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Root System of Tropical Trees 1. Ectotrophic Mycorrhizae of *Afzelia africana* Sm.

Kořenový systém tropických dřevin 1. Ektotrofní mykorhizy u *Afzelia africana* Sm.

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Abstract — *Afzelia africana* Sm. (*Caesalpiniaceae*) exhibits ectotrophic mycorrhizae. The structure and development of these organs have been described in detail. A comparison with the few tropical trees showing similar symbiosis has been done. The mycorrhizae were studied both in nature and in cultivation.

Introduction

The rarity of ectotrophic mycorrhizae in the Tropics has not been properly appreciated. Quoted mostly together with endotrophic mycorrhizae, the ectotrophic type of fungus-root association in the Tropics is assumed to be at least of the same frequency and importance as in other climatic regions (Holttum 1954, p. 202; Taylor 1962, p. 20—21; Nielsen 1965, p. 48). This assumption, however, is contrary to the data in the pertinent literature.

In the classical survey of the mycorrhizal associations in Java (Janse 1897) only endotrophic symbiosis has been described. More than fifty years elapsed before Johnston (1949), after extensive research in Trinidad, found no evidence of the occurrence of ectotrophic mycorrhizae. The first indigenous plant in Tropics with ectotrophic mycorrhizae seems to be *Gilbertiodendron dewevrei* (De Wild.) J. Léonard, as discovered by Peyronel and Fassi (1957) in Congo. This record was later succeeded by findings of ectotrophic mycorrhizae in a few tree species all belonging to the family *Caesalpiniaceae* (Peyronel et Fassi 1960; Fassi et Fontana 1961, 1962*a*, 1962*b*). Among sixty forest tree species examined in Western Nigeria by Redhead (1960) only one species exhibited ectotrophic mycorrhizae. According to the literature available no occurrence of this kind of symbiosis is reported from the tropical regions of Central and South America. A few subtropical species of the genera *Pinus* and *Eucalyptus* (see Asai 1934; Chilvers and Pryor 1965), both in natural stands and in cultivation are known to form ectotrophic mycorrhizae.

Material and Methods

The roots of *Afzelia africana* Sm. were studied near Weija in Southern Ghana, in a small riverian thicket. The trees are growing in association with *Baphia nitida* Lodd., *Dialium guineense* Willd., *Drypetes floribunda* (Muell. Arg.) Hutch., *D. parvifolia* (Muell. Arg.) Pax & K. Hoffm., *Ceiba pentandra* (L.) Gaertn. and *Uvaria ovata* (Dunal) A. DC. The stony soil is covered with a shallow humus layer which is richly penetrated with feeding tree roots. Many end-roots in this topsoil showed evidence of abundant fungal hyphae growing in their close vicinity. The

samples collected in FAA and later studied in the laboratory proved the presence of ectotrophic mycorrhizae.

Seeds of *A. africana* were collected near the coast on Freetown Peninsula (Sierra Leone) and later grown in pots (Plate III, phot. 1) in the greenhouse of the Department of Botany, Legon. Soil used in the pots was supplied from a natural forest near Aburi, Ghana.

Morphology of the roots was studied under stereoscopic microscope. Selected root samples were dehydrated and embedded in paraffin. The stain combination used was safranin-fast green.

Root morphology

The morphology of the big skeleton roots was omitted in the present study. Attention has been paid to the rootlets of the last order distributed in the surface soil up to a depth of 10 cm. The branched system of these end-roots

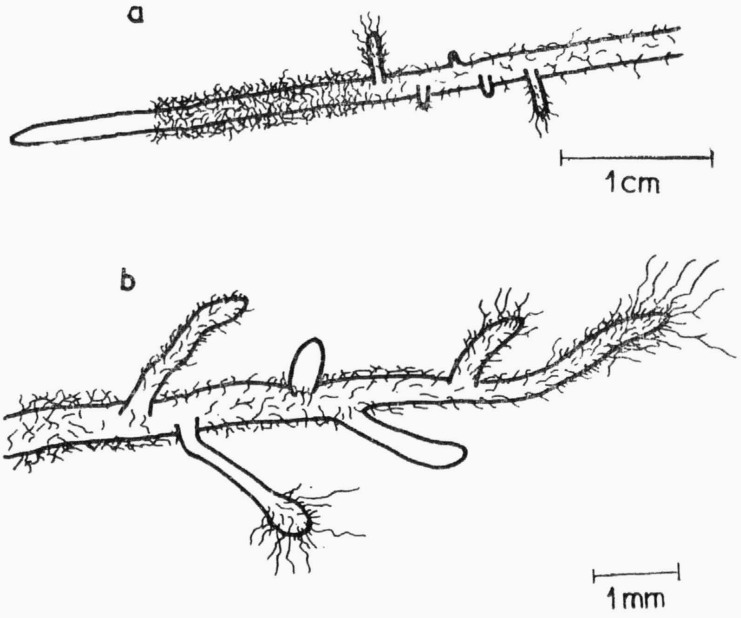


Fig. 1. — External appearance of end-roots in *Afzelia africana* after H_2O_2 treatment: a — a vigorously growing macrorhiza with a few laterals: the hyphous covering behind the smooth tip is formed by loose hyphae attached to the mucilagenous sheath of the rhizodermis; b — a branched system of macrorhizae and ectotrophic mycorrhizae.

(Fig. 1) exhibits a distinct heterorhizis, i.e., a differentiation into bigger leading roots (macrorhizae) and smaller laterals (brachyrhizae) — see nomenclature in Jeník et Sen (1964). The relatively rare macrorhizae (Fig. 1a) attain in the topsoil, a diameter of about 2.0 mm (measurements taken behind the narrowing portion of the root tip); they are smooth, yellow green in colour, lacking root hairs and are never transformed into mycorrhizae. The brachyrhizae (Fig. 1b) have an average diameter of 0.2 mm; they are

variously coloured and frequently transformed into distinct ectotrophic mycorrhizae. The branching gradient is very steep; in a 1 year old seedling branches of the III. order are invariably the utmost root-ends.

In natural conditions as well as in pots the end-roots cling closely to the surrounding soil particles. This is due to either the mucilagenous sheath occurring on the surface of the rhizodermis and/or due to loose fungal hyphae in the soil or the communication hyphae extending from the mycoclenae. The attached soil is not easily removed even by repeated washing with water. Treatment with H_2O_2 breaks the soil-root contact and makes possible a distinction of independent rhizospheric hyphae (peritrophic mycorrhiza sensu JAHN) from communication hyphae of the ectotrophic mycorrhizae. Transitions between the peritrophic and ectotrophic mycorrhizae are frequent.

Morphologically, there are two types of hyphae associated with *A. africana* roots: 1. thick, dark and septate hyphae laid down as more or less straight strands in the surroundings of the root, 2. whitish, richly branched and thin hyphae with woolly and wavy appearance.

Root hairs in true morphological sense were not observed either in nature or in cultivation.

A branched system of end-roots (Fig. 1) may consist of several organs: simple brachyrhizae, ectotrophic mycorrhizae (which may be smooth or hairy, elongated or club-shaped), and slightly elongated brachyrhizae in transition into macrorhizae, and well developed, vigorously growing macrorhizae.

Anatomy of the end-roots

The anatomical structure of the vigorously growing macrorhizae exhibits a very steady histological gradient: even 3 cm behind the cap in transverse section there are no clearly differentiated vascular bundles and the secondary thickening and periderm formation rarely occur within 7 cm from the root tip. The macrorhizae are polyarch, their cortex is very thick and underneath the rhizodermis there is a collenchymatic exodermis which gradually replaces the destroyed rhizodermis. The surface of these roots is covered by a mucilagenous layer in which loose fungal hyphae may be embedded. No compact mycoclenae and no penetration inside the primary cortex were observed.

The brachyrhizae (diameter approx. 0.2 mm) have a diarch stele, a thin cortex and are always covered with surface mucilage. Their root caps are poorly developed or entirely missing. No root hairs have been recorded. This type of root is richly colonized by fungi and frequently transformed into various ectotrophic mycorrhizae.

The consistent fungal mantle shows variability in surface features, thickness and layering (Fig. 2; Plate IV, phot. 3—6). The simplest case is a smooth fungal mantle (Fig. 2a; Plate IV, phot. 3 and 4) composed of a uniform pseudotissue, which has either a pseudoparenchymatic structure ("cells" approx. 3 μ in diameter) or a pseudoprosenchymatic pattern (interwoven hyphae approx. 1.4 μ in thickness). The next type exhibits similar uniform mantle with radiating "communication" hyphae from the surface (Fig. 2b). The colour, length, thickness and density of these hyphae might be well used as a basis for further classification of the ectotrophic mycorrhizae in *A. africana*.

More complicated mycoclenae are frequently composed of two distinct

pseudoprosenchymatic tissues: externally, there is a more or less transparent layer formed by thin, interwoven hyphae (thickness 1.4 μ approx.) with a relatively thin cell wall. Beneath this layer there is a pseudoprosenchymatic tissue composed of thicker hyphae (thickness 2.3 μ approx.), which have a thicker cell wall and are efficiently stained by safranin. (See Fig. 2c). In a few cases we observed peculiar outbursts of this coarser tissue, forming short ridges or "thorns" on the root surface (see Plate IV, phot. 5).

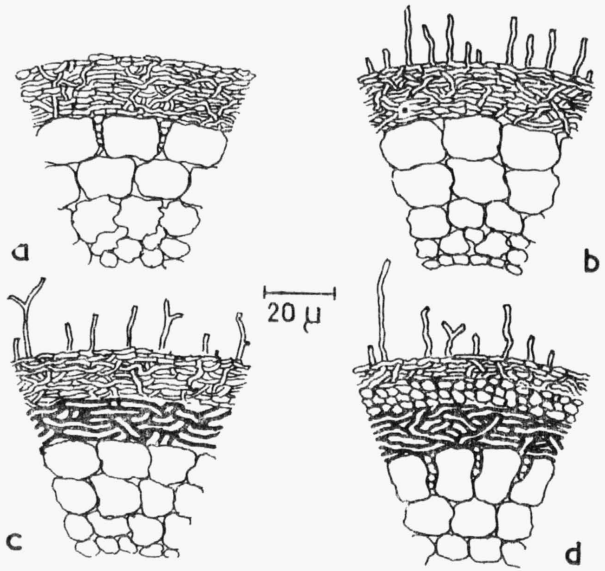


Fig. 2. — Transverse section of the ectotrophic mycorrhizae in *A. africana*; a — smooth and simple mycoclena with Hartig net; b — hairly mycoclena composed of fine pseudoprosenchyma; c — double mantle consisting of fine and coarse pseudoprosenchyma; d — complex structure of mycoclena and Hartig net.

There are also mycoclenae with a very complicated structure in which layers of fine pseudoprosenchymatic tissue alternate with coarse pseudoprosenchyma and pseudoparenchyma (Fig. 2d; Plate IV, phot. 6).

The Hartig net is seldom distinctly differentiated. In most cases the external layer of the root cortex (rhizodermis) undergoes structural changes: the cells are either tangentially or radially elongated. The fungal hyphae or their derivatives or the pseudoparenchymatic cells penetrate only in between the two surface layers of the cortex. Occasionally, there was an intracellular penetration by the coarse hyphae.

The fungal mantle was extended, in some cases, far behind the root tip; secondary thickening under a compact and integrate mantle was also observed (see Plate III, phot. 2). As usual in ectotrophic mycorrhizae, the mycoclenae of *A. africana* covers the entire root tip (Plate IV, phot. 3). The apical meristems seem to cease their growth under the hyphal mantle and the mycorrhizae as a whole die off after some time.

The structure of the ectotrophic mycorrhizae is often complicated by the presence of a surface mucilage which thickly covers all brachyrhizae. The

mucilage seems to be a pectinoid substance which is sometimes colonized by fungi which may through successive growth gradually exclude the mucilage from the root surface.

Discussion

The record of the ectotrophic mycorrhiza in *Afzelia africana* is in line with the recent discoveries from Congo by PEYRONEL, FASSI et FONTANA (op. div.) and from Nigeria by REDHEAD (1960). All nine species so far recorded belong to seven genera of the family *Caesalpiniaceae*. This apparent restriction of ectotrophic mycorrhizae to a single family in Tropical Africa is very peculiar and raises many theoretical problems. The species concerned grow in a wide range of habitats thus indicating that the causative fungi are widely distributed in the forest areas of Tropical Africa. Why then do the members of one legume family only enter into ectotrophic root symbiosis? REDHEAD (op. c., p. 45) quoting HARLEY's experiments suggests, that the soil temperature in Tropical Africa is too high for the optimal development of *Basidiomycetes* which are known to be mycorrhizal in the temperate region. Another explanation might be sought in the specific features of the root systems of tropical trees; this aspect is the topic for further research of the present authors.

Legumes are reported from other parts of the world as species mostly with endotrophic mycorrhizae. Another detail deserving further research is the relation of ectotrophic mycorrhizae to the presence of root nodules in *Caesalpiniaceae*. They were not observed in *A. africana* end-roots. There was, on the other hand, a conspicuous abundance of fungi related to these roots.

As far as the structure is concerned, the mycorrhizae of *A. africana* have many common features with the structures described in detail by FASSI et FONTANA (1961; 1962a) for *Julbernardia seretii* (DE WILD.) TROUPIN and *Brachystegia laurentii* (DE WILD.) LOUIS ex HOYLE. Among the characteristic features the layering of the mantle is of interest. The two types of the pseudoprosenchymatic tissue belong apparently to two different types of fungi, showing more or less constant diversity in size (1.4 μ against 2.3 μ) and thickness of the cell wall (thin, staining light blue against thick, staining dark brown-red). This diversity of mycoclena structure corresponds with the diversity which is recognized among the loose hyphae in the peritrophic mycorrhizae. Mention of two types of hyphae does not imply that only two species of fungi are involved in the colonization. Two types of hyphae are also recorded in the drawings by FASSI and FONTANA (op. c.) and their layering seems to be characteristic for tropical ectotrophic mycorrhizae. The complex multiple layering in *A. africana* with three types of pseudotissues has no counterpart in the descriptions by the above mentioned authors. The development of the peculiar outbursts in the mycoclena seems to be in relation to the more vigorous growth and subsequent extension of the inner layer composed of coarse hyphae. Many of the mycorrhizal types classified by FASSI et FONTANA (op.c.) for the Congo trees were not observed in *A. africana* which may be due to limited material used in this study. One detail in anatomical pattern does not agree with the usual structures found in ectotrophic mycorrhizae: the tangential elongation of the outer layer of primary cortex cells when transformed into a Hartig net.

Contrary to the observations by REDHEAD (1960, p. 15) we did not observe the ectotrophic mycorrhizae in big end-roots (macrorhizae). Contrary to

Chilvers and Pryor (1965, p. 251—252) we consider the mucilage present in some of the mycoclenae and on their surface as a product primarily of the outer cell wall of the rhizodermis. Compared with the roots of temperate tree species, the roots of tropical trees seem to develop a thicker layer of this pectinoid mucilage which may also affect (positively or negatively) the frequency of the ectotrophic mycorrhizae.

The cultivation of *A. africana* proved that there is no difficulty in artificial infection of the seedlings with the appropriate fungi. Since the role of the ectotrophic mycorrhizae in the nutrition of trees in generally proved, there may be some practical use of the present knowledge of the occurrence of this symbiosis in *Caesalpiniaceae* which includes some important and potentially important timber trees in West Africa.

Summary

Afzelia africana Sm. (*Caesalpiniaceae*), a widely distributed tree in Tropical Africa, forms ectotrophic mycorrhizae. Well differentiated mycoclenae develop on the end-roots of this species both in nature and in cultivation. The natural stand studied was a riverain forest in Ghana; the cultivated plants were grown from seeds collected in Sierra Leone. The ectotrophic mycorrhizae of *A. africana* originate through infection and successive histological transformation of short lateral end-roots which occur abundantly in the topsoil rich in humus. Externally, the fungal mantle is either smooth or hairy. The structure of the mycoclena is either a uniform pseudotissue (pseudoparenchyma or pseudoprosenchyma) or a multiple layer composed of a combination of pseudoparenchyma and modifications of pseudoprosenchyma. Additionally, in the juvenile stages of infections, a mucilagenous sheath is generally present. The Hartig net is poorly differentiated. This record of ectotrophic mycorrhizae in *A. africana* extends the short list of the members of *Caesalpiniaceae* which, so far, is the only family in Tropical Africa showing this kind of symbiosis.

Souhrn

Afzelia africana Sm. (*Caesalpiniaceae*), velmi rozšířený strom tropické Afriky, vytváří ektotrofní mykorhizy. Charakteristické hyfové pláště na koncových kořenech této dřeviny lze najít v přirozených podmínkách i v kultuře. Morfologické, anatomické a ekologické zvláštnosti této symbiosy byly studovány v lužním lese v Ghaně; vypěstované rostliny vzešly ze semen sebraných v Sierra Leone. Ektotrofní mykorhizy vznikají houbovou infekcí a následnou histologickou přestavbou postranních koncových kořenů, které jsou nejpočetnější v mělké humósní vrstvě lateritické půdy. Houbový plášť je na povrchu buď hladký nebo vlasatý a štětinatý. Vnitřní struktura houbového pláště je tvořena buď jednotným pseudoparenchymatickým či pseudoprosenchymatickým pletivem, nebo se skládá z několika různorodých pletiv. Kromě vnějších vrstev houbového původu lze na mladých mykorhizách často pozorovat obalnou rosolovitou vrstvu, která je produktem rhizodermis. Hartigova síť je vytvořena jen málo výrazně. Nález ektotrofní mykorhizy u *A. africana* rozšiřuje zatím nevelkou řadu zástupců *Caesalpiniaceae*, které jsou jedinou čeledí tropické Afriky, u níž je tento typ symbiosy znám.

Acknowledgement

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See also plates III and IV in the appendix

Zprávy o literatuře

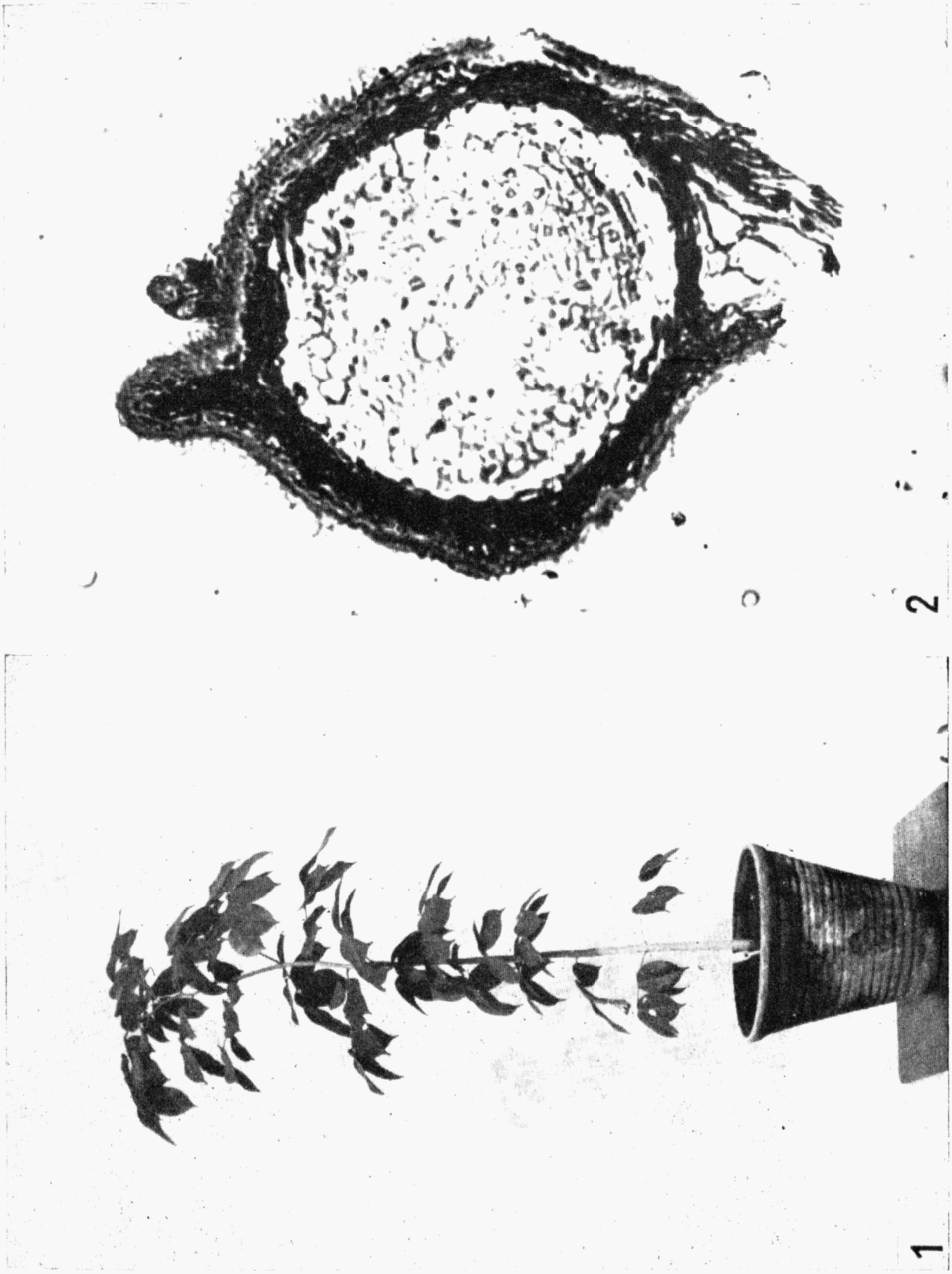
J. Dagys et al. (red.):

Botanikos terminų žodynas

Leidykla „Mintis", Vilnius 1965, 663 stran., cena váz. 1,61 rublů. (Kniha je v knihovně ČSBS.)

Tento litevský slovník botanických termínů je kolektivní dílo. Kromě předmluvy a vysvětlení užitých zkratek obsahuje 3 části, jež tvoří jádro publikace. V první části je věcný výklad litevských botanických termínů (v litevštině), uspořádaných abecedně, k nimž se pojí na konci jednotlivých hesel odpovídající termíny v latině a ruštině (p. 9—502). Druhou část tvoří latinsko-litevský slovník (p. 503—557) a konečně třetí rusko-litevský slovník botanických termínů (p. 559 až 654). Publikaci ukončuje seznam literatury, z níž komise, která slovník připravovala, excerpovala hesla.

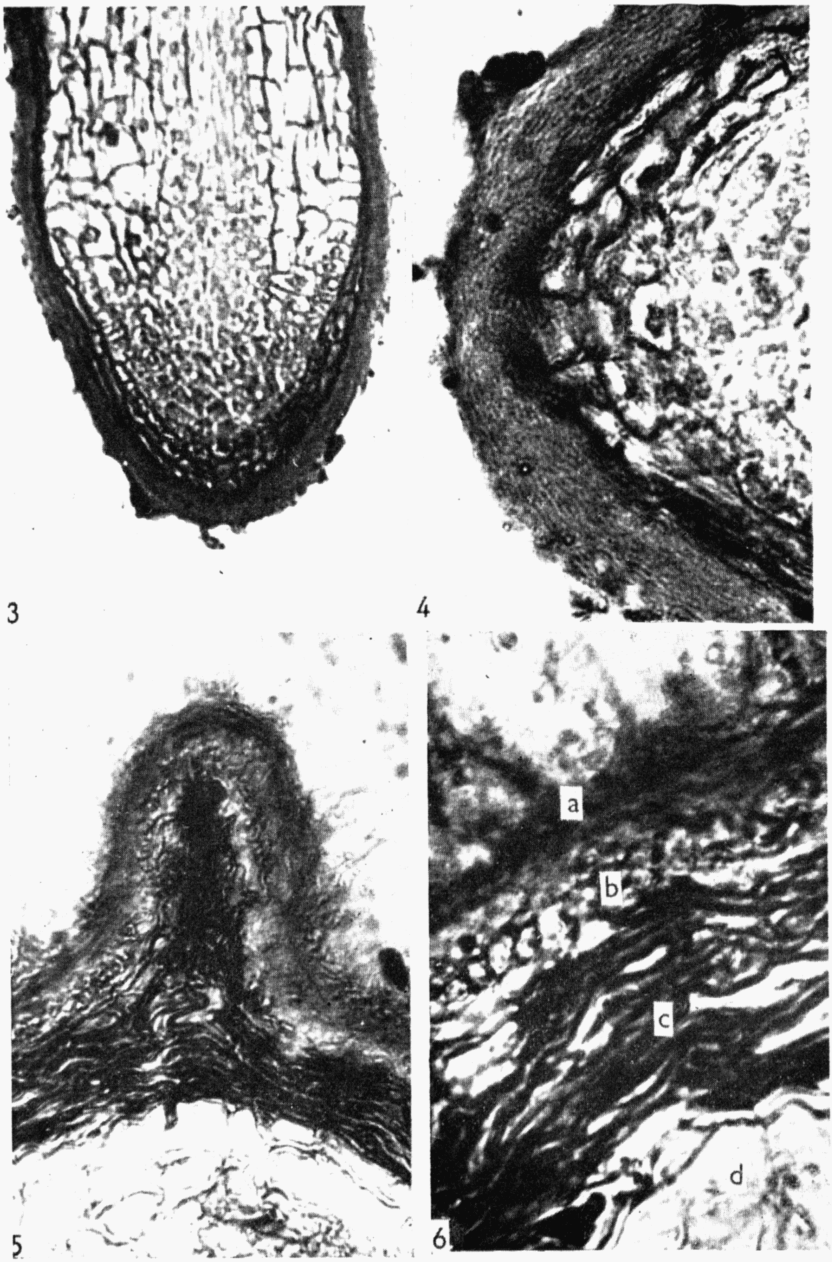
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Phot. 1. Less than 1 year old seedling of *Afzelia africana* from cultivation in greenhouse.

Phot. 2. Multiple structure of the mycoclena covering an older end-root of *A. africana*.

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3. Longitudinal section of an ectotrophic mycorrhiza in *A. africana*. 4. Detail of the mycoclena composed of fine pseudoprosenchyma. 5. Characteristic outburst of the mycoclena. 6. Complex structure of the mycoclena; a — fine pseudoprosenchyma; b — pseudoparenchyma; c — coarse pseudoprosenchyma; d — primary cortex.

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