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Root System of Tropical Trees 4. The Stilted Peg-roots of *Xylopia staudtii* ENGL. et DIELS

Kořenový systém tropických dřevin 4. Kolíkovité pneumatofóry s opěrnými kořeny u *Xylopia staudtii* ENGL. et DIELS

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Abstract — A new type of pneumatophore is described in *Xylopia staudtii* ENGL. et DIELS (*Annonaceae*) growing in forests and swamps in Ghana, West Africa. From the depth of waterlogged soil, larger horizontal roots of this tree send slender aerotropic roots which reach a height of up to 2 metres above ground. The lower portion of this aerotropic root-branch bears numerous laterals which grow downward, in a positively geotropic direction. Several of these laterals anchor in the surrounding mud, and, successively, develop into a set of stilt-roots which prop the slender aerotropic root. These are the characteristic features of a peculiar kind of pneumatophore which can be called „stilted peg-root", and regarded as a highly specialized adaptation among breathing roots in tropical mangroves and swamps.

Introduction

Xylopia staudtii ENGL. et DIELS (*Annonaceae*) is a frequent component of the West African forests. A middle-sized tree reaching a maximum height of about 25 metres, this species grows both in free-drained and in waterlogged soils. It can be encountered both in "mesic" rain forest and in freshwater swamps on the valley bottoms. Regions of higher rainfall seem to be preferred by this species. In Ghana, *Xylopia staudtii* is a characteristic tree in the *Lophira-Cynometra-Tarrietia*-Association (TAYLOR 1960) which represents the climatic climax in areas with rainfall totals exceeding 1500 mm.

Current botanical monographs dealing with African trees describe *Xylopia staudtii* as a tree possessing characteristic stilt-roots and buttresses. SCHNELL (1950, p. 212) notes "racines aériennes arquées, aplaties dans le plan vertical". HUTCHINSON et al. (1954, p. 41) mention "buttresses and stilt roots". TAYLOR (1960, p. 89) puts down "thin stilt roots, which do not spread far". IRVINE (1961, p. 25) comments on "buttresses short or sometimes flattened stilt roots up to 6 feet high". STEENTOFT NIELSEN (1965, p. 90) records just "having stilt roots". Remarkably, there is a note on „adventitious roots" in *Xylopia aethiopica* A. RICH. in Chevalier's description of the Ivory Coast's forests (CHEVALIER 1909, p. 119). LEBRUN et GILBERT (1954, p. 42) report formation of pneumatophores in unspecified *Xylopia* trees, possibly in *Xylopia rubescens* (op. c., p. 43), in Congo.

In view of scanty information on roots of tropical trees, we could take the preceding account of referencies for relatively good evidence of the roots of *Xylopia* species. There is no doubt that the stilt-roots of this genus are a familiar feature to experienced foresters in West Africa. In their conspicuousness they are matched only by the stilt-roots of *Musanga cecropioides* and *Uapaca* species. In the undergrowth of tropical forests, well developed stilt-roots provide a convenient point in identification of *Xylopia staudtii*. According to our experience, stilt-roots form a thick tangle of flattened roots at the base of mature trees of *Xylopia staudtii* frequently up to 3 metres height. A view of a characteristic cone of stilt-roots in this species is given on Plate II, Photo 1.

In spite of the above mentioned familiarity, a unique root modification escaped attention of both foresters and botanists. In the flooded bottoms of valleys with waterlogged mud, this tree develops a highly specialized kind of pneumatophore which can be best called "stilted peg-root" (see Plate III, Photo 2 and 3). Earlier, in our preliminary list of root modifications of West African trees (Jeník 1967), we used the term "stilt pneumatophores" which appears to be less suitable than the above proposed name. In the present paper, we take the opportunity of describing this root modification in detail.

Localities observed

Stilted peg-roots of *Xylopia staudtii* were first discovered in 1965, during a botanical expedition to the western region of Ghana. The first site of our observation ("locus classicus") of this root structure is situated in the Tano-Nimiri Forest Reserve (description see below). Independently J. B. Hall has collected specimens of the same roots in the area of Takoradi. In 1966 we saw stilted peg-roots south of the Ankasa Forest Reserve. Three separate localities provided reliable material for the description of the pneumatophores of *Xylopia staudtii*. Since their discovery in 1965, we have inspected many *Xylopia staudtii* trees on several sites of the rain forest zone in Ghana. Though the ordinary stilt-roots in mature trees were always present, stilted peg-roots were never found on free-drained soils.

The following is a short description of the three localities concerned:

1. Compartment No. 116 in the Tano-Nimiri Forest Reserve, north-west of Sambreboi, close to the road. Longitude 2°35′ W, latitude 5°40′ N. Annual rainfall total approx. 1600 mm, annual average temperature 26 °C. Flat bottom of a valley with waterlogged soils. Acid gleisol related to the Oda series described by Ahn (1961). Closed swampy forest composed of *Xylopia staudtii* Engl. et Diels, *Alstonia boonei* De Wild., *Mitragyna ciliata* Aubrév. et Pellegr., *Carapa procera* DC., *Symphonia globulifera* Linn. f., *Cynometra ananta* Hutch. et Dalz., *Raphia hookeri* A. Chev., *Ancistrophyllum opacum* Drude, *Marantaceae* indet., etc.

2. Freshwater swamp 25 km west of Takoradi, 8 km north of Agona Junction. Longitude 1°55′ W, latitude 4°50′ N. Swampy depression with acid gleisol, saturated for the greater part of the year with water. Trees of *Xylopia staudtii* grow in association with *Nauclea diderichii* (De Wild. et Th. Dur.) Merrill, *Mitragyna ciliata* Aubrév. et Pellegr., *Spondianthus preusii* Engl., *Symphonia globulifera* Linn. f., *Raphia hookeri* A. Chev., *Cyrtosperma senegalense* Engl., *Cyclosorus striatus* (Schum.) Ching, etc.

3. Bottom of a narrow ravine near the Mpataba-Elubo road, approx. 8 km south of the southern boundary of the Ankasa Forest Reserve. Longitude 2°40′ W, latitude 5°10′ N. The slopes of the ravine were covered by mesic rainforest with *Combretodendron africanum* (Welw. ex Benth. et Hook. f.) Exell, *Sacoglottis gabunensis* (Baill.) Urb., *Dialium aubrevillei* Pellegr., *Chrysophyllum subnudum* Bak., etc. Trees of *Xylopia staudtii* grow both on the slopes and on the bottom of the ravine; stilted peg-roots only on the flooded gleisols.

Description of specimen trees

Specimen trees of *Xylopia staudtii* were studied in the Tano-Nimiri Forest Reserve. Mature trees of about 20 metres height and 150 cm girth possessed numerous stilt roots which formed a thick cone of anastomosing roots at the base of the bole. Young lateral branches of these stilt roots with suspending tips and light-brown apices showed that the formation of adventitious roots — future stilt roots — was still in progress.

Around the *Xylopia* trees the ground was covered by numerous smaller structures which, in the first instance, resembled scattered dry twigs stuck in the mud. A closer view and subsequent excavations revealed that the apparent "twigs" were living aerial roots attached to deeply buried horizontal roots (Fig. 1). In spite of their different size, their morphology repeatedly showed similar features: a slender vertical root with an aerotropic apex was propped by a set of stilts which rooted in the surrounding mud. There were hundreds of these stilted peg-roots in the vicinity of a mature specimen tree. Around a single tree the area of distribution of stilted peg-roots stretched up to 10 metres from the bole.

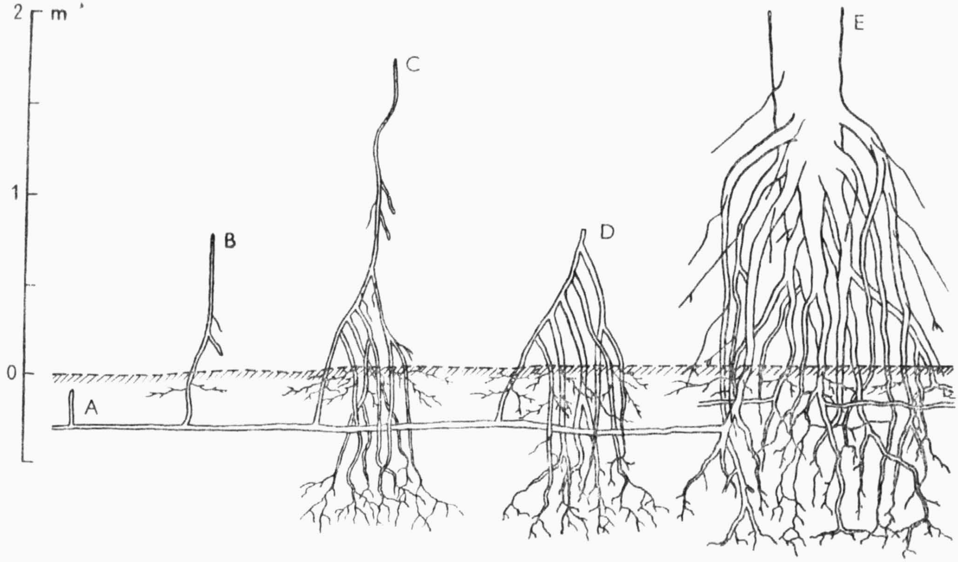

Fig. 1: A diagrammatic sketch of the morphogenesis of stilted peg-roots of *Xylopia staudtii*. *A* — initial stage, *B* — advanced initial stage, *C* — mature stage, *D* — disintegration stage, *E* — the base of a tree with stilt-roots.

Excavations showed that the leading aerotropic root arises as a lateral branch of larger horizontal roots creeping in the waterlogged subsoil at about 20 to 30 cm depth. A big apex and its vigorous growth suggest that this leading root has the characteristic of a prominent macrorhiza, i.e. an end-root with great potential meristematic activity. In the initial stage of its development this aerotropic root protrudes 20 to 50 cm above ground, thus resembling single peg-roots well known in certain mangrove and freshwater species. In spite of its slender shape and very light tissues, the leading root, which can ultimately reach a length of even 2 metres, does not keep an upright position and a straight shape: the lower aerial portion of this root tends to bend down, and the slender root tip twists amidst the stems of larger forbs, e.g. Marantaceae and Zingiberaceae species, frequently growing in the undergrowth of swampy forests.

On the curved lower part of the leading root, new lateral roots successively arise, all pointed towards the ground in a positively geotropic direction. The oldest of these laterals gradually reach the ground surface, anchor in the soil, and richly branch spreading deeper than was the original position of the mother horizontal root which gave rise to the pneumatophore. A set of firm stilts supporting the main aerotropic root thus originates. Owing to the oblique position of the lower part of the leading root, the stilts tend to be arranged in a single plane on one side of the main root. This characteristic pattern is marked on Fig. 2 and Plate III, Photo 2. Above the branching point of the rooted stilts, many more laterals can arise. They hang like little appendages and soon die off, never reaching the surface of the ground. The general morphology of mature stilted peg-roots is shown in Fig. 2.

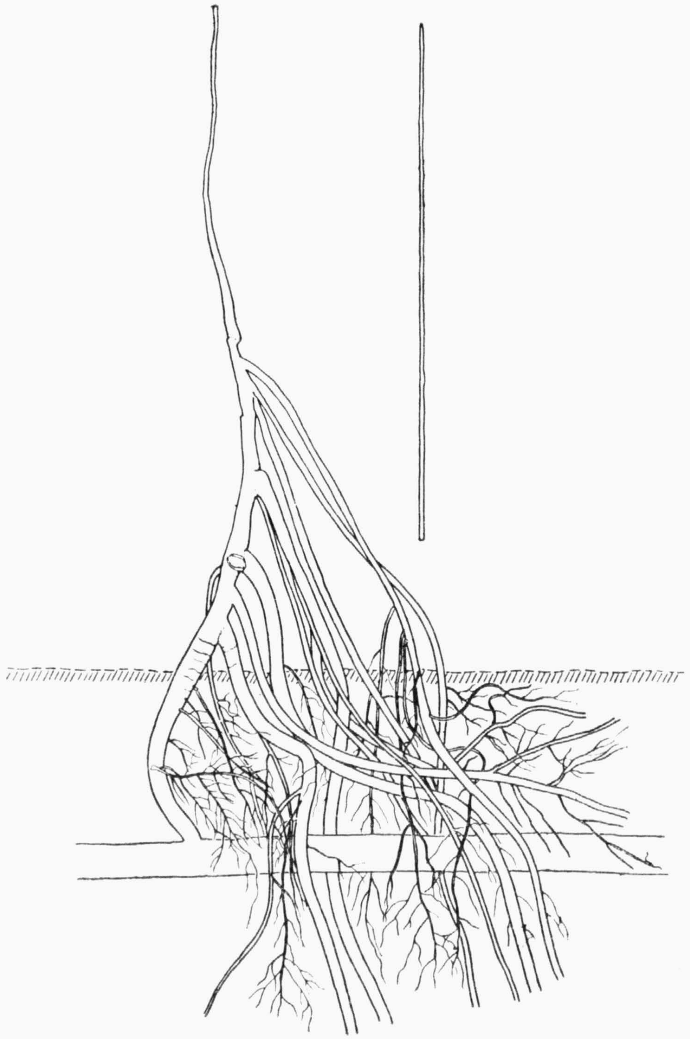

Fig. 2: A stilted peg-root of *Xylopia staudtii* in the mature stage of development. Reduced 8 ×.

As mentioned above, more vigorous geotropic sinkers penetrate below the level of the parent horizontal root, and create numerous branches. Additionally, the subterranean portion of the aerotropic leading root bears abundant laterals. However, none of these underground roots derived from the stilted peg-root turn upward and repeat the formation of the pneumatophore.

Comparing the morphology of dozens of stilted peg-roots distributed around specimen trees in a mixture of different sizes and developmental phases, we could describe five successive stages which are usual in the morphogenesis of this pneumatophore. Table 1 and Fig. 1 summarise the characteristic features of the single stages. In the absence of annual rings, the duration of the whole cycle is difficult to estimate. Three to five years appear to be an average period necessary for the formation of a mature pneumatophore; crippled stilted peg-roots in the stage of disintegration can survive many more years.

Table 1. Successive development of stilted peg-roots of *Xylopia staudtii* as observed in the swamps of the Tano-Nimiri Forest Reserve in Ghana

Stage	Morphology
Initial stage	A root-branch arises on a horizontal underground root, and starts growing in negatively geotropic direction
Advanced initial stage	Having reached the soil surface, the root keeps growing upwards; laterals with positively geotropic growth arise on its aerial portion
Mature stage	Lower laterals anchor in the soil and develop as firm stilts; the slender upper part of the main root gradually elongates reaching a height up to 2 metres
Senescent stage	The main aerotropic root ceases growing and dies off; the stilts become thicker than the leading root
Disintegration stage	The tip of the upper part of the main root decays leaving a stump above the branching point of the upper stilt; gradually the whole organ above ground withers away

Anatomical observations

In a move which can be called "applied anatomy", tropical foresters use slashes of the bark and wood in order to identify tropical trees. In the tangle of the swamp forest, slashes can be very useful in the identification of pneumatophores protruding above ground. Stilted peg-roots of *Xylopia staudtii* when cut on the thicker aboveground parts possess a slightly scented slash and, after a few minutes, the original whitish colour of wood changes into brown. Slashes of the bole and large stilt roots give a similar pattern, thus, we can use this method for easy recognition of the pneumatophores. Anybody who has the experience with troublesome excavations of roots in tropical swamps will appreciate this relatively simple procedure.

The leading aerotropic root of the future pneumatophore originates endogenously in the pericycle of the horizontal roots creeping in the subsoil. While underground and during the subsequent growth towards the ground surface and above the surface, the vertical root possesses a large pith, polyarchous vascular cylinder, and thick cortex. Usually, the cortex occupies

2 thirds of the radius. The transverse sections of vigorously growing aerotropic roots showed the primary anatomical structure even 10 cm below the apex. At that distance, approximately, the vascular cambium originates. Still farther from the tip, the rhizodermis disintegrates, being substituted first by the exodermis, later by the exogenously formed periderm. The cortex is very compact and does not possess any intercellular spaces which are a common feature in pneumatophores of tropical trees.

In the stage of secondary anatomical structure, wood occupies a greater part of the entire diameter of the pneumatophore: phloem, remnants of cortex and periderm represent less than 1 fourth of the radius. On transverse sections, secondary wood of the aerotropic root gives an appearance of a fairly compact and homogeneous tissue. The predominant component of the wood are septate tracheids and xylem parenchyma. Larger vessels are irregularly scattered over the transverse section. Very thin walls of tracheids and vessels are richly pitted. No fibres were observed in this wood. Altogether the wood is exceptionally light (see Table 2).

Table 2. Specific gravity of the dry wood in various roots of *Xylopia staudtii* as sampled in the swamps of the Tano-Nimiri Forest Reserve

Kind of root	Environment	Specific gravity
Stilted peg-root	above ground under ground	0.1 0.09
Stilt root of the bole	above ground under ground	0.6 0.5

The periderm and secondary phloem of older root branches of the stilted peg-roots is also very compact and does not show intercellular spaces similar to those in the pneumatophores of *Laguncularia racemosa*. Groups of phloem fibres reinforce the mechanically weak aboveground parts of the stilted peg-roots.

Transverse section of the distal parts of the stilted peg-roots showed a great variability in numbers of protoxylem groups, and differencies in the anatomical gradient from the primary towards the secondary structure. The steepness of this gradient, obviously, varies according to the morphogenetic stages, and is influenced by the environment.

The anatomical structure of the geotropic laterals of the stilted peg-roots does not differ from the mother root. The majority of these roots start with four protoxylem poles; they keep their primary structure as long as they hang above ground. Once rooted in the soil, they develop secondary xylem, secondary phloem and periderm in a similar pattern to that in the mother root. The radial growth of these stilts can, ultimately, exceed the growth of the aerotropic root; in the sensecent stage these roots can be thicker than the original mother root.

For comparison, sections of underground roots and stems of *Xylopia staudtii* were studied. Larger horizontal roots were all distinct by the presence of large vessels, a feature well known in the anatomy of roots of many trees. The cortex of young underground roots contains numerous cells filled with tannins. The secondary wood of the normal stilt roots and of the bole of *Xylopia staudtii* showed similar xylem elements described in pneumatophores, however, the cell walls of all tracheary elements were thicker, which makes the wood heavier and harder.

Discussion

Modifications of roots in tropical trees attract attention of both foresters and botanists. In the helter-skelter of the forest interior, the abnormal shape of roots provides valuable diagnostic points which serve for the identification of trees. Many flora and keys for identification of tropical trees bring separate keys for recognition of species after their roots (e.g. SCHNELL 1950; VOORHOEVE 1965). In spite of this importance, the current knowledge of roots of African trees is very limited. Until recently, only trees of West African mangroves were known as to their formation of the pneumatophores. For example, none of the dicotyledonous trees in freshwater swamps were recognized as species with peg-roots similar to *Avicennia* pneumatophores in mangroves. OGURA (1940) and TROLL (1941—42) described peg-roots in freshwater swamps of South East Asia. Most recently, *Anthocleista nobilis* (JENÍK 1965) and *Voacanga thouarsii* (unpublished) were found with distinct peg-roots in freshwater swamps of Ghana and Sierra Leone.

The above outlined morphology of the stilted peg-roots of *Xylopia staudtii* represent a new type of pneumatophore, unknown to science hitherto. All types of currently known pneumatophores, i.e. knee-roots, root-knees, single peg-roots, branched peg-roots and peg root-tips, are held for adaptations to waterlogged soils in which gaseous exchange between the living roots and oxygen-rich atmosphere is impeded. Both morphology and physiological observation support this idea of "breathing roots".

Stilted peg-roots of *Xylopia staudtii* appear to be a fairly advanced type among these pneumatophores. The maximum length of the aerotropic root (2 metres length recorded) and successive development of stilts propping the slender aerotropic root, suggest a highly specialized adaptation to fluctuations of water in flooded valleys of the rain-forest zone. All localities observed are situated in the high-rainfall areas of Ghana where occasional showers can raise the water level within a single hour 1 metre above ground. In this ecological setting the structure of stilted peg-roots appears as a successful adaptation which can secure the gaseous exchange of the submersed root system.

From the point of view of growth physiology, the strictly opposite behaviour of the apex of the main aerotropic root and the apices of geotropic laterals is of the utmost importance. The student of tree growth will find here interesting material for experiments.

However, the anatomy of the stilted peg-roots does not provide a straightforward support for the breathing function of these organs. The compact cortex, persisting rhizodermis or exodermis, and the compact periderm and secondary phloem give no signs of ventilating tissues commonly observed in pneumatophores. Scattered lenticells on the older parts of the aerotropic root and adjoining stilt roots are the only external features suggesting breathing function. It was beyond the scope of this study to investigate these problems.

One aspect of our observations should be emphasized: the occurrence of stilted peg-roots is limited to waterlogged soils. These organs do not develop in free-drained soils and *Xylopia staudtii* grows with ordinary subterranean roots and ordinary stilt roots only. This fact makes the adaptation theory and the ventilation background of this root modification very probable.

Acknowledgment

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Souhrn

Článek popisuje nový typ pneumatofórů nalezených u stromovité *Xylopia staudtii* ENGL. et DIELS (*Annonaceae*) v bažinách Jižní Ghany. V dlouhodobě zamokřených půdách vysílají horizontální kořeny tohoto stromu svisle vzhůru postranní větve, které pronikají nad povrch půdy, pnou se po bylinách podrostu a dosahují výšky až 2 m. Na spodní vzdušné části aerotropického kořene vz… kají postranní kořenové větve, které jsou všechny pozitivně geotropické. Nižší z těchto větví zakořeňují v půdě, postupně tloustnou a vytvářejí opěry, které podpírají štíhlý hlavní kořen. Tak vzniká ustálený tvar pneumatofórů, pro něž byl zvolen název „kolíkovité pneumatofóry s opěrnými kořeny" (anglicky: "stilted peg-roots"). Výkopy kořenového systému *Xylopia staudtii* na více lokalitách potvrdily, že jde o dobře vyhraněnou modifikaci stromových kořenů, kterou možno považovat za případ velmi specializované adaptace na zamokřené půdy tropických sladkovodních bažin. Na rozdíl od jiných pneumatofórů je primární kůra, druhotné lýko i periderm těchto kořenů velmi kompaktní a bez intercelulár, takže tu nelze dokládat jejich dýchací funkci jen pomocí anatomických řezů. Dřevo starších kořenových větví pneumatofórů je mimořádně lehké a složené převážně z článkovaných tracheid a dřevního parenchymu. Morfogenese kolíkovitých pneumatofórů s opěrnými kořeny probíhá v pěti ontogenetických fázích, které lze pozorovat v okolí jediného stromu v neutříděné směsici. Na dobře drenovaných půdách kolíkovité pneumotofóry s opěrnými kořeny nevznikají a *Xylopia staudtii* roste jen s normálními zemními kořeny a shlukem opěrných kořenů na bazi kmene.

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Recensent: Z. Černohorský

See also plates II.—III. in the appendix.

Berichtigung

zum Aufsatz: MARTINOVSKÝ J. O. et SKALICKÝ V.: Zur Nomenklatur einiger *Stipa*-Sippen der *Pennatae*-Gruppe. — Preslia, Praha, 41 : 327—341, 1969.

Durch ein Versehen unterlief in diese Abhandlung ein Druckfehler, der wesentlich den Sinn neuer Namenskombination verändert. Seite 331, Zeilen 17—19 von oben herab sollen lauten:

Stipa pennata L. emend. STEVEN subsp. *eriocaulis* (BORB.) MARTINOVSKÝ et SKALICKÝ comb. nova

Basionym: *Stipa eriocaulis* BORB. Math. term. tud. Közl. 15 : 311, 1878.

Plate II., Photo 1. — A characteristic cone of stilt-roots at the base of a tree of *Xylopia staudtii* in the Atewa Range, Ghana.

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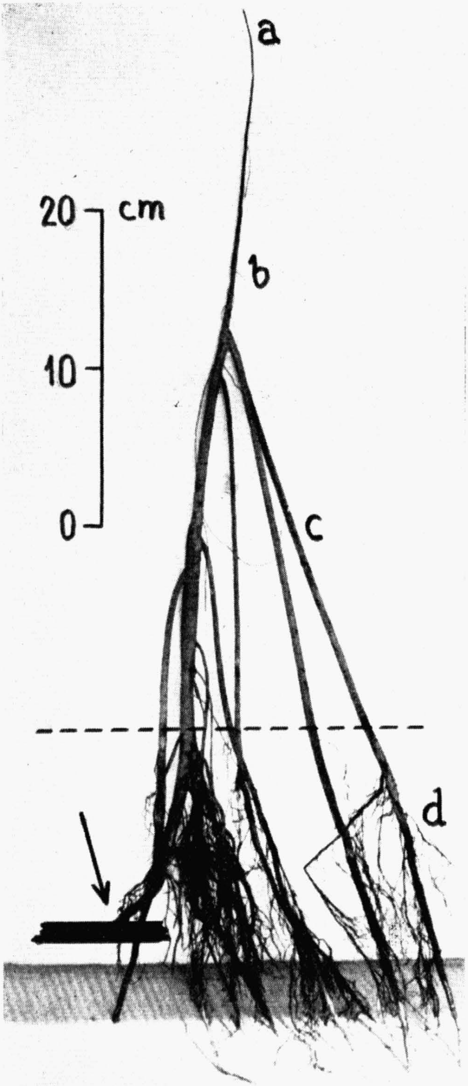

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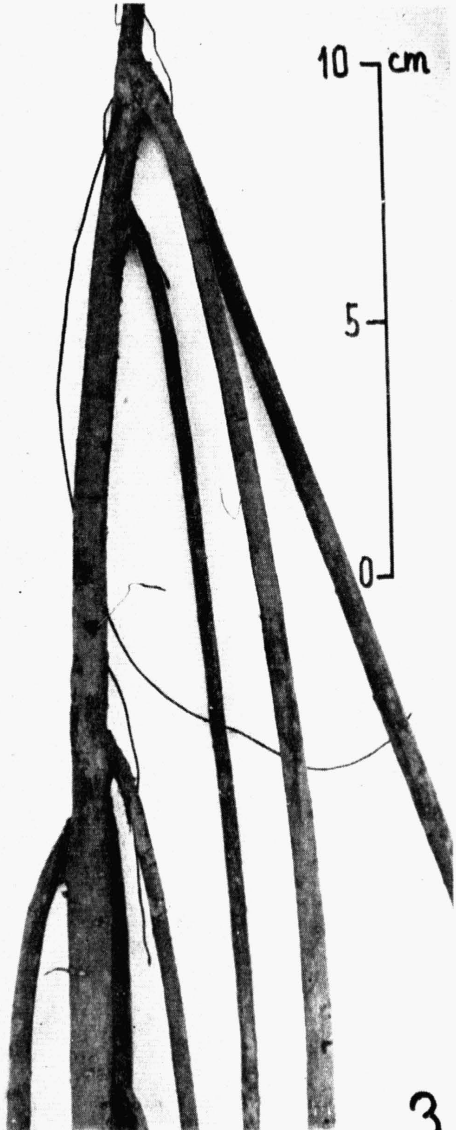

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Plate III., Photo 2. — A middle-sized specimen of the stilted peg-root of *Xylopia staudtii*. *a* — apex of the aerotropic root, *b* — freely hanging laterals, *c* — geotropic laterals developed into stilt roots of the pneumatophore, *d* — richly branched system of underground roots. The broken line indicates the level of the ground, the arrow marks the point of the connection with the main horizontal root of the tree.

Photo 3. — A detail of the stilted peg-root on Photo 2.

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