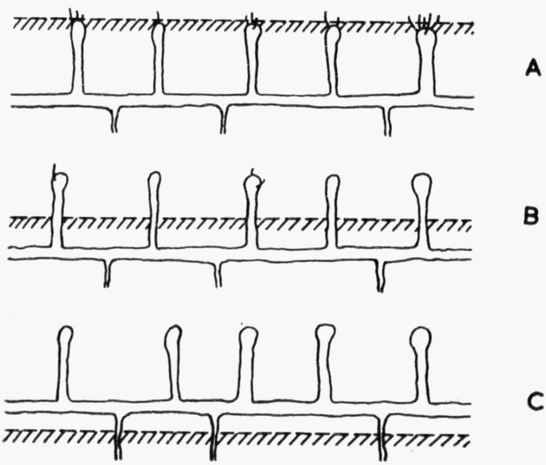

Fig. 3. — Diagram of three stages in the successive exposure of roots of *Laguncularia racemosa* on a site affected by erosion (S-5). *A* — normal development of underground peg-roots and aerial pneumathodes; *B* — exposed tips of the peg-roots with remainders of pneumathodes; *C* — exposed peg-roots and their parent horizontal root.

tip enlarges. Successively, the entire peg-roots, frequently together with their parent horizontal roots get exposed, and thus appear "above the ground". In this stage, large parts of the root system of older *Laguncularia* trees are propped by single sinkers growing in positively geotropic direction from the horizontal roots (**S-5**). Fig. 3 gives diagrammatic pictures of this successive development in trees growing on the ship-canal in the Niger Delta. Eventually, the entirely exposed rows of peg-roots cease growing, get covered by epiphytic algae and mosses, and die off.

Occasionally, the underground peg-roots of *Laguncularia racemosa* can fork as can be seen on Plate VII., Photo 2.

The anatomy

Transverse sections of roots of *Laguncularia racemosa* show a pattern which is different from other West African mangrove and freshwater swamp trees. Fig. 4 and 5 present diagrammatic sketches of the structures observed on root specimens collected on **S-1** and **S-3**.

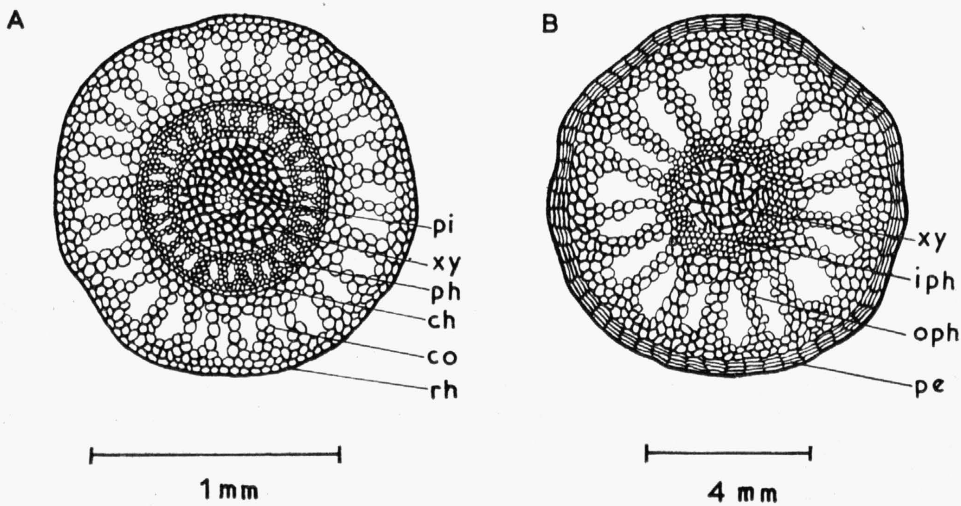

Fig. 4. — Transverse section through a young (*A*) and older (*B*) peg-root of *Laguncularia racemosa*. *pi* — pith, *xy* — xylem, *ph* — phloem, *ch* — endodermis, *co* — cortex, *rh* — rhizodermis, *iph* — inner phloem, *oph* — outer phloem, *pe* — periderm. The size of the cells not in scale.

In normal subterranean roots creeping horizontally in soil, the cambial activity starts very soon. Roots of about 1.5 mm in diameter showed layers of secondary xylem and secondary phloem, while the rhizodermis and the cortex with large intercellular spaces remained in full function. The extraordinary thickness of the secondary phloem in the slender distal roots deserves particular attention.

In roots of about 2.5 mm thickness, the secondary phloem starts forming larger air spaces, and both the rhizodermis and the cortex appear in disintegration.

Still larger roots of 5 mm thickness shed the cortex, and develop a sheath of periderm with numerous lenticels in the cork layer. The periderm originates in the pericycle of the root. The woody cylinder remains small in proportion to the thick secondary phloem. Large intercellular spaces in the secondary phloem suggest the aerating function of this tissue.

In older roots above 1 cm in diameter, the outer layer of the phloem gradually disintergrates and the tube of the periderm is loosely attached to the inner part of the phloem. This living part of the secondary phloem consists of radiating rows of parenchymal cells surrounding radially extended intercellular spaces. The woody cylinder remains small, the pith is still marked, but its parenchymatous cells possess lignified walls.

The subterranean portions of the negatively geotropic roots (underground peg-roots) show on transverse section very similar structure to what has been described above. All peg-roots thicker than 0.5 cm were covered by periderm ruptured by numerous lenticels. Their secondary phloem with large air spaces occupied more than 2/3 of the entire radius of the root. There are comparatively few large vessels in the secondary wood of these roots.

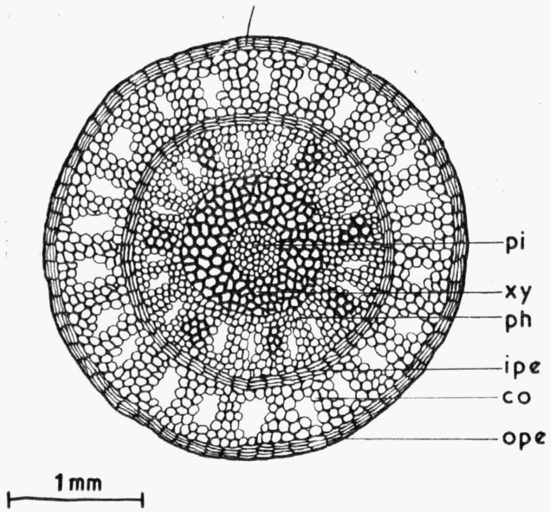

Fig. 5.— Transverse section through an adventitious root on the lower part of the stem of *Laguncularia racemosa*. *pi* — pith, *xy* — xylem, *ph* — phloem, *ipe* — inner periderm, *co* — cortex, *ope* — outer periderm. The size of the cells not in scale.

The examined sections of the pneumathodes confirmed that these aerial organs remain in the stage of primary anatomical structure. A few of them, however, showed cambial activity, though cork cambium never appeared. Under the microscope, the loose white tissue derived from the cortex consists of rod-like living cells with a large nucleus and numerous plastids. We have observed similar cells even in the lenticels of the underground roots.

An anatomical peculiarity was met with on adventitious roots arising on the lower part of the stems of *Laguncularia racemosa* (**S-3**). Transverse sections of these roots showed the presence of two periderms (Fig. 5). One of them derives from a superficial phellogen in the subepidermal layer of the cortex. Simultaneously, the other cork cambium originates in the pericycle. Further radial growth of these roots is marked by disintegration of the cortex and gradual approaching of both periderm layers.

Discussion

The above described features of the root system of *Laguncularia racemosa* deserve further comments. We have to keep in mind that our observations were limited to the shores of tropical West Africa. Schenck (1889) and Chapman (1944), on the other hand, derive their observation from the mangroves of the New World. However, in both areas concerned *Laguncularia racemosa* seems to be identical species without taxonomical problems. Also, the environmental setting in which this species occurs seems to be identical; Chapman's (op.c.) description of the Jamaican mangrove vegetation resembles the conditions found in tropical West Africa very closely. Thus, we can assume that the details of the morphogenesis of the root system in *Laguncularia racemosa* may not differ substantially in the two regions in question.

As mentioned above the puzzling pneumatophores incidentally met with in the mangroves are secondarily exposed underground peg-roots. Though no long-term observations could be carried out, the process of their gradual exposure can be deduced from the various stages observed on the same tree, and from the comparison with roots of *Avicennia germinans* spread in the close vicinity of the *Laguncularia* roots. In both species thick horizontal roots bearing the negatively geotropic laterals never develop above the ground. Thus, exposed horizontal roots with their pneumatophores must have developed in the soil.

In an attempt to explain the evolution of aerotropic roots in *Avicennia* and *Laguncularia*, SCHENCK (1889, p. 87) pointed out that both species grow on sites where soil is frequently eroded by water currents. According to this author, in the long run of the evolution, the occasionally exposed roots of these trees became inherited features. SCHENCK did not recognize that unlike in *Avicennia* the exposure of the pneumatophores in *Laguncularia racemosa* is not genetically fixed. However, taking in view the underground peg-roots with their aerial pneumathodes, the evolutional trend in the root adaptation as suggested by SCHENCK seems to be confirmed.

In our opinion, the above quoted photographs of *Laguncularia* roots by IRVINE (1930), and LÖTSCHERT (1969) were erroneously labelled, and represent organs of *Avicennia germinans*. In mixed stands, without special attention to the interlacing root systems, such a mistake is understandable.

CHAPMAN (1944, p. 440) expressed the view that no pneumatophores were formed in sand mangroves, thus, introducing the problem of the effects of soil texture on root morphogenesis. It was not clear whether the large peg-roots ("tuberous pneumatophores") or small pneumathodes were in question. In our observations the formation of larger peg-roots and their appearance above the ground were mainly controlled by soil erosion and soil accretion. More numerous and detailed observations would be necessary in order to clarify the impact of the soil texture.

The modified white roots of *Laguncularia racemosa*, spreading primarily above the ground, are designated by the term "pneumathodes". This term was originally coined by JOST (1887) to name all histological structures functioning as aerating channels on plant organs, e.g. stomata, lenticels, etc. In a paper on roots of *Elaeis guineensis* (*Arecaceae*), YAMPOLSKY (1924) has slightly extended the meaning of this term: a root predominantly covered by aerating tissues is also called as "pneumathode". Moreover, TOMLINSON (1961) in his summarizing work on palms, has shifted the meaning of this term towards morphological content. We find this approach very suitable and in the same sense apply it in denomination of root forms in *Laguncularia racemosa*.

In conjunction with the study of *Laguncularia* roots, the term "pneumatophore" requires an explanation. This term, too, has passed through gradual changes of its meaning. Literally, it has designated any plant organ bearing ventilating tissues, including organs of some algae. It was mainly in the English literature where the meaning of this term was narrowed to aerotropic roots of mangrove and freshwater swamp plants. In the absence of another suitable term this terminological alteration seems to be acceptable, though in the future a less ambiguous term might be found (pneumorhiza?).

If applied to the tree root, however, the pneumatophores must be further classed in various forms, like "peg-roots", "stilted peg-roots", "knee-roots", etc. In this sense we can consider the above described underground peg-roots bearing pneumathodes on their tip as "pneumatophores".

With regard to the anatomy of *Laguncularia* roots, we did not extend the knowledge much beyond the point reached by SCHENCK (1889). The early development of thick secondary phloem with large air spaces belongs to the most astonishing features found in the adaptations of tropical roots. Also, the simultaneous formation of two periderms on both sides of the cortex is a unique feature not known in other trees. Not much can be added to the nature of the white, mealy-like tissue of the pneumathodes. According to YAMPOLSKY (op.c.) we can regard this tissue as a sort of aerenchyma evolved as a channel for gaseous interchange. Alternatively, we can view it as pathological cell proliferation induced by excessive moisture (see KÜSTER 1916, p. 34). In our opinion, the pathological nature of a regularly originating tissue is rather doubtful.

Souhrn

Článek je pokusem vysvětlit zatím neznámý původ a vývoj dýchacích kořenů u stromu *Laguncularia racemosa* GAERTN. (*Combretaceae*), rostoucího v mangrovech tropické západní Afriky a v mangrovech Nového světa. Rhizologické výkopy a odběr srovnávacího materiálu byly provedeny na dvou lokalitách v Ghaně (Elmina Lagoon a ústí Volty) a v deltě Nigeru u přístavu Port Harcourt (Nigerie-Biafra). Výsledky ukázaly, že vývoj kořenového systému tohoto stromu probíhá odlišně od druhu *Avicennia germinans* (LINN.) LINN., který je v literatuře s naším druhem bezdůvodně srovnáván. U *Laguncularia racemosa* přirozeně pronikají nad povrch půdy jen konce drobných distálních kořínků, které prodělávají ve vzdušném prostředí histologickou proměnu: jejich rhizodermis puká a primární kůra se přeměňuje v bílé, moučnaté pletivo složené z tyčinkovitých buněk. Tyto modifikované kořínky — pneumatódy — vytrvávají jen krátkou dobu a po odumření a rozkladu jsou opakovaně nahrazovány novými pneumatódami adventivně vyrůstajícími na špičce podzemních kolíkovitých pneumatofórů. Tyto pneumatofóry jsou vytrvalé orgány s druhotnou anatomickou stavbou, na níž je nápadné tlusté druhotné lýko s velkými intercelulárami. U velmi starých pneumatofórů je špička tvořící nové pneumatódy kulovitě ztloustlá, což je důsledek abnormální aktivity kambia a vzniku hojivého pletiva v obvodu odumírajících a regenerujících pneumatódů. Na mořských březích ovlivněných vlnobitím i na březích kanálů odvodňujících a zavodňujících porosty mangrovů při mořském dmutí mohou být podzemní kolíkovité kořeny (pneumatofóry) druhotně obnaženy. Objeví se nad povrchem půdy postupně i se svými matečnými horizontálními kořeny. V tomto stadiu se však již nové pneumatódy netvoří a kolíkovité kořeny odumírají. V nitru zapojených porostů mangrovů, kde je povrch půdy stabilizován anebo kde dochází k ukládání mangrovového bahna, se vytrvalé kolíkovité kořeny nad povrchem půdy neobjevují. V některých půdách podzemní kolíkovité pneumatofóry vůbec nevznikají a pneumatódy se tvoří jen jednotlivě na distálních koncích některých kořenů rostoucích při povrchu půdy.

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Recensent: Z. Černohorský

See also plate VII. in the appendix.

L. van der Pijl:

Principles of dispersal in higher plants

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Nová publikace z oboru karpobiologie ,,Principles of dispersal in higher plants" od van der PIJLA je vlastně jakýmsi tematickým pokračováním kolektivní práce autora s K. FAEGERIM ,,Principles of pollination ecology", vydané v roce 1966. Vychází po delší časové mezeře v tomto oboru — 14 let po příručce P. MÜLLERA-SCHNEIDERA a 12 let po knize R. LEVINY. Při práci čerpal autor jednak z vlastních poznatků a zkušeností, dále pak ze starších a novějších karpobiologických příruček a prací speciálních i ze širší botanické literatury.

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Pro svoji stručnost, přehlednost a komplexnost se stane tato nová publikace jistě vítanou příručkou nejen pedagogů a studentů, ale také všech botaniků a věřím, že tak vykoná další záslužnou práci v další propagaci a rozšíření zájmu o toto dosud poněkud opomíjené odvětví botaniky.

M. Lhotská

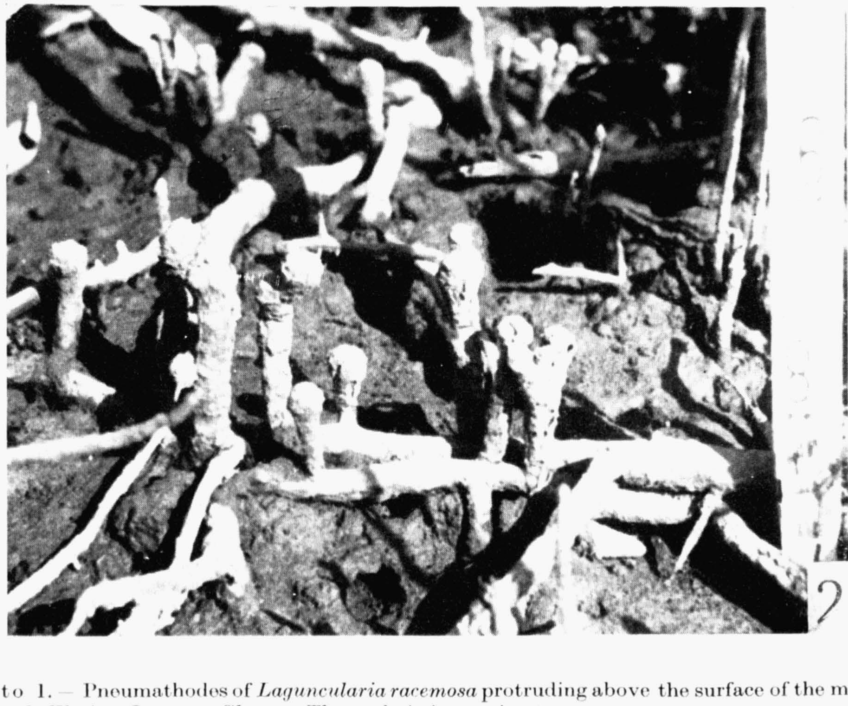

Photo 1. — Pneumathodes of *Laguncularia racemosa* protruding above the surface of the mangrove mud (Elmina Lagoon, Ghana). The scale is in centimetres.

Photo 2. — Peg-roots of *Laguncularia racemosa* exposed by erosion on the margin of a channel (Elmina Lagoon, Ghana).

J. Jeník: Root System of Tropical Trees 5. The Peg-roots and the Pneumathodes of *Laguncularia racemosa* GAERTN.