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Root System of Tropical Trees 8. Stilt-Roots and Allied Adaptations

Kořenový systém tropických dřevin 8. Opěrné kořeny a příbuzné adaptace

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Stilt-roots and allied forms of aerial adventitious roots can be arranged in a series of more or less overlapping "organisation models" which are associated with particular tropical species, and can thus be regarded as genotypical adaptations. *Palmae, Pandanaceae, Euphorbiaceae, Guttiferae, Moraceae, Myristicaceae, Rhizophoraceae* and *Sapotaceae* contain the majority of genera and species developing aerial roots. General appearance of these roots is affected by the place of emergence and distribution pattern over the trunk, by their anatomical structure and rate of both longitudinal and radial growth, by their branching and anastomosing, and by the age of the tree. Formation of aboveground root primordia, and survival and successful growth of unprotected root apices in aerial environment are enhanced by waterlogged soil, high atmospheric humidity, equable temperature and reduced illumination in the interior of tropical forests. Stabilization of large trunks in soft soil, "snowshoe effect", and "short cut" in the nutrition supply and gaseous exchange between the root and shoot, seem to be the main adaptive trends in stilt-root formation. Lack of stilt-rooted trees in tropical mountains and temperate forests can be explained by negative selection for trees with susceptible aerial root apices and high surface/volume ratio of the trunk base — heat exchange and frost being the critical factors.

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Introduction

A cylindrical trunk base is the predominant feature in the majority of trees all over the world. In tropical forests, however, there are numerous deviations from this "normal" appearance of a tree. The lower part of the bole can be dissected into various outgrowths and subsidiary organs which are seldom, if at all, seen in temperate countries, such as plank buttresses, flying buttresses, stilt-roots, spine-roots, hanging roots, broom-like clusters of roots, etc. Buttresses attracted attention of many students in tropical botany and forestry which is well reflected in the RICHARDS' (1952 : 59—74) and SCHNELL's (1970—1971) large reviews, and in a thorough paper by SMITH (1972). Various kinds of aerial adventitious roots including the most conspicuous stilt-roots, on the other hand, were never studied in detail.

The descriptions of tropical trees frequently refer to organs which are, in the anglophonic literature, vaguely called "aerial roots", „adventitious roots", "stilt roots", "prop roots", "strut roots", "hanging roots", "clasping roots", etc. (see IRVINE 1961, 1963; HUTCHINSON, DALZIEL et al. 1954—1971; KEAY et al. 1960; etc.). Tropical foresters often distinguish between "short" and "high" stilt-roots (TAYLOR 1960), or "simple", "branched", "straightened" and "arched" stilt-roots (LETOUZEY 1969) associated with particular species. WILDEMAN (1930), TROLL (1941 to 1942), RICHARDS (1952: 59—62), KUNKEL (1965a), LETOUZEY (1969), KRASILNIKOV (1970) and SCHNELL (1970—1971) summarized the most interesting data referring to this phenomenon.

In the present paper, an attempt is made to describe stilt-roots and allied organs of tropical trees from the morphogenetical and ecological points of view. It appears that the broad spectrum of the aerial adventitious roots can be tentatively classed as a set of partly overlapping "organisation models", and that this approach can be fruitful in adaptation and evolution hypotheses. The author has been biased, necessarily, by his experience with African trees and forests which explains the greater part of examples quoted in the text.

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Tab. 1. — Approximate equivalents for "stilt-root" used in various languages (with referrence to their etymology)

	Mechanical function	Environment	Morphogenesis
English	stilt root prop root strut root	aerial root	adventitious root
French	racine-échasse	racine aérienne	
German	Stelzwurzel Stützwurzel	Luftwurzel	sprossbürtige Wurzel stammbürtige Wurzel
Russian	choduľnyj koren'		pridatočnyj koreň
Czech	vzpěrný kořen podpůrný kořen chůdovitý kořen	vzdušný kořen	adventivní kořen přídatný kořen
Slovak	oporný koreň barlovitý koreň		advetívny koreň

Terminological notes

Not only in English but in other languages as well the organs which are in the focus of the present paper are termed by various names, the etymology of which is connected with their statistical and mechanical function (1), surrounding environment (2) or morphogenetical features (3). Table 1 summarizes the usual equivalents encountered in the pertinent literature dealing with tropical vegetation.

Terms given in a single horizontal line of the Table 1 can possess different meaning and may not substitute each other. Indeed, all roots arising on the trunk and branches of the tree can be classed as "adventitious"in the broad sense of this term (Esau 1960 : 472). However, the same term refers to adventitious laterals on subterranean roots as well, which makes it unspecific for the aerial organs. Using the terminology of Troll (1959 : 383) the term "adventitious" would not fit anyhow; instead of it Troll's "sprossbürtige Wurzel" (stem-born root) or Guttenberg's (1940 : 41) "Beiwurzel" would be appropriate. For practical use we shall adhere to the broader sense (Esau l.c.) of the above mentioned term and use the compound term "aerial adventitious root" contrary to "subterranean adventitious root".

Names denominating the organs in question according to the surrounding aerial environment only, i.e. "aerial root", "racine aérienne", "Luftwurzel", can be also rather vague, especially in the tropics where numerous kinds of pneumorhizae (= pneumatophores) protrude into the atmosphere.

For certain cases of larger and well developed aerial adventitious roots anchored in the soil, the term "stilt-root"*) referring to the mechanical function of the root seems to be useful. On the other hand, the terms "prop

*) The author prefers the orthography used, for example, by Hutchinson et al. (1954—1971): "stilt-root" as a hyphened word.

root", "racine-échasse" and "Stelzwurzel" could be misleading and create wrong impression that an uplifting force is exerted on the tree. In Czech the term "opěrný kořen" will be recommended.

It is only exceptional that we encounter a single stilt-root at the trunk base. Usually a number of these roots branches and anastomoses at the tree base forming a compact system: this will be termed "stilt-root system"

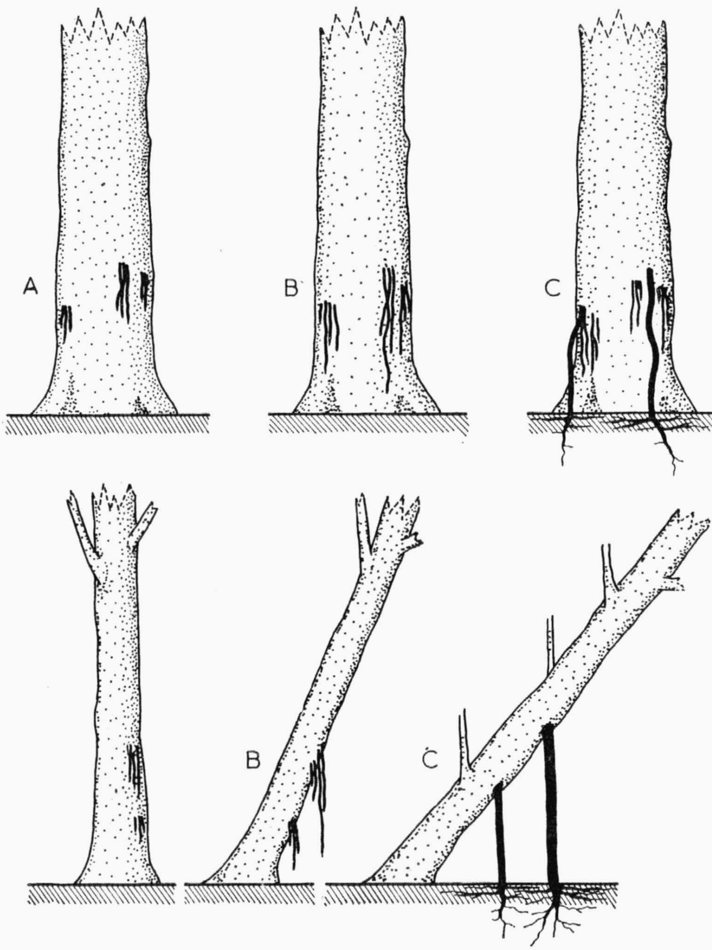

Fig. 1. — Three stages (A, B, C) in the development of the aerial adventitious roots in the models *Afrosersalisia* (above) and *Protomegabaria* (below).

[compare also "Stelzwurzelsystem" by KUNKEL (1965a : 642)] though the plural "stilt-roots" will be used in a similar sense.

PITOT's (1958) investigation into the anatomy of *Rhizophora racemosa* G. F. W. MEY. suggests, however, that the term "root" itself may turn rather doubtful in connection with certain organs we are going to deal with.

Morphogenesis

A certain number of tropical trees shows the capability of formation of root primordia on the aboveground parts of their trunk and branches. The root primordia may arise in the early period of the secondary thickening, and remain concealed in a latent stage, in a similar pattern observed in European *Salix* spp. Or they may develop *de novo* in the cambial zone, secondary phloem or lenticels at any age of the tree under the impact of a physiological or environmental factor. Thus there can be a pause between the actual formation of the primordium and the emergence of the adventitious root. No data are available hitherto to decide this question in tropical trees. The observations confirm that the occurence of root primordia on aboveground organs is limited to particular species and tends to appear within particular families; this suggests, that the phenomenon is rather an inherited feature and genotypical adaptation than a phenotypical modification of individual specimens influenced by environmental stress or injury.

The emergence of aerial adventitious roots is another morphological and ecological problem. The usual anatomy of the tender root apex and primary body seems to be unfavourable for the survival and active growth in the open atmosphere. However, both the primary and secondary structure of the aerial adventitious roots show several deviations from the normal pattern. Some species, such as *Pentadesma butyracea* Sabine or *Anthocleista nobilis* G. Don possess a suberized sheath temporarily protecting the apex; many of them develop the periderm in the subepidermal layer, contrary to the usual formation in the pericycle; and most of them start cambial activity very early so that the emerging root acquires a stiff structure and protection against desiccation and temperature fluctuation from the very beginning. On the other hand, the equably warm, humid and dim micro-climate of tropical forests promotes the growth of adventitious roots in the aerial environment.

The general appearance of individual aerial adventitious root and the entire system of these organs depend on following factors:

i) place of emergence of adventitious roots;

ii) distribution pattern of adventitious roots over the tree surface;

iii) anatomical structure and mechanical features of young adventitious roots;

iv) longitudinal growth of adventitious roots;

v) radial growth of adventitious roots;

vi) branching and anastomosing of individual roots.

We shall successively deal with the above mentioned features in the following paragraphs.

The adventitious roots can arise at any height above the ground, both on the main trunk and from the underside of branches in the crown. Most frequently they develop on the lower part of the trunk, within its 2 metres height, occasionally up to 5 metres height. If the longitudinal growth of these roots is satisfactory, typical stilt-root system can be formed, such as in *Uapaca* and *Xylopia* spp. In some trees, adventitious roots develop along the entire trunk and they can occur even on branches of the crown. Further development of these flying adventitious roots depends on the rate of their longitudinal growth. They remain as clusters of short roots on the stems (Bünning 1947 : 165) or as freely hanging roots (Gill 1969). In West Africa, we have observed adventitious roots never reaching the ground level in *Raphia* palms, *Spondianthus preussii* Engl., *Pachystela brevipes* (Bak.) Baill. ex Engl. and *Myrianthus serratus* (Trécul)

Benth. et Hook. f. The adventitious roots in some *Ficus* species, on the other hand, can resume vigorous growth and cross the distance between the crown and ground surface: this results in the formation of the special form of stilt-roots called sometimes "column-roots" which are well known in *Ficus benghalensis* L. On the contrary *Pycnocoma macrophylla* Benth., a small pachycaulous tree in the undergrowth of African rain forests, develops short adventitious roots in the leaf axils filled with crown humus.

The distribution of adventitious roots over the tree surface shows diverse pattern. Some trees start developing adventitious roots early in the seedling or sapling stage, e.g. *Musanga cecropioides* R. Br. and *Cecropia* ssp., other produce similar roots only in mature age, e. g. *Penta-*

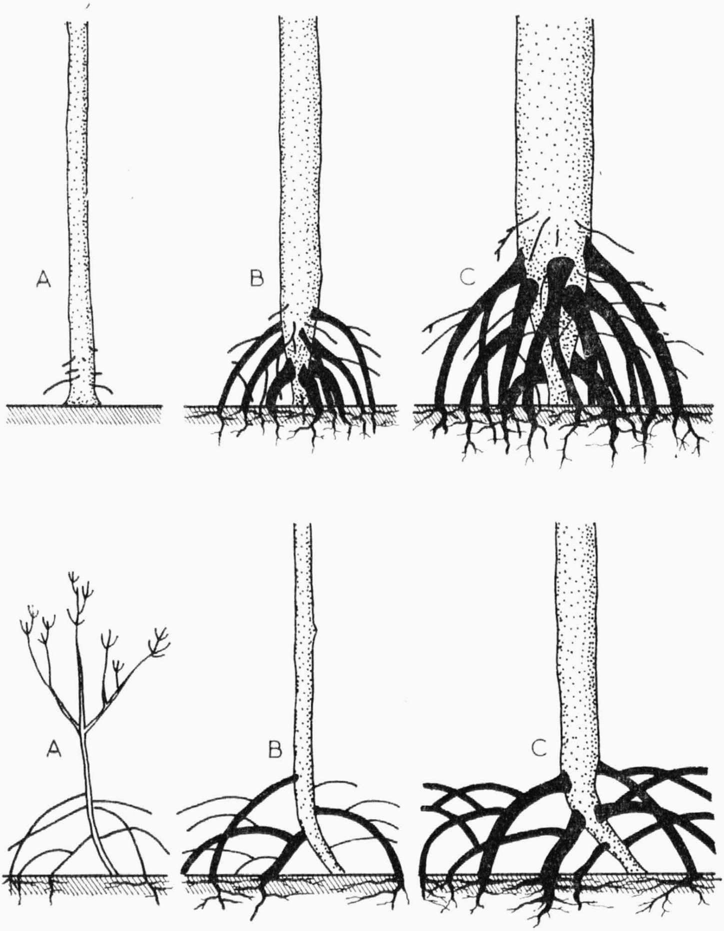

Fig. 2. — Three stages (A. B.C) in the development of the aerial adventitious roots in the models *Uapaca* (above) and *Rhizophora* (below).

desma butyracea Sabine. The environment can alter this pattern markedly. *Anthocleista nobilis* G. Don, for example, usually develops small stilt-roots only in mature age; in dense undergrowth of freshwater swamps and under the influence of reduced illumination and high atmospheric humidity, the adventitious roots arise in the seedling stage and produce stilt-roots in very young trees (Jeník 1971). The resulting system of stilt-roots depends on the density of adventitious roots over the surface of the parent tree. Trees such as *Bridelia micrantha* (Hochst.) Baill. or *Macaranga barteri* Müll. Arg. develop abundant adventitious root-spines and spine-roots which can extend in a system of dense stilt-roots. On the other hand, *Uapaca* spp. or *Santiria trimera* (OLIV.) AUBRÉV. tend to develop scattered and large adventitious roots.

The shape of stilt-roots depends on mechanical feature and growth direction of young adventitious roots. These properties are affected by the anatomy of their primary body, and speed of their secondary thickening. Two marginal cases can be distinguished: (1) The root remains soft and freely hanging along the trunk of the parent tree. Provided with sufficient longitudinal growth such a root can enter the soil close to the foot of the tree and never form an efficient stilt. On a leaning trunk similar root can anchor in a greater distance from the tree base and thus create an efficient stilt. (2) The root is stiff and grows first plagiotropically or obliquely toward the ground, eventually anchoring in a certain distance from the tree base. Though some of the adventitious roots acquire stiff structure in the primary stage, most of the tropical trees can project their roots in a greater distance, mainly due to the early differentiation of secondary xylem and rigid periderm. In *Rhizophora* spp. adventitious roots start growing even obliquely upwards and develop arch-like structure.

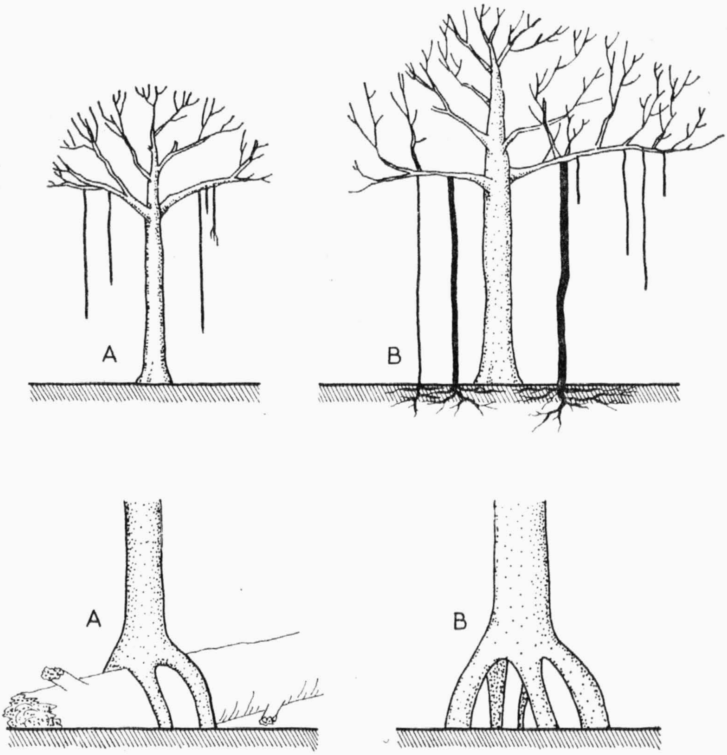

Fig. 3. — Two stages (A, B) in the development of the aerial adventitious roots in the model *Ficus benghalensis* (above) and the development of phenotypical modification of roots in *Picea excelsa* LINK. (below).

The transition from a young adventitious root into an anchored stilt-root depends on the longitudinal growth. This can be rather limited, as it is frequent in species where the secondary thickening starts late or never commences, e.g. in the short roots of *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB. and in *Raphia* spp. In species of the temperate zone the longitudinal growth of occasional aerial adventitious roots seems to be interrupted by adverse conditions of a dry or cold period when most of these roots are killed, e.g. in *Alnus glutinosa* (L.) GAERTN. and *Salix pentadra* L. This could be the reason for the scarcity of stilt-roots in savannah region with marked dry season. In the equable climate of tropical forest, aerial adventitious roots can grow without interruption and reach the soil even at greater distance. Upon entering the soil, these roots change their anatomical structure, branche intensively and enhance the growth of the both underground and aboveground parts.

Radial growth gives the old roots a characteristic shape. Emerging adventitious roots show various thickness ranging from 1 mm to 1 cm diameter in dicotyledons. The palms and screw-pines develop thick adventitious roots, the latter being often quoted as example with huge apices (TROLL 1959 : 379). Old and progressively thickened aerial roots can achieve a diameter of 20 to 30 cm near the point of their attachment to the trunk. Mature trees of *Uapaca* spp., *Santiria trimera* (OLIV.) AUBRÉV., *Tarrietia utilis* (SPRAGUE) SPRAGUE and *Rhizophora mucronata* LAM. were found to possess the largest stilt-roots. Normally, the larger stilt-roots are tapered towards their basal end which gives the stilt-root systems the appearence of an inverted crown. The conical or cylindrical shape of the larger roots (see Plate I, Fig. 5) can be altered by excessive secondary growth in the vertical plane (Plate III, Fig. 9) which creates the "flying buttresses". In many tropical trees only thin stilt-roots are usually found which can be the result of their late formation of the short life span of the respective species. In monocotyledons the secondary thickening is completely lacking and their stilt-roots remain relatively thin.

Finally, the branching and anastomosing affect the shape and general habit of stilt-root system and related adaptations. Three kinds of branch root can be distinguished: (1) laterals arising endogenously in acropetal sequence, (2) laterals arising as adventitious organs in secondary tissues of the parent root, and (3) laterals promoted by the injury of the parent root. — According to the author's experience, in the atmospheric environment the first kind of lateral roots is rather rare. Branching in the aboveground space proceeds mainly by the development of adventitious roots on progressively thickened roots: with regard to the adventitious origin of the parent root, and similar origin and structure of the lateral root, a strict differentiation between stem-born root (sprossbürtige Wurzel sensu TROLL 1959 : 68) and adventitious root seems to be at least inconvenient. — Brittle and frequently palatable young roots exposed in the forest undergrowth attract insect and browsing mammals which cause their frequent injury. This affects the translocation of hormons which enhance the emergence of lateral roots on the proximal side of the damaged tissues. Repeated damage results in the formation of above mentioned broom-like clusters. Desiccation of the apices have similar effects. — In very old trees with a tangle of stillt-roots closely packed together, anastomoses between individual roots can be frequently observed. Successive branching and the anastomoses between individual branches transform the system of stilt-roots into a firm structure supporting the tree on the soft ground.

Distribution and ecology

The diversity of aerial adventitious roots considered in this paper is not limited to the intertropical regions. In swampy forests of the Central Europe, *Salix* spp. and *Alnus* spp. can develop adventitious roots on the trunk base and on leaning branches during wet periods and floods. Obviously the formation of root primordia, emergence of aerial and aquatic adventitious roots can be enhanced by spring and summer flooding. Under favourable conditions even short stilt-roots can develop as known in *Alnus glutinosa* (L.) GAERTN., *A. lanuginosa* GILIB., *Padus avium* MILL. and *Salix cinerea* L.

In Europe, however, the term "stilt-root" has also been applied to structures which are merely phenotypical modifications caused by erosion. In certain species of the conifers, e.g. *Picea abies* (L.) KARSTEN and *Pinus silvestris* L., part of the root system can get exposed and stout skeleton roots emerge from the soil (Fig. 3, below) resembling the genuine stilt-roots (WILLKOMM 1887; KAVINA 1930; SVOBODA 1939). Only recently DOSTÁL et FUTÁK (1966 : 190) have suggested a term "radix pseudogralliformis" which distinguishes between the phenotypical modification of the European trees and usually genotypical adaptation in tropical trees. MOWSZOWICZ et HEREŹNIAK (1969) rightly prefer the term "uncovered roots" in connection with eroded roots of *Pinus silvestris* L.

Wet habitats in subtropical regions, both along the rivers and in foggy mountains, can harbour tree species which can develop short or long adventitious roots on the aboveground stems. GILL (1969) listed 22 species of trees and shrubs with aerial roots in the elfin forest of Puerto Rico. In the equatorial region, various kinds of roots occur not only in wet sites but spread over the "well drained" and mesic parts of rain forests, including secondary stands in both natural and artificial clearings. It appears that the stout stilt-roots which "in a graceful curve" (RICHARDS' 1952 : 59) bend downwards and enter the soil, are to be found only in the tropical region.

In the riverain forest, freshwater swamps and mangroves, the aerial adventitious roots can be abundant, though the number of species possessing these organs is not necessarily too high. New adventitious roots emerge both on the flooded parts of the trunk and over the aerial part during the period of waterlogged soil and lack of aeration in the soil. Along the river Tano in West Africa we have observed a number of arising adventitious roots on trunks of *Spondianthus preussii* ENGL., *Pachystela brevipes* (BAK.) BAILL. ex ENGL., *Myrianthus serratus* (TRÉCUL) BENTH. et HOOK. f. and *Raphia hookeri* MANN et WENDL.; some of these roots emerged as high as 4 to 5 metres above the ground which suggested that they could not arise in the aquatic environment; their formation was induced by the waterlogged soil. In freshwater swamps of Central Africa *Aeschynomene elaphroxylon* (GUILL. et PERR.) TAUB. develops slender adventitious roots which cover the trunk base like a thick brown coat (JENÍK et KUBÍKOVÁ 1969). The majority of these roots are brachyrhizae with limited longitudinal and radial growth; only a few of them can acquire vigorous longitudinal and radial growth and develop into stilts which penetrate into the substratum. Usual pattern of stilt-roots can be seen in *Ficus congensis* ENGL., *Uapaca staudtii* PAX and *U. paludosa* AUBRÉV. et LEANDRI which dominate some African swamps. In the same conditions *Anthocleista nobilis* G. DON develops well differentiated stilt-roots, while similar organs can be missing in well-drained habitats (JENÍK 1971). Altogether the number of tree species forming large stilt-roots in swamp forests is not as high as might be expected from old descriptions. For example, among 106 tree species of the swampy forests in the Congo Basin, ÉVRARD (1968) listed only 4 species (= 3,8%) possessing stilt-roots. In the humid Liberia, KUNKEL (1965b) enumerated only 26 tree species developing stilt-roots. CORNER (1940) describing the trees of the Malaya quotes only a couple of species belonging to *Dillenia*, *Elaeocarpus*, *Xylopia* and *Palaquium*.

In mangrove woodlands the stillt-rooted *Rhizophora* spp. are a dominant tree habit all over the tropical world. Seven species belonging to the genus *Rhizophora*, however, represent only a small fraction of mangroves which in their majority do not form aerial adventitious roots. Occassional "stilt-roots" in *Avicennia africana* P. BEAUV. can only be classed as phenotypical modifications caused by injury and tidal erosion.

In mesic tropical forests stilt-root systems achieve large size and belong to the peculiarities of the undergrowth. Among the numerous tree species of the upper and middle tree-layers, the number of stilt-rooted species is mostly below 5 per cent. In the West African mesic forest, for example, *Uapaca vanhouttei* DE WILD., *U. acuminata* (HUTCH.) PAX et K. HOFFM., *U. esculenta* A. CHEV. ex AUBRÉV. et LÉANDRI, *U. guineensis* MÜLL. ARG. (Plate XXI, Fig. 5), *Xylopia staudtii* ENGL. et DIELS (Platte XXI, Fig. 4 and Plate XXII, Fig. 6) and *Tarrietia utilis* (SPRAGUE) SPRAGUE (Plate XXIII, Fig. 9) develop large stilts which spring out of the main trunk as high as 5 metres above the ground. In *Myrianthus arboreus* P. Beauv. (Plate XXIII, Fig. 8) only short stilts are usually formed. It is quite common that in all these species the shape of the main trunk is markedly tapered towards their base, suggesting that the total wood volume of large stilts and the trunk base approximately equals the volume of a cylindrical trunk referring to the diameter above the insertion of the stilt-roots. In secondary stands of the African rain forest, stilt-rooted *Musanga cecropioides* R. Br. often occurs. In this species aerial adventitious roots can be very vigorous and in old specimens a dense system of anastomosed stilt-roots can be observed. Permanent rejuvenation and luxuriance of these roots led Chipp (1913) to a wrong assumption that *Musanga cecropioides* R. Br. was reproduced "entirely vegetatively". According to our observations in West Africa, buds are never formed on stilt-roots and shoot can arise only from a seedling. In some habitats and in parts of its area of distribution adventitious roots of *Musanga cecropioides* R. Br. can be missing (Richards 1952 : 61). Stilt-rooted *Bridelia* spp. and *Macaranga* spp. are also frequent in secondary forests of the tropical Africa: Jeník and Harris (1969) pointed out that the spines encountered over their trunk are potential roots which can at certain age and in a particular biotope develop into stout stilt-roots. Species of the above genera can grow even in clearings and secondary forests of the lower mountains.

In the savannah region with pronounced dry season, and in high mountains with night frosts the phenomenon of aerial adventitious roots is missing. Obviously there was a negative selection for stilt-rooted trees in these regions in the course of evolution.

In conclusion we want to emphasize some characteristic phytogeographical and ecological features referring to aerial adventitious roots:

i) the phenomenon has its centrum of distribution in the tropics, but it does occur in extratropical countries as well;

ii) its frequency within the tropical region is strongly affected by the biotope and biome;

iii) the development of aerial adventitious roots is enhanced by waterlogged soil, damp atmosphere, equable temperature and dim light within the undergrowth of forests;

iv) the occurence of perennial aerial roots is adversely affected by the periods of drought and/or frost which injure the susceptible apices and primary tissues of the freely exposed organs.

Occurrence in families and relationship to individual species

Stilt-rooted tree species have been repeatedly listed in various parts of the tropical world (Corner 1940; Schnell 1950; Voorhoeve 1965). Less known are small aerial roots which, only occasionally, may enter the soil and develop into stilts (Gill 1969). Table 2 gives a survey of families and genera which contain a majority of trees and shrubs showing various forms of aerial adventitious roots. Among the dicotyledons 5 families include more than 3 genera: *Euphorbiaceae*, *Guttiferae*, *Moraceae*, *Myristicaceae* and *Sapotaceae*. Among the monocotyledons *Palmae* contain the majority of genera with the capacity for rhizogenesis on the aboveground stems. As for the genera, *Pandanus* (approx. 600 spp.) and *Ficus* (approx. 800 spp.) contain the highest number of stilt-rooted woody plants in the plant kingdom. In Africa, *Bridelia*, *Macaranga*, *Rhizophora* and *Uapaca* include more than two stilt-rooted

Tab. 2. — Tropical families and genera containing trees and shrubs with aerial adventitious roots (incl. stilt-roots); the genera possessing short aerial roots only are marked by an asterisk

Dicotyledones		*Dicotyledones*	
Annonaceae Juss.	*Xylopia* L.	*Myristicaceae* R. Br.	*Coelocaryon* Warb. *Myristica* Gronov. *Pycnanthus* Warb. *Virola* Aubl.
Barringtoniaceae Rudolphi	*Barringtonia* J. R. et G. Forst		
Burseraceae Kunth.	*Canarium* L. *Santiria* Blume *Santiriopsis* Engl.	*Myrsinaceae* R. Br.	**Grammadenia* Benth. **Wallenia* Sw.
Dilleniaceae Salisb.	*Dillenia* L.	*Myrtaceae* Juss.	**Calyptranthes* Sw. *Eugenia* L.
Dipterocarpaceae Bl.	*Hopea* Roxb.		
Euphorbiaceae Juss.	*Amanoa* Aubl. *Bridelia* Willd. corr. Spreng *Macaranga* Thou. *Protomegabaria* Hutch. **Pycnocoma* Benth. **Spondianthus* Engl. *Uapaca* Baill.	*Rhizophoraceae* R. Br.	*Ceriops* Arn. *Carallia* Roxb. *Rhizophora* L.
		Sapotaceae Juss.	**Afrosersalisia* A. Chev. **Chrysophyllum* L. **Micropholis* (Griseb.) Pierre *Neoxythece* Aubrev. et Pellegr. *Pachystela* Pierre ex Radlk. *Palaquium* Blanco
Guttiferae Juss.	*Calophyllum* L. *Clusia* L. *Garcinia* L. *Pentadesma* Sabine *Symphonia* L. f. *Tovomita* Aubl.	*Sterculiaceae* Vent. *Tiliaceae* Juss.	*Tarrietia* Blume *Elaeocarpus* L.
Irvingiaceae Pierre	*Kleinedoxa* Pierre ex Engl.	*Monocotyledones*	
Loganiaceae Mart.	*Anthocleista* Afzel.	*Agavaceae* J. G. Agardh.	*Dracaena* Vand. ex L.
Melastomataceae Juss.	**Calycogonium* DC. **Mecranium* Hook. f. **Miconia* Ruiz. et Pav.	*Palmae* Juss.	*Eugeissona* Griff. *Euterpe* Gaertn. *Iriartea* Ruiz. et Pav. **Prestoea* Hook. f. **Raphia* Beauv. *Verschaffeltia* H. Wendl.
Moraceae Link.	*Cecropia* Loefl. *Ficus* L. *Musanga* C. Sm. R. Br. *Myrianthus* Beauv. *Treculia* Decne ex Tréc.	*Pandanaceae* R. Br.	*Pandanus* L. f. *Freycinetia* Gaudich.

species. For example, out of the 9 *Uapaca* spp. growing in West Africa, at least 6 possess distinct stilt-roots: *Uapaca staudtii* PAX, *U. heudelotii* BAILL., *U. paludosa* AUBRÉV. et LÉANDRI, *U. togoensis* PAX, *U. esculenta* A. CHEV. ex AUBRÉV. et LÉANDRI and *U. guineensis* MÜLL. ARG.

The occurrence of stilt-roots and related adaptations within a limited number of genera and families suggests that the capacity for the formation of root primordia and their further development on aboveground organs is an inherited character deeply anchored in the genotype. The same seems to be confirmed by the repeated findings of stilt-roots and related adaptations in a particular species by different authors in different parts of the area of its distribution. For example, the list of stilt-rooted trees growing in West Africa is essentially the same in works referring to various countries (HUTCHINSON et al. 1954—1971; SCHNELL 1950; TAYLOR 1960; KEAY et al. 1960; IRVINE 1961; KUNKEL 1965b; VOORHOEVE 1965). We can assume that this phenomenon represents a genotypical adaptation selected in the course of the evolution under particular environmental conditions.

Adaptations and evolution hypotheses

The function of aerial adventitious roots and their adaptive value has been subject to much consideration and speculation. So far, neither physiological nor mechanical experiments have been carried out. Thus we have to rely on comparative ecological observations and evolutionary hypotheses.

In the course of evolution large bodies of tropical trees faced the problem of (1) stability, (2) nutrition and (3) oxygen supply. Though similar problems occured in temperate zone, the peculiarities of tropical climate and soil required different adaptations. Additionally, in the equable climate of the tropical forest, there was a different rate of both positive and negative selection. Frequent immigration, enhanced speciation and lower rate of extinction affected the current diversity of tropical plants (STEBBINS 1972) which could be one reason of the greater variety of root forms.

The problem of stability in a tall tree appeared to be pressing due to the shallow physiological profile of tropical soils, i.e. due to the absence of nutrients and low aeration in the subsoil, and owing to respective shallow-rootedness. Swallen spurs and plank buttresses were one adaptive trend; aerial adventitious roots transformed into stilt-roots was another solution. The stilt-roots provided not only mechanical support against uprooting, but also produced favourable "snowshoe effect" dispersing the tree's compressive force over a greater area and thus reducing trunk settling and associated root damage (compare similar consideration for buttressing by SMITH 1972 : 37). With regard to the tapered shape of the trunk base and individual stilt-roots, a well developed stilt-root system does not require more energy to be built than a usual cylindrical trunk base. However, its higher surface/volume ratio is a disadvantage in the heat exchange between the tree and surrounding atmosphere, a factor, which might have played important role in the negative selection for this adaptation in extratropical countries (compare again SMITH 1972).

In various kinds of gleisols and muds, tropical trees face the difficulty of efficient mineral nutrition by roots. The absorption roots are repeatedly damaged or killed by anaerobic conditions in the waterlogged soil. Regeneration of these physiologically active roots takes place either by formation of adventitious roots on large subterranean roots or by emergence of adventitious roots on aboveground stands. These roots can branch and root over a great area in the surroundings of the tree, and by this "short-cut" they supply shoot with required amount of water and nutrients. The same morphogenesis seems to be favourable for oxygen supply to roots.

The question of oxygen supply in heavily inundated areas has been discussed in many papers. Bünning (1947) reviewed the contraversial points. Crawford (1972) pointed out that in flooded trees the oxygen supply from the shoot to root is not sufficient for respiratory needs. There are various metabolic adaptations to the anaerobic environment of trees, however, in most plants anaerobiosis is a process that is avoided wherever possible (Crawford op. c.: 311). This is why the spreading of roots and their regeneration after injury caused by anaerobic conditions, find successful alternative in the development of aerial roots which keep the main passage organs (large skeleton roots) outside the soil and when nesessary regenerate only the terminal branches. Various growth substances which are translocated and synthetized under the impact of environmental stress can be assumed as trigger factor for the emergence of new adventitious roots.

Kunkel (1965a) has recently proposed that the important reason for stilt-root formation can be the competition-factor. The author assumes that stilt-root systems enable the tree to escape "suffocation" by the tangle of undergrowth shrubs and trees. This kind of explication, however, does not fit the actual mechanism of tree growth: by no means the longitudinal and radial growth of stilt-roots lift the whole tree up. On the contrary, young aerial roots can contract by means of tension wood in them (cf. Zimmermann et al. 1968).

Models of stilt-root system and related adaptations

As explained in the preceding chapters, the variety of aerial adventitious roots in tropical trees cannot be described in terms of static morphology. Similar structures can result from different development and function. We have to consider the entire architecture of these organs in a similar way as Hallé and Oldeman (1970) studied the shoots of tropical trees. Obviously, the variety of root forms can best be described by means of "organisation models" in which structure, function and temporal changes are integrated. Following is the description of 10 models (see also Figs. 1—3 and Plates XXI—XXIV) which should cover the most characteristic cases of adventitious roots on the trunk of tropical trees.

1. **Model Spondianthus.** — This model is found in trees growing in the riverain forests and swampy depressions where soil is seasonally waterlogged and flooded. Adventitious roots arise on the submerged part (aquatic roots) and on emerged parts of the trunk and branches (aerial roots). Young aerial roots are brittle and flexible, hanging freely along the trunk and from the branches. They undergo secondary thickening only very late, and their longitudinal growth is limited. Thus they never reach the ground and successively die off. They have no mechanical function and may possibly assist in the gaseous exchange between the tree and atmosphere. Observed on *Spondianthus preussii* Engl. in a riverain forest of the river Tano in SW Ghana. *Myrianthus serratus* (Trécul) Benth. et Hook. f. and *Pachystela brevipes* (Bak.) Baill. ex Engl. from African fringing forests belong to the same model.

2. **Model Afrosersalisia** (Fig. 1 above and Plate XXIV, Fig. 10). — Aerial adventitious roots develop on the trunk of mature trees in the humid climate of mountain forests. The roots arise in groups and slowly undergo secondary thickening. They can branch and develop a system of thin and short hanging roots. Single roots can elongate and enter the soil near the foot of the

trunk. The maximum diameter of such a root is below 10 cm. None of these roots have any statical importance in the life of the tree. This model has been described on *Afrosersalisia afzelii* (ENGL.) A. CHEV. in the Atewa Range, Ghana. Similar behaviour of roots can be found in *Chrysophyllum subnudum* BAK. Possibly some shrubs and trees described by GILL (1969) in elfin forest of Puerto Rico belong to the same model.

3. **Model Protomegabaria** (Fig. 1, below and Plate XXIV, Fig. 11). — In the wet part of the African rain forest upright trunks of *Protomegabaria stapfiana* (BEILLE) HUTCH. rarely develop thin adventitious roots near the base. However, on the underside of a leaning trunk vigorous adventitious roots can arise. In the young stage they are soft and freely hanging, but after reaching the ground they grow radially and create stout stilts supporting the weight of the tree. This development can be important for the stability of the tree since many epicormic shoots usually develop on the upperside of the trunk. It is difficult to distinguish between genotypical adaptation and phenotypical modification in this model.

4. **Model Uapaca** (Fig. 2, above and Plate XXI, Fig. 5). — Over the lower part of young trunks numerous adventitious roots arise, and readily acquire vigorous longitudinal growth. They bend down in an arch-like curve, anchor and branch in the soil, and grow radially achieving cylindrical or conical shape. Tapered trunk in old specimens suggests that the total volume of wood required for the stilt-roots system does not markedly surpass the volume of a cylindrical trunk base in a comparable tree. *Uapaca guineensis* MÜLL. ARG. and *Santiria trimera* (OLIV.) AUBRÉV. in African rain forests develop stilts with the upper diameter as large as 30 cm. Some species, such as *Xylopia staudtii* ENGL. et DIELS and *Tarrietia utilis* (SPRAGUE) SPRAGUE also belong to this model. Their large stilt-roots show hastened thickening in vertical plane, and tend to resemble plank buttresses (Plate XXII, Fig. 6 and Plate XXIII, Fig. 9); they are sometimes called "flying buttresses". Some species form short stilt-roots, such as *Myrianthus arboreus* P. BEAUV. (Plate XXIII, Fig. 8), while other species develop few adventitious roots on very old trunks, e. g. *Pentadesma butyracea* SABINE (Plate XII, Fig. 7). Model *Uapaca* includes the most characteristic cases of stilt-root system. High adaptive value of this feature can be anticipated in its mechanical support against uprooting, "snowshoe effect" and efficient spreading of seasonally injured root system.

5. **Model Rhizophora** (Fig. 2, below). — Both on young trunks and lower branches, thick adventitious roots occur, spreading in an arch-like direction towards the ground. PITOT (1958) studied the anatomy of *Rhizophora racemosa* G. F. W. MEY and realised that in the aerial part these organs are neither shoots nor roots; their archaic anatomical structure suggests a special organ called by the author „rhizophore". Stiff and arch-like lateral branches are formed on the top of rhizophores and, successively, an impressive stilt-root system spreads in the surroundings of a single tree. Anchorage and gas exchange appear to be the most adaptive value of this system, while "snowshoe effect" can be anticipated only in very old trees. In younger trees the rhizophores remain thin and possess a markedly uniform thickness; very old trees, e.g. *Rhizophora mucronata* LAM. in East Africa, form cylindrical aerial roots surpassing 20 cm in diameter.

6. **Model Bridelia.** — In a paper by JENÍK and HARRIS (1969) the development of stilt-roots from spines arising on stems of *Bridelia* and *Macaranga* spp. have been described. Only a small part of these root-spines possesses the capacity for longitudinal growth and gradual secondary thickening. Though the resulting stilts are not as stout as in *Uapaca* spp., they can achieve a diameter of more than 10 cm. While the sharp-pointed root apices provide an efficient protection of the trunk base against browsing animals, the elongated stilt-roots have similar mechanical function as in the model *Uapaca*.

7. **Model Ficus benghalensis** (Fig. 3, above). — Numerous *Ficus* spp. develop diverse forms of adventitious roots, including strangling roots, freely hanging roots and stilt-roots. Banyan (*Ficus benghalensis* L.) develops an advanced form of stilt-roots which can also be termed "column-roots". The aerial adventitious roots of this species arise high up in the crown from the underside of the branches, and in juvenile stage hang freely in the air. Upon reaching the ground they branch intensively in the soil and undergo rapid secondary thickening of the aerial portion. In this way upright pillars supporting the crown arise. Successively the tree may horizontally extend its crown and form a large grove. ZIMMERMANN et al. (1968) described the morphology and anatomy of these roots in *Ficus benjamina* L. and showed that tension wood and considerable contraction appear at the early stage of their secondary growth.

8. **Model Raphia.** — Among the monocotyledons this model is a counterpart of model *Spondianthus* in dicotyledons. In wet sites and mostly on old palms short adventitious roots can arise on the trunk as high as 4 to 5 metres above the ground. For a certain time they remain concealed under the decaying bark. Only a few of those emerging near the ground can enter the soil. Compared with the model *Spondianthus*, these roots never show secondary thickening. Their adaptive value is doubtful. Observed on *Raphia hookeri* MANN et WENDL in West Africa.

9. **Model Iriartea.** — This is an advanced type of stilt-roots among monocotyledons. It has been observed on palms of the genus *Iriartea* in South America and on *Eugeissona minor* in Borneo (ASHTON 1964, photo 34). These palms can develop stiff aerial adventitious roots on the lower part of the trunk. They grow obliquely towards the soil and become straightened by contraction. Successively a cone of stilts anchored in the soil surrounds the tree. Unless damaged by browsing animals these roots never branch, and as it is usual in monocotyledons they never form secondary body. Both mechanical and physiological functions comparable with those in model *Uapaca* can be anticipated.

10. **Model Pandanus.** — The majority of screw-pines develop thick aerial adventitious roots with large apices that are said to be the largest in the plant kingdom. These aerial roots can branch and create a tangle of stilts resembling that of the model *Rhizophora*. Observed on *Pandanus candelabrum* P. BEAUV. in the summit area of the Atewa Hills in Ghana. It is the most advanced model of stilt-roots among monocotyledons, very frequent in the paleotropical region where hundreds of *Pandanus* and *Freycinetia* species produce large stands. HOLTTUM (1954) uses the term „strut-roots" for this model.

Souhrn

Tropické stromy vytvářejí širokou stupnici vzdušných adventivních kořenů, jež jsou v některých formách známy také u dřevin mírného pásma. Jejich nejvýraznějším typem jsou opěrné kořeny, které jako obloukovité větve vyrůstají z dolní části kmene a zakořeňují distálními konci v různé vzdálenosti od stromu. Opěrné kořeny byly dosud v literatuře bezdůvodně popisovány jako vyhraněné orgány bez spojitosti s volně visícími kořeny, kořenovými trny, objímavými kořeny škrtičů a sloupovitými kořeny některých fíkovníků. Nebyla brána v úvahu morfogenese těchto orgánů, jejíž různá stadia vývoje se při statickém nazírání jeví jako různé "typy" kořenů. Nedostatečně byly rozlišovány fenotypické modifikace a genotypické adaptace.

Autor dává poprvé do souvislosti rozmanité formy vzdušných adventivních kořenů a na širokém výběru příkladů srovnává jejich strukturu, vývoj a funkci. Všímá si různých aspektů morfogenese, které rozhodují o konečné organizaci kořenového systému: velikost a stáří stromu, místo založení kořenových základů, rozložení a četnost adventivních kořenů na povrchu kmene a větví, mechanické vlastnosti mladých kořenů, podélný a radiální růst, větvení a srůstání kořenových větví. Popisuje ekologické podmínky, které ovlivňují vznik a růst vzdušných adventivních kořenů: zamokření půdy, zaplavení půdy, vlhkost vzduchu, vyrovnaná teplota, snížená světelná intenzita a okus zvěří. Uvažuje o adaptivní hodnotě rozličných forem vzdušných adventivních kořenů: u výrazných opěrných kořenů předpokládá mechanické funkce (ochrana před zapadáním do měkké půdy — tzv. sněžnicový efekt, ochrana před vyvrácením), regenerační funkce (obnova odumírajících terminálních kořenů po záplavách) a fyziologické funkce (zajištění minerální výživy „krátkým spojením" od regenerovaných terminálních kořenů přes vzdušné kosterní kořeny, výměna kyslíku a kysličníku uhličitého mezi nadzemními orgány a kořeny obdobnou cestou a translokace růstových látek).

Na podkladě morfogenese a ekologie autor popisuje 10 organizačních modelů vzdušných adventivních kořenů: model *Spondianthus*, model *Afrosersalisia*, model *Protomegabaria*, model *Uapaca*, model *Rhizophora*, model *Bridelia*, model *Ficus benghalensis*, model *Raphia*, model *Iriartea* a model *Pandanus*. Jsou to většinou dědičně založené adaptace, které jsou vázány na omezený počet čeledí, rodů a druhů. Největší část rodů je obsažena v čeledích *Euphorbiaceae*, *Guttiferae*, *Moraceae*, *Myristicaceae*, *Sapotaceae* a *Palmae*. Nejvíce druhů se vzdušnými adventivními kořeny je zastoupeno v rodech *Ficus* a *Pandanus*.

References

ASHTON P. S. (1964): Ecological studies in the mixed Dipterocarp forests of Brunei State. — Oxford Forestry Memoirs, Oxford, 25 : 1—75.

BÜNNING E. (1947): In den Wäldern Nord-Sumatras. — Bonn.

CHIPP T. F. (1913): The reproduction of Musanga smithii. — Kew Bull., Kew, 2 : 96.

CORNER E. J. H. (1940): Wayside trees of Malaya. Tom. 1. — Singapore.

CRAWFORD R. M. M. (1972): Some metabolic aspects of ecology. — Trans. Bot. Soc. Edinb., Edinburgh, 41 : 309—322.

DOSTÁL J. et J. FUTÁK (1966): Morfologická terminológia. — In: J. FUTÁK [Ed.], Flóra Slovenska, p. 27—596. — Bratislava.

ESAU K. (1960): Plant anatomy. — New York et London.

ÉVRARD C. (1968): Recherches écologiques sur le peuplement forestier des sols hydromorphes de la Cuvette centrale congolaise. — Publ. I. N. É. A. C., Bruxelles, 110 : 1—295.

Gill A. M. (1969): The ecology of an elfin forest in Puerto Rico, 6. Aërial roots. — Journ. Arnold Arbor., Cambridge, Mass., 50 : 197—209.
Guttenberg H. (1940): Der primäre Bau der Angiospermenwurzel. — Berlin.
Hallé F. et R. A. A. Oldeman (1970): Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. — Paris.
Holttum R. E. (1954): Plant life in Malaya. — London, New York et Toronto.
Hutchinson J., J. M. Dalziel et al. (1954—1971): Flora of West Tropical Africa. Ed. 2. — London.
Irvine F. R. (1961): Woody plants of Ghana. — London.
— (1963): West African botany. Ed. 2. — London.
Jeník J. (1971): Root system of tropical trees 7. The facultative peg-roots of Anthocleista nobilis G. Don. — Preslia, Praha, 43 : 97—104.
Jeník J. et B. J. Harris (1969): Root-spines and spine-roots in dicotyledonous trees of tropical Africa. — Österr. Bot. Zeitschr., Wien, 117 : 128—138.
Jeník J. et J. Kubíková (1969): Root system of tropical trees 3. The heterorhizis of Aeschynomene elaphroxylon (Guill. et Perr.) Taub. — Preslia, Praha, 41 : 220—226.
Kavina K. (1930): Oekologie vzpěrných kořenů konifer. — Věstn. Čs. Akad. Zeměd., Praha, 6 : 487—488.
Keay R. W. J., C. F. A. Onochie et D. P. Stanfield (1960): Nigerian trees. Tom. 1. — Lagos.
Krasilnikov P. K. (1970): Klasifikacija kornevych sistem derev'ev i kustarnikov. — Lesovedenie, Moskva, 1970 (3): 35—44.
Kunkel G. (1965a): Der Standort: Kompetenzfaktor in der Stelzwurzelbildung. — Biol. Zentralbl., Leipzig, 8 : 641—651.
— (1965b): The trees of Liberia. — München, Basel et Wien.
Letouzey R. (1969): Manuel de botanique forestière. Afrique tropicale. Tom. 1. — Nogent s/Marne.
Mowszowicz J. et J. Hereźniak (1969): Odsłonięcie korzeni u sosny zwyczajnej (Pinus silvestris L.) — Ekologia Polska, Seria B, Warszawa, 16 : 153—159.
Pitot A. (1958): Rhizophores et racines chez Rhizophora sp. — Bull. de I.F.A.N., Sér. A, Dakar, 20 : 1102—1138.
Richards P. W. (1952): The tropical rain forest. — Cambridge.
Schnell R. (1950): La forêt dense. — Paris.
— (1970—1971): Introduction à la phytogéographie des pays tropicaux. Tom. 1 et 2. — Paris.
Smith A. P. (1972): Buttressing of tropical trees: A descriptive model and new hypotheses. — Amer. Naturalist, Chicago, 106 : 32—46.
Stebbins G. L. (1972): Ecological distributioun of centers of major adaptive radiation in angiosperms. — In: Valentine D. H. [Ed.], Taxonomy, phytogeography and evolution, p. 7—34. — London et New York.
Svoboda P. (1939): Lesy Liptovských Tater. — Praha.
Taylor C. J. (1960): Synecology and silviculture in Ghana. — Edinburgh.
Troll W. (1941—1942): Vergleichende Morphologie der höheren Pflanzen. Tom. 1/3. — Berlin-Zehlendorf.
— (1959): Allgemeine Botanik. Ed. 3. — Stuttgart.
Voorhoeve A. G. (1965): Liberian high forest trees. — Wageningen.
Wildeman E. (1930): Empattements, contreforts, racines-échassess. — Bull. Acad. Roy. Belg., Cl. Sc., Sér. 5, Bruxelles, 16 : 989—995.
Willkomm M. (1887): Forstliche Flora von Deutschland und Oesterreich. — Leipzig.
Zimmermann M. H., A. B. Wardrop et P. B. Tomlinson (1968): Tension wood in aerial roots of Ficus benjamina L. — Wood science and technology 2 : 95—104. [Separatum.]

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See also plates XXI—XXIV in the appendix.

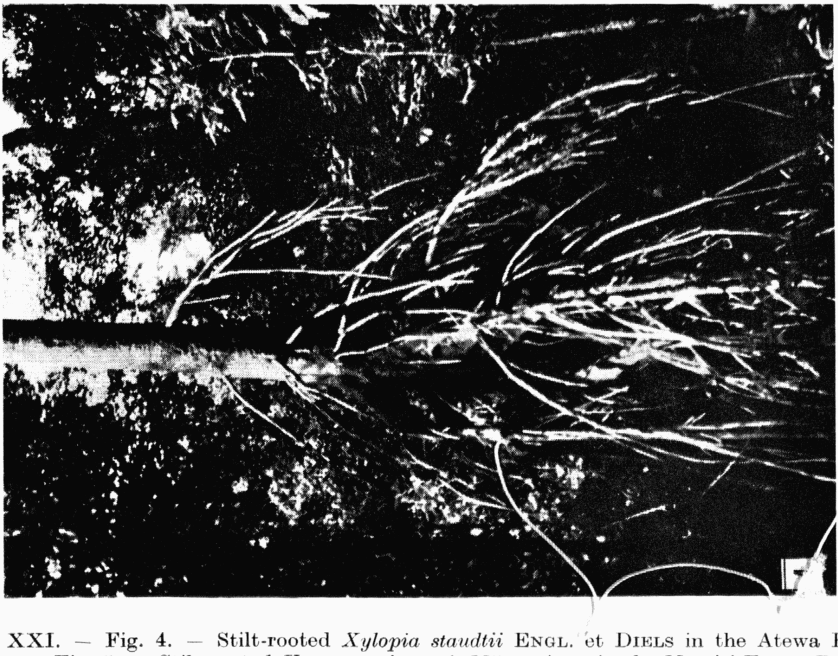


Plate XXI. — Fig. 4. — Stilt-rooted *Xylopia staudtii* ENGL. et DIELS in the Atewa Range Ghana. — Fig. 5. — Stilt-rooted *Uapaca guineensis* MÜLL. ARG. in the Mamiri Forest Reserve Ghana.

J. Jeník: Root System of Tropical Trees 8. Stilt-Roots and Allied Adaptations

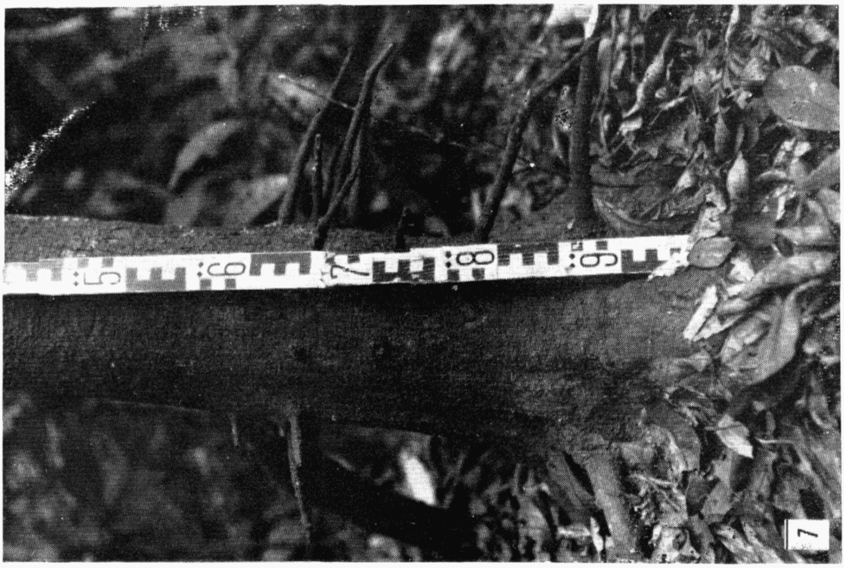
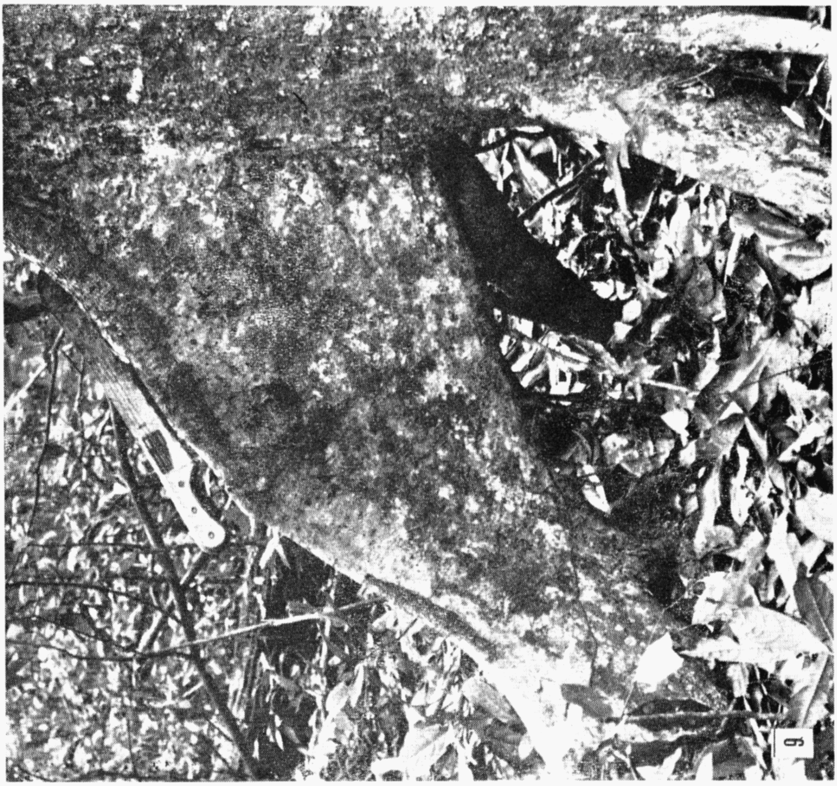


Plate XXII. — Fig. 6. — Close-up view of the stilt-roots in *Xylopia staudtii* ENGL. et DIELS in the Fure Forest Reserve, Ghana. — Fig. 7. — Short aerial adventitious roots (one root in the background and another at the level of the litter, rooted in the soil) in *Pentadesma butyracea* SABINE in the Fure Forest Reserve, Ghana.



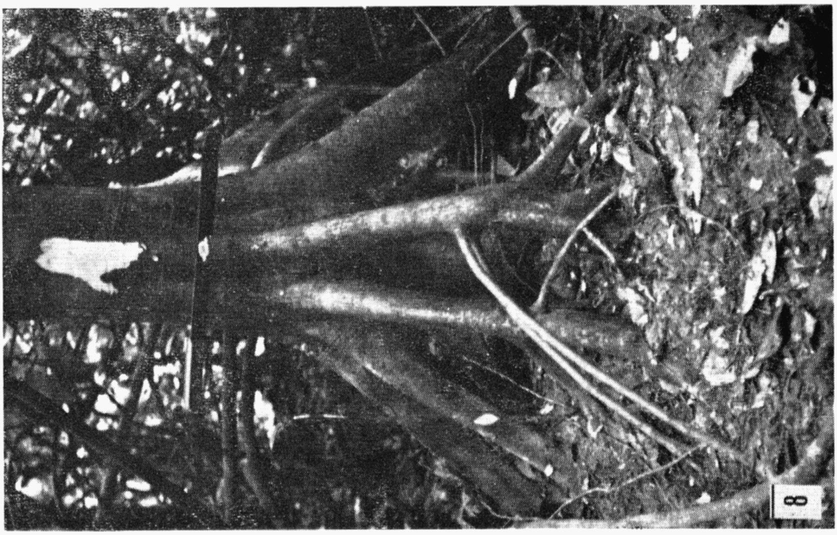


Plate XXIII. — Fig. 8. — Short stilt-root system in *Myrianthus arboreus* P. Beauv. in the Tano-Anwa Forest Reserva, Ghana. — Fig. 9. — Flying buttresses in *Tarrietia utilis* (Sprague) Sprague, developed by hastened thickening of stilt-roots in vertical plane; the Ankasa Forest Reserve, Ghana.

J. Jeník: Root System of Tropical Trees 8. Stilt-Roots and Allied Adaptations

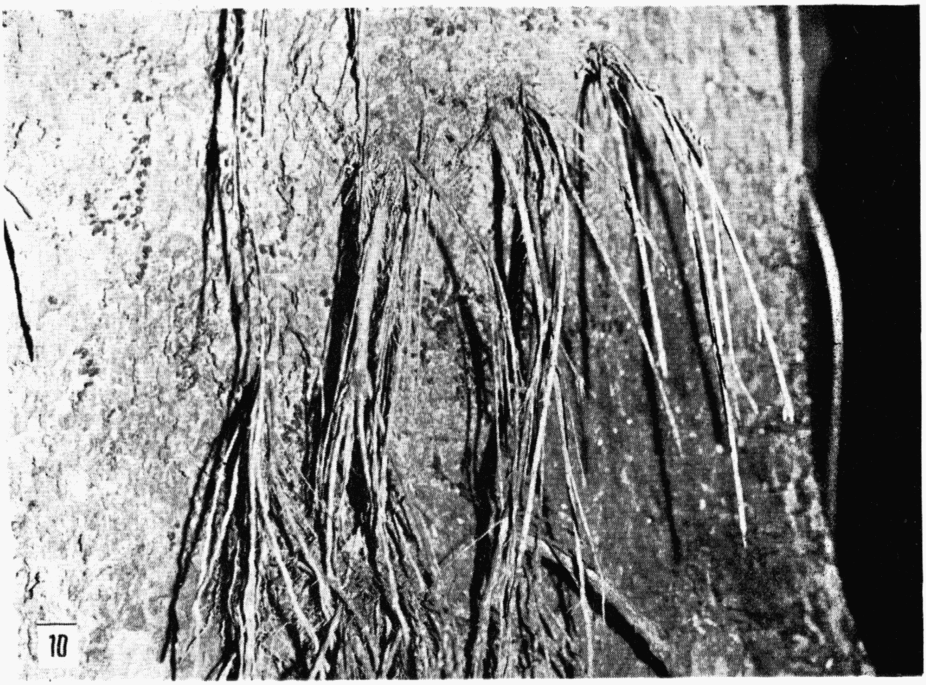


Plate XXIV. — Fig. 10. — Freely hanging aerial adventitious roots on the trunk of *Afrosersalisia afzelii* (Engl.) A. Chev. in the Atewa Range, Ghana. — Fig. 11. — Stilt-roots on a leaning trunk of *Protomegabaria stapfiana* (Beille) Hutch. in the Ankasa Forest Reserve, Ghana.

J. Jeník: Root System of Tropical Trees 8. Stilt-Roots and Allied Adaptations