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Root System of Tropical Trees 3. The Heterorhizis of *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB.

Kořenový systém tropických dřevin 3. Heterorhizie u *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB.

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Abstract — In tropical swamps of Ghana, *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB. develops a peculiar root system possessing prominent dimorphism of end-roots. The distal roots are differentiated into macrorhizae and brachyrhizae, a feature commonly called heterorhizis. Contrary to the majority of temperate and tropical trees, the heterorhizis of *Aeschynomene elaphroxylon* is very well defined both morphologically and anatomically. The numerous brachyrhizae develop as adventitious laterals in dense longitudinal rows connected with bigger medullar rays of larger skeleton roots developed from macrorhizae. All brachyrhizae are uniform in size and shape, lacking secondary growth and further branching. They develop a marked exodermis with suberized inner tangential cell walls. The thick coat of brachyrhizae covers the loose system of skeleton roots, and both types together represent a unique type of "intensive root system" sensu BÜSGEN. This root-form seems to be well adapted to the free movement of nutrients in water and water-logged bottom of lakes. A new type of bacteroidal nodules has been observed on the aboveground parts of the stem.

Introduction

The ambatch tree, *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB., is a small leguminous tree (family *Papilionaceae*) widespread in freshwater swamps in Africa and Madagascar. Its exceedingly light wood attracted attention of African peoples who made rafts and net-floats of pieces of its stem. Moreover, many other sophisticated products, e.g., sandals, shields against the sun's rays were manufactured of this wood (see IRVINE 1961). Since the first description of this species by GUILLEMIN and PERROTTET in 1830, several attempts have been made to investigate various aspects of the anatomy of this tree. Leaving aside the smaller papers, the works by JAENSCH (1884), KLEBAHN (1891), SOLEREDER (1908), and BEIJER (1927) deserve attention. In the course of our expeditions to the Lower Volta region, Ghana, various ecological and morphological features of the ambatch tree were investigated. Compared with other freshwater swamp trees, this species is remarkably adapted towards the water-logged sites and fluctuating water level in rivers and lakes. During a detailed study on the natural stands a well differentiated root dimorphism was discovered and later confirmed by anatomical examination. A brief description of the more interesting structures observed in this tropical tree is given in the following chapters.

Root morphology

Numerous specimen trees were investigated on the margin of the Eka Lagoon, Ke Lagoon and Avu Lagoon (approx. 6°N lat., 0°40 E long.), near the Volta Estuary, Southern Ghana. The ambatch tree is a dominant plant in swampy thickets covering wide stretches of waterlogged banks and shallow waters of the above-mentioned lakes (see Plate XV, Photo 1). Some of these thickets form a sort of floating mats (floating islands) adapting themselves to the seasonal changes of the fluctuating water level. *Aeschynomene elaphroxylon* is accompanied by *Ficus congensis*, *Alchornea cordifolia*, which are the other frequent woody species surviving in these swamps.

Among the grasses and herbs associated with the ambatch tree following species were encountered: *Leersia hexandra, Oriza barthii, Cyclosorus striatus, Commelina gerardi, Polygonum tomentosum, Ipomoea aquatica, Pentodon pentandrus* and *Zehneria capilacea*.

Mature ambatch trees achieve a height of about ten metres, reaching a stem diameter of up to 50 cm at breast height. Inspecting an older stem the observer is struck by the conspicuous coat of rust-brown "hairs" covering the base of the bole and adjoining root spurs (see Plate XV, Photo 2). Closer inspection discovers that these "hairs" are unbranched roots of equal thickness (approx. 0,5 mm) and of similar length (approx. 5 to 10 cm). Further observation and excavation showed that similar uniform roots occur also in water and in the waterlogged soil. On the other hand some of the distal roots were thouroughly different because of their conspicous thickness (3—5 mm) and unlimited growth in length. Thus the distal roots of the ambatch tree could be distinguished in two kinds (see also Fig. 1; Plate XVI, Photo 3): bigger macrorhizae developing gradually into main skeleton roots and smaller brachyrhizae persisting in a stage of uniform restricted size. (The terminology of roots follows the suggestion of Jeník and Sen 1964.)

The number of macrorhizae within the entire root system of a specimen tree is relatively small. This kind of end-roots develops both as primary tap root of the seedling and as the main lateral branches of the root. They also occur as bigger adventitious roots on the submersed stems and branches.

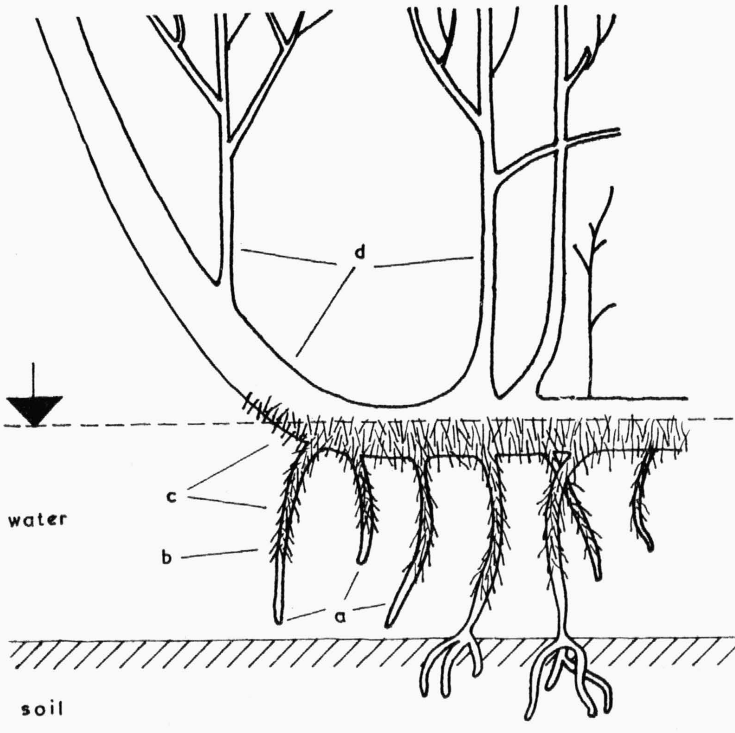

Fig. 1. Adventitious root system developed on the floating stems of *Aeschynomene elaphroxylon*; a — macrorhizae, b — skeleton roots developed from macrorhizae, c — brachyrhizae, d — stems.

The growth in length and the secondary growth of the macrorhizae is very vigorous, and results in a considerable thickness of the skeleton roots, achieved not far from the apex. The skeleton roots derived from these macrorhizae are conical in shape and light brown in colour. While growing in the loose organic mat and in the open water, the activity of the apical meristems of macrorhizae is not disturbed by any adverse mechanical factor; this results in straight, uncurved growth in these roots. Yet at the bottom of the lake, in contact with the waterlogged soil, the apex is frequently damaged and, subsequently, irregular bunches of regenerating roots may appear (Fig. 1). No genuine root hairs were observed above the elongation zone of the macrorhizae.

Except for the apical zone, the macrorhizae bear plenty of laterals which only exceptionally originate endogenously; the majority of them arise adventitiously under the well developed periderm of the bigger root which is progressively thickening through cambial activity. However, even on the older skeleton roots the laterals are regularly arranged in longitudinal rows affected by the position of bigger medullar rays (see below). All these laterals can be classified as brachyrhizae: they show a constant thickness over their entire length and never branch; they keep a uniform diameter over the entire specimen tree regardless their position in water, underground or aboveground.

No doubt, the above-mentioned root dimorphism of *Aeschynomene elaphroxylon* represents a remarkable example of the heterorhizis. Unlike any other tree described in the literature hitherto, the ambatch tree shows a distinct gap between both different kinds of end-roots which are clearly differentiated without any transition forms.

Old trees frequently curve down, their stems and branches touching the soil or water surface, sometimes floating as components of the vegetation mat covering shallow waters. Numerous adventitious roots develop on these prostrate stems and submerged parts. Among these adventitious roots only few are differentiated as macrorhizae forming future skeleton roots; however, the majority of them are the brachyrhizae.

During our study of the roots of *Aeschynomene elaphroxylon*, we tried to discover true rhizobial nodules commonly attached to the roots of leguminous plants. On the localities studied in Ghana no genuine nodules could be observed in our species. Yet our attention was attracted by numerous hemispherical protuberances situated on the bark of the stems and over the root spurs close to the water surface. Subsequent anatomical inspection proved the occurrence of active bacteroidal tissue different from the usual rhizobial nodules (Plate XVI, Photo 4). A preliminary examination by O. N. Allen and E. K. Allen (personal communication) showed that the tissue is entirely filled with Gram positive pleomorphic rods of different size, structure and staining properties than are the symbiotic rhizobia.

Root anatomy

Though various aspects of stem anatomy were studied in older works, no adequate investigation has been carried out into the root structure. Thus, paraffin sections stained with safranine and aniline blue, and freezing microtome sections were used for the completion of our study. Cell wall was examined by usual histochemical reactions.

The primary structure of the macrorhizae as seen on the transverse section upto 12 protoxylem groups can be counted not far from the apical meristems. Pericycle and cortex parenchyma are relatively thick, though without any noteworthy features. None of the sections showed endophytic fungi in the cortex.

The cambial and felogen activity begin very soon, only approx. 5 cm behind the apex the periderm is fully developed and the cortex starts disintegrating. The structure of the secondary xylem has similar features as described in the stem of *Aeschynomene elaphroxylon*. The substantial volume of the wood is formed by regular layers of palisade-like tracheids, with cell walls unlignified. Isolated vessels are scattered in this tracheidal mass, accompanied by tangentially arranged groups of libriform. Two kinds of medullar rays occur in the secondary xylem: (1) uniseriate parenchymatous rays, and (2) bigger multiseriate rays containing radial vessels.

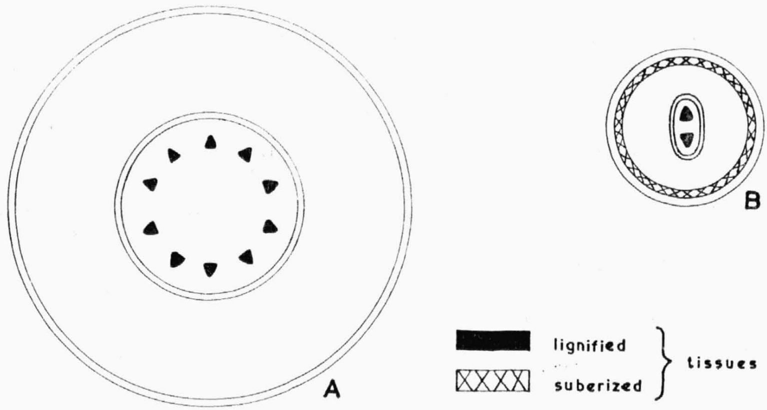

Fig. 2. Transversal sections of a macrorhiza (A) and brachyrhiza (B) in 5 mm distance from the apex to compare different sizes and different number of protoxylem groups, and the formation of suberized exodermis in the brachyrhiza.

The structure of the brachyrhizae (see Fig. 2B) differs profoundly and the diarch vascular bundle is very restricted in size. The thin cortex is limited to three parenchymatous layers. Under the thin-walled rhizodermis, the one-layered exodermis is clearly developed (see Plate XVI, Photo 5), having a thickened inner tangential cell wall containing suberin lamellae which do not dissolve in 50% chromic acid. Root hairs do not develop on the brachyrhizae. Also, no epiphytic as well endophytic fungus was observed in connection with these roots. The most characteristic feature of the brachyrhizae is the absence of the secondary growth; no cambial activity, no periderm formation could be spotted.

With regard to the morphogenesis the most interesting point is the origin of lateral roots and the way branching of the entire root system. In our material, normal endogenous branching initiating deeply in the pericycle close to the apical meristem occurred only exceptionally. The bulk of the laterals develops as adventitious roots initiated near the medullar rays of the mother roots derived from the macrorhizae. As seen on the sections, all laterals (brachyrhizae) are connected through one of the bigger medullar rays with one of the isolated vessels scattered in the secondary xylem.

Limited size, strictly cylindrical shape and absence of secondary growth of the brachyrhizae in *Aeschynomene elaphroxylon* seem to corespond with the anatomical structure of the secondary xylem. Obviously, the connection of the root with a single vessel running through a single medullar ray and attached to a single longitudinal vessel, does not permit any subsequent anastomosis with other vessels of the secondary wood and prevents the successive growth of the lateral root. The restricted size and lack of branching in brachyrhizae is compensated by their abundance, long lasting persistence and by their new formation in the area of lenticels on roots and stems in any stage of the morphogenesis.

Discussion

The prominent root dimorphism of the ambatch tree, manifested in the clear cut differentiation of two kinds of distal roots is a very interesting phenomenon among root-forms of woody plants. Undoubtedly, a characteristic case of heterorhizis is encountered in this species. As discussed in an earlier paper (KUBÍKOVÁ 1967), the phenomenon of heterorhizis in trees is not yet properly understood and generally accepted. Owing to the common transitions observed between the bigger and smaller end-roots, many authors prefer to view the dimorphism better as a matter of a size gradient. Indeed, such a gradient in size of the distal end-roots is a prevailing feature not only in the temperate zone, but also in the tropical trees. In *Aeschynomene elaphroxylon* we find a unique case among the trees. The bigger end-roots are qualitatively different from the mass of the smaller laterals. Their difference is obvious from their anatomy and growth capacity.

Though the ambatch tree was subject to many botanical investigations, no data were published about this particular feature. SCHWEINFURTH (sec. KLEBAHN 1891, p. 133) observed "filzartiges Geflecht" of roots of *Aeschynomene elaphroxylon* in swamps along the Nile; we can only assume that Schweinfurth observed the thick coat of brachyrhizae.

The paper by KLEBAHN (op. c.) discusses in detail the origin of adventitious roots in the aboveground branches. According to his work, the root primordia are formed in connection with the bigger medullar rays and are always present in the bark in a latent stage. According to our observations, the connection of brachyrhizae with the mother root occurs similarly, however, we cannot say anything certain about the permanent presence of undeveloped root primordia in the bark of bigger skeleton roots.

Another interesting point is the life-span of brachyrhizae. In most of the temperate trees brachyrhizae occur only ephemerally, e.i. persit just several months or a couple of years. Usually, an estimate of the duration of these organs is very inaccurate. As for *Aeschynomene elaphroxylon* the actual life-span of the brachyrhizae can be estimated according to the length of the transverse vessel linking the lateral root with the longitudinal vessel in the mother root. The older brachyrhiza is connected with one of the inner vessels, the younger one is linked with one of the peripheral vessels. Accordingly, we can assume the age of the laterals which persist over a period of many years. Such a durability in a structure built up mainly of primary tissues can be explained only in terms of the efficient protection by a well differentiated exodermis.

A contraversial point in our observations is the presence and structure of the root nodules. KLEBAHN (1891, p. 135) described numerous spherical and ovoid nodules developed on the rootlets excavated from the mud of the Nile. No proper nodules were recorded in our specimen trees inspected in Ghana. However, peculiar hemispherical protuberances with bacteroidal tissues were found on the above ground parts of thicker stems and root spurs.

From the ecological point of view we can classify the root system of *Aeschynomene elaphroxylon* as an intensive root system (sensu BÜSGEN) which is characterised by its restricted volume of space occupied in the substratum. This kind of root system seems to be an adequate adaptation to the free movement of nutrients dissolved in water and water-logged sites where *Aeschynomene elaphroxylon* usually occurs. Finally the question of gaseous exchange within the submersed root system of the ambatch tree should be examined. The majority of swamp trees in the tropical Africa develop a sort of breathing roots (pneumatophores, knee roots, root kness, stilt roots); in the ambatch tree this adaptation seems to be resolved by an easy formation of adventitious roots richely developing at the lower part of the bole above the water level.

Acknowledgements

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Souhrn

Ve sladkovodních bažinách Ghany vytváří *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB. význačný typ kořenového systému s vyhraněným dimorfismem koncových kořenů. Tyto kořeny jsou jasně rozlišeny v makrorhizy a brachyrhizy a představují tedy typický případ tzv. heterorhizie. Podobně jako v mírné zoně, i v tropických oblastech projevují stromy heterorhizii spíše jako kvantitativně odstupňovaný gradient bez výrazného hiátu mezi oběma mezními formami. U *Aeschynomene elaphroxylon* jsou však oba typy koncových kořenů zřetelně morfologicky i anatomicky diferencované. Brachyrhizy postrádají druhotný růst a nikdy se nevětví; mají zcela jednotný cylindrický tvar, zběžně připomínající spíše velké trichomy; jejich cévní svazek je diarchní, primární kůra slabá a vždy opatřena výraznou exodermis. Makrorhizy jsou v rámci celého systému jen ojedinělé, mají vždy energický druhotný růst a nesou po celé délce postranní větve — brachyrhizy. Většina brachyrhiz vzniká adventivně v druhotných pletivech pokročile ztloustlých kořenů. Po stránce anatomické i morfogenetické je významná skutečnost, že postranní kořeny se napojují na mateřský kořen jen v místech větších dřeňových paprsků obsahujících radiální cévu, která kořen spojuje s některou z isolovaně zastoupených cév sekundárního xylému. Anatomická stavba dřeva *Aeschynomene elaphroxylon* i systém napojení postranních kořenů nedovoluje zvětšování brachyrhiz a je asi příčinou vyhraněného typu heterorhizie u této dřeviny. S hlediska ekologického lze kořenový systém této dřeviny charakterizovat jako „intensivní“ (ve smyslu BÜSGENOVĚ), protože soubor brachyrhiz s omezeným růstem může prokořeňovat jen velmi omezený objem půdního resp. vodního prostoru. Tato „redukce“ je nejspíše v souvislosti s relativně volným pohybem živin ve vodě a v trvale zamokřených biotopech, kde se vždy rozměry kořenů zmenšují, jak je známo ze studia bylinných vodních rostlin. U studovaného druhu *Aeschynomene elaphroxylon* byly na lokalitách v Ghaně vytvořeny na basi bakterioidní hlízky, jejichž pletiva jsou naplněna grampositivními pleomorfními tyčinkami, lišícími se rozměry, strukturou i barvením od symbiotických rhizobií.

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Recensent: Z. Černohorský

See also plates XV. — XVI. in the appendix

G. H. M. Lawrence, A. F. G.Buchheim, G. S. Daniels et H. Dolezal [ed.]:

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V. Skalický

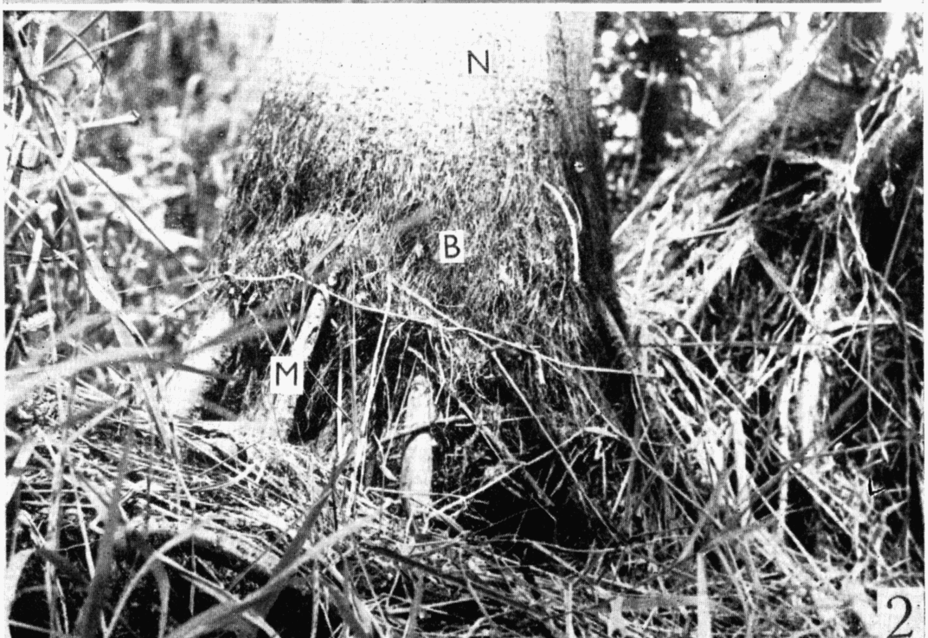

Photo 1. General view of the stands of *Aeschynomene elaphroxylon* on the banks of Ke Lagoon, Ghana.
Photo 2. The base of the ambatch tree stem with adventitious roots developed from macrorhizae (M), numerous brachyrhizae (B), and hemisphaerical nodules (N).

J. Jeník and J. Kubíková: Root system of Tropical Trees 3. The Heterorhizis of *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB.

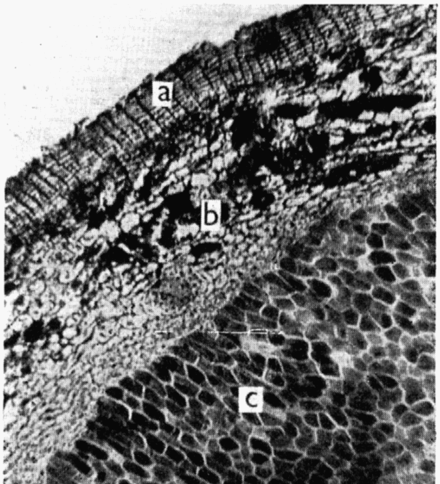

Photo 3. A detail of a prostrate branch with bigger adventitious roots developed from macrorhizae (m), and abundant brachyrhizae (b) forming a thick hair-like indumentum.
Photo 4. Transverse section through a stem nodule showing the bark with a prominent cork layer (a), vaulted part of the secondary phloem (b) and bacteroidal tissue (c). Enlarged 75×.
Photo 5. Transverse section through a brachyrhiza showing disintegrating rhizodermis (a), thickened exodermis with peculiar inner suberin layer (b), and cortex parenchyma (c). Enlarged 270×.