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Contribution to the Classification of Root Systems of Woody Plants

Příspěvek ke klasifikaci kořenových systémů dřevin

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Abstract — Heterorhizis is a characteristic feature of root systems of all woody plants: end roots are differentiated into macrorhizae and brachyrhizae. Macrorhizae (long end roots of relatively unlimited growth) and brachyrhizae (short roots of limited growth) are characterized in detail. The main differentiating feature of macrorhizae is their capability of secondary growth. Secondary growth is absent in brachyrhizae or is limited in time. Woody plants may be divided into two big groups according to their type of root system: 1. woody plants with intensive root system, with typical heterorhizis and ectotrophic mycorhizae (anatomically the primary roots are characterized by the absence of external protective tissues); 2. woody plants with extensive root system, with atypical heterorhizis and endotrophic mycorhizae (characteristic feature of root anatomy is the presence of external protective tissues — for instance cutinization of rhizodermis, suberization of exodermis, cork layers in cortex etc.).

The problems of root systems have been neglected in botanical and forestry literature. Forestry literature restricts its studies to the main skeleton secondary roots and to their distribution in soil space (differentiation of deep and shallow rooting woody plants). Botanical literature is then interested in the general principles of origin and branching of roots, in their anatomical structure and histological differentiation, mainly in more easily handled herbaceous plants.

Several authors, at the beginning of this century, devoted their studies to root systems, to the morphology and anatomy of primary and secondary roots (see Büsgen 1905, 1927, Tschirch 1905, Noelle 1910, Flaskämper 1910, Alten 1909, Krömer 1903); their work resulted in a detailed description of the anatomy and morphology of plants studied and in the introduction of the new terms: heterorhizis (denoting formation of different root apices in one plant), and extensive and intensive root systems (according to the character of root branching in certain soil space).

The term heterorhizis was first used by Tschirch (1905) for two types of herbaceous roots: Ernährungswurzeln — feeding (absorbing) roots with primary structure, and Befestigungswurzeln — anchorage roots with secondary structure. From his description, however, it is to be seen that these root types were only differently old stages of one root and there was no reason to form two different categories. This weakness in Tschirch's concept was soon recognised by Alten (1909), Flaskämper (1910), and Noelle (1910). Flaskämper completely rejected Tschirch's heterorhizis, Alten and Noelle used the term in a new context. According to them, heterorhizis is the ability of plants to form qualitatively different types of end roots.

Alten (1909) characterized the two following types: long roots (Bereicherungswurzeln) have a big diameter, rapid longitudinal growth, anatomically they are characterized by a large number of protoxylem groups and prolonged differentiation of tissues; feeding roots (Ernährungswurzeln) have a small diameter, a small number of protoxylem groups, a large number of root hairs and rapid differentiation.

Anders (1907, p. 68) described the phenomenon as follows: pioneer (Triebwurzeln) and absorptive (Saugwurzeln) roots may be differentiated in perennial roots of trees and shrubs; the first are perennial, of rapid growth and serve for the enlargement of root system, the second are mostly ephemeral and only short.

NOELLE (1910, p. 255) defined heterorhizis as the ability of one plant to form different types of roots. He considered differences between roots to be qualitative, not only quantitative. In conifers, it was always possible to differentiate long roots (Bereicherungswurzeln, Langwurzeln) and short feeding roots (Ernährungswurzeln, Kurzwurzeln). The third category (in some woody plants) formed roots of the last but one order, which had an intermediate position between the first two types. The fourth category were ectotrophic mycorhizae. The types differed in root diameter, in the number of cortex layers and in the number of protoxylem groups.

BÜSGEN et MÜNCH (1927, p. 267) described the development of root system as follows: "... it is comprised of long roots (Triebwurzeln auch Bereicherungswurzeln, resp. Langwurzeln), which are characterized by strong, long continued, longitudinal growth and facilitate the enhancement of the root system. They branch at different distances from the apex; the lateral roots may again be long roots or they may remain short and after some time die off.." BÜSGEN et MÜNCH called them feeding roots (Saugwurzeln). They mediate complex exhaustion of the soil space occupied by the long root.

From the preceding citations it is clearly seen that heterorhizis was proved and described in detail. The authors of the subsequent rhizological and mycorhizal studies were well aware of results achieved. PRAT (1926) studied endotrophic mycorhizae in *Taxus baccata* and differentiated two types of end roots called pioneer and short feeding roots. Infection in pioneer roots was local, in short roots systemic. HATCH et DOAK (1933) studied root system of the pine and differentiated long, growing roots (the main root of the seedling, lateral "mother" roots and pioneer roots), and short feeding roots, mostly changed into mycorhizae.

TROLL (1941, p. 2271) in his big compendium on plant morphology, on the contrary, denied heterorhizis in underground roots, he took the differences in size to be only end points in a continuous series of values. It is possible that his authority is the reason why new text-books on dendrology, general botany or plant anatomy and morphology, known to me (for instance SVOBODA 1953–1957, GUTTENBERG 1952, EAMES et MACDANIELS 1947, ČERNOHORSKÝ 1957, ESAU 1965), do not contain the term heterorhizis as a general phenomenon occurring in all woody plants. It is possible that the long time interval from formation of basic principles in the beginning of this century also played a role. New American dendrological literature is mostly physiological (KRAMER et KOZLOWSKI 1960, KOZLOVSKI 1962, STEWARD et SUTCLIFFE 1959); when the cited authors work with roots, they do not typify them, although the physiological activity of long and short roots in particular must be very different.

Nevertheless, later specialized workers continue to use terms "long" and "short" root, and "heterorhizis" in papers which deal with mycorhiza problems in more detail and consider the whole root system (ROBERTSON 1954, HARLEY 1959). JENÍK (1957) studied the root system in the oak and found clear differences between the end roots — long roots, and short roots of limited growth. He clarified again the term heterorhizis and showed that the mycorhizal roots belonged to the type of short roots. ZGUROVSKAYA (1958) somewhat complicated the problem: she differentiated three types of roots — pioneer, absorbing (feeding) and leading. Thus, she made the same mistake as TSCHIRCH — she took for leading roots older parts of feeding and pioneer roots; the precise limit, where one type begins and second type ends, cannot be determined. SEN (1962) studied the root system of the lime, where again the two above types might be differentiated. JENÍK et KUBÍKOVÁ (1961) in the work about mycorhiza in *Fraxinus excelsior* have shown heterorhizis also here regardless the opinion of BÜSGEN et MÜNCH (1927, p. 267) who reported only long roots in the ash. BELICOVÁ (1963) described heterorhizis in *Euonymus europaea, Sambucus nigra, Cornus sanguinea, Prunus spinosa, Corylus avellana.* JENÍK et SEN (1964) took heterorhizis for a typical phenomenon of the root system of woody plants and suggested the new terms: brachyrhizae for roots of limited growth and macrorhizae for long, pioneer rots.

On the contrary, there are a number of mycorhizal works dealing with the morphology and anatomy of mycorhizal roots, which do not consider the problems of the whole root system (see DOMINIK 1961 and other works of his collaborators).

Since the term and the phenomenon of heterorhizis in woody plants is not quite clear and is not generally used in the literature, I suggest, on the grounds of data in the literature (NOELLE, ALTEN, BÜSGEN et MÜNCH, ANDERS, PRAT, JENÍK, SEN etc.) and my own experiences, this definition:

Heterorhizis of woody plants is the ability of their root system to form two qualitatively different types of end roots: macrorhizae and brachyrhizae.

M a c r o r h i z a e (long, pioneer roots; Langwurzeln, Bereicherungswurzeln, Triebwurzeln; rostovyje korni; dlouhé růstové prodlužovací kořeny) are thick intensively growing roots, which enlarge the space occupied by

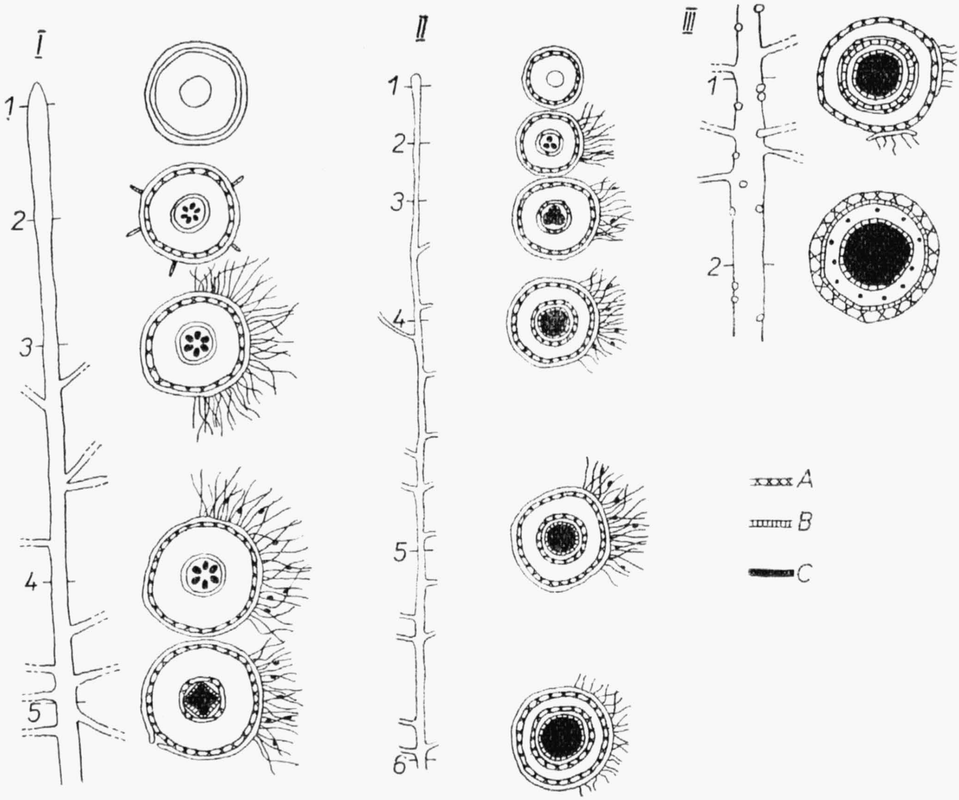

Fig. 1 — The scheme of the differentiation of the macrorhizae and the brachyrhizae in the ash (the example of atypical heterorhizis): I. macrorhiza — description of the layers from periphery to centre: 1 — rhizodermis, exodermis, cortex, stele; 2 — rhizodermis with first root hairs, exodermis suberized, cortex, endodermis, stele with 6 protoxylem groups; 3 — rhizodermis with abundant root hairs, exodermis, cortex, endodermis, stele with 6 protoxylem groups; 4 — as I/3; 5 — rhizodermis with root hairs begins to disintegrate, exodermis, cortex, endodermis begins to suberize, differentiation of metaphloem and metaxylem; II. brachyrhiza: 1 — rhizodermis, suberized exodermis, cortex, stele; 2 — rhizodermis with root hairs, exodermis, cortex, endodermis, stele with 3 protoxylem groups; 3 — rhizodermis, exodermis, cortex, endodermis begins to suberize, first metaphloem and metaxylem; 4 — rhizodermis, exodermis, cortex, suberized endodermis, phloem, cambium, xylem; 5 — as II/4; II/6 — rhizodermis with hairs begins to disintegrate, further see II/4; III. skeleton root: 1 — remainders of rhizodermis and root hairs, exodermis, cortex, endodermis partly suberized, pericycle, phloem with parenchyma, cambium, xylem; 2 — cork, phelogen, secondary parenchyma with groups of sclereids, phloem, cambium, xylem; (skeleton root is an older part of macrorhiza)
A — suberized tissues, B — dividing tissues (cambium, pericycle, phelogen), C — lignified tissues

a certain root system. Anatomically, they are characterized by a large number of protoxylem groups (definite number depends on the woody plant taxon) and by the presence of pith in the stele. The apex is composed of many cell layers, has a distinct root cap and is more or less pointed. The histological differentiation of tissues begins at a greater distance from apical meristem (formation of endodermis, or of exodermis and the impregnation of their walls with lignin and suberin). The cambium begins to function relatively late. According to the woody plant species the root remains for a differently long time at a stage when stele already has secondary structure, but the primary cortex still persists. Only afterwards does the pericycle begin to divide, then the cortex dies off and the periderm is formed. At this stage the development of the secondary anatomical structure of the macrorhiza culminates and by progressive thickening the skeleton root develops, forming later one of the branches of the root system skeleton (see Fig. 1 and 2). These final stages of differentiation occur on the part of the root which is about one year old and has many lateral branches. The apical meristem stops and renews its activity according to ecological conditions (JENÍK 1957, ZGUROVSKAYA 1958) but not indefinitely. After its final dying off its function is taken over by the meristem on a lateral endogenous branch. The capability of secondary growth, i.e. the function of lateral meristems, is not touched by the death of apical meristem. Macrorhizae do not change into mycorhizae; in some cases only local infection was observed. Macrorhizae occur with limited frequency in the root system.

B r a c h y r h i z a e (short, absorbing roots, feeding roots; Kurzwurzeln, Ernährungswurzeln, Saugwurzeln; vsasyvajuščije, sosuščije korni; krátké, savé kořeny omezeného růstu[1])) are thin, primary roots with two or three branches, concerned mainly with the intake of water and salts. Anatomically they are characterized by a small number of cortex layers, a small number of protoxylem groups (1—2—3) and by the absence of pith. The apex is composed of several cells, it is often rounded and the root cap is badly differentiated. Histological differentiation of the endodermis (resp. exodermis) goes up to the apical meristem. The formation of root hairs depends on the taxon (some species have abundant root hairs, some are devoid of them). The cambium begins to function much nearer to the apex. Mostly, the pericycle does not begin to divide, or its activity is limited: brachyrhiza lives for certain time in the primary structure and then dies off, i t w i l l n o t t h e r e f o r e b e c o m e a s k e l e t o n r o o t. As a rule brachyrhizae are infected by fungi. Ectotrophic (epiphytic) or endotrophic (endophytic) mycorhizae then form according to the woody plant species (typification of mycorhizae see MELIN 1927, DOMINIK 1961). The life of a single brachyrhiza depends on the character of its anatomical structure (presence of exodermis, exogenous cork, impregnation of rhizodermis) and on infection with mycorhizal fungi. Generally, it is possible to say that the presence of protective surface layers and the formation of epiphytical fungous mantle (mycoclena) lengthens the life of brachyrhiza to more than one growing season. In dependence on ecological conditions the lifespan of brachyrhizae may fluctuate between several days to several years. The apical meristem is able to renew the growth activity several times and to live through unfavourable periods in a latent state. Finally, it dies off and with it, as a rule, the whole brachyrhiza up to the base. It is possible to observe scars remaining on macrorhizae after the shedding of brachyrhizae. The active surface of died brachyrhizae is compensated by the endogenous formation of new roots by

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[1]) The term absorbing, feeding root does not precisely coincide with purely morphological term brachyrhiza: the primary parts of macrorhizae are also able to absorb water and nutrients.

branching of macrorhizae. Brachyrhizae form the main part of woody plant end roots.

The elementary difference between macrorhizae and brachyrhizae, therefore, does not lie in the limited or unlimited activity of the apical meristem (the activity of the apex being limited in both types), but in the secondary growth (both cambium and pericycle functioning) of older parts of the

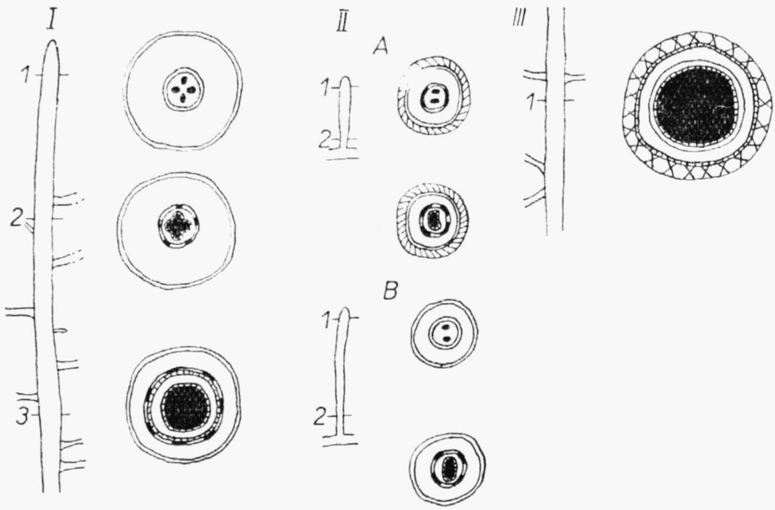

Fig. 2 — The scheme of differentiation of the macrorhizae and the brachyrhizae in the lime (example of typical heterorhizis) I. macrorhiza — description of layers from periphery to centre: 1 — rhizodermis, cortex, endodermis, stele with 4 protoxylem groups; 2 — rhizodermis, cortex, endodermis with single cells impregnated by tanin, stele with first metaphloem and metaxylem; 3 — rhizodermis, cortex, endodermis impregnated by tanin, pericycle, phloem with parenchyma, cambium, xylem; II. brachyrhiza: A — brachyrhizae changed in epiphytic mycorhizae: 1 — mycorhizal mantle (mycoclena), rhizodermis, cortex, endodermis impregnated with tanin, stele with 2 protoxylem groups; 2 — mycorhizal mantle, rhizodermis, cortex, endodermis with tanin impregnation, phloem, cambium, xylém; B — non-infected brachyrhizae: 1 — rhizodermis, cortex, endodermis, stele with 2 protoxylem groups; 2 — rhizodermis, cortex, endodermis with tanin cells, phloem, cambium, xylem. III. skeleton root: 1 — cork, phelogen, cortex, phloem, cambium, xylem; For symbols of lignified, suberized and dividing tissues see Fig. 1.

macrorhiza and in the independence of older parts of macrorhiza on possible disintegration of apical meristem (in such a case, brachyrhiza will die off).

Heterorhizis occurs in all woody plants, nevertheless it is possible to differentiate two groups:

1. typical heterorhizis (e.g. oak, beech, lime, pine etc.): the frequency of macrorhizae on the root system is relatively higher, brachyrhizae are very strikingly shortened (length in mm.) and frequently changed in ectotrophic (epiphytic) mycorhizae. Mycorhizae are distinct by their special morphology and anatomy (see Harley, Dominik, Sen, Robertson). Notwithstanding the high frequency of mycorhizae, some brachyrhizae are without infection, depending on ecological conditions. Macrorhizae are mostly without infection, sometimes only a Hartig net may be formed, i.e. the intercellular hyphal infection of the cortex. (Plate XIX, photo 1 and 2).

2. atypical heterorhizis (e.g. ash, maples, *Taxus*, most shrubs): brachyrhizae in relation to macrorhizae are not very strikingly shortened (length in cm.), ectotrophic (epiphytic) mycorhizae are not formed. As a rule, the roots are inhabited by endophytic fungus, which does not influence their morphology and anatomy (see MOSSE, NICOLSON, DEMETER, PRAT, JENÍK et KUBÍKOVÁ). Infection of the endophyte in the cortex is local to systemic depending on the physiology of both the fungus and the woody plant, and on the ecological conditions. The infection of macrorhizae is mostly only local. Brachyrhizae may secondarily thicken to a certain degree and they may get mother roots of further brachyrhizae (see NOELLE 1910, third type of end roots). Macrorhizae develop mainly in older trees and then mostly on the periphery of root system. (Plate XX, photo 3 and 4).

In connection with the problematics of root system morphology, I would like to point out the great significance of a genetically based, for certain species characteristic anatomical structure. The root anatomy is far from being so uniform, as presented in anatomy text-books. Very important is the formation of exodermis (hypodermis), its impregnation (with lignin and formation of suberin layers) or impregnation of rhizodermis (tanin layers, cutinization), or in some cases the formation of cork layers on the periphery of the cortex. From the comparison of anatomical structure and mycorhiza formation it can be seen, that epiphytic mycorhizae are formed only on roots without exodermis or otherwise strengthened outer primary cell layers. Such protective layers are formed in some woody plants already in the apical meristem and are impregnated very soon (compare Fig. 1 — exodermis in ash); they represent a barrier for the fungi forming epiphytic mycorhizae (*Basidiomycetes*). The endophyte occurring in these roots belongs to quite a different systematic group (*Phycomycetes*) and is so physiologically active (pathogenic) that it can pass through this barrier. Mycorhizal *Basidiomycetes* are restricted only to brachyrhizae, which have thin - walled rhizodermis and cortex without any impregnation.

Examples of plants, whose roots have exodermis, impregnated rhizodermis or other types of protective layers: *Pseudolarix, Cedrus, Cunnighamia, Sequoia, Cryptomeria, Taxodium, Callitris, Libocedrus, Thuja, Cupressus, Juniperus,* (NOELLE 1909); *Acer, Fraxinus* (ZGUROVSKAYA 1958); *Taxus* (PRAT 1926); *Valeriana, Digitalis, Ranunculus, Mentha* (ALTEN 1910); *Cornus sanguinea, Euonymus europaea, Sambucus nigra, Prunus spinosa* (BELICOVÁ 1963); *Primulaceae, Saxifragaceae, Rosaceae* (with the exception of *Dryas octopetala*), *Gentianaceae, Compositae* (LUHAN 1951, 1952, 1954, 1959); *Salix herbacea* (JENÍK et KUBÍKOVÁ 1963); *Liliodendron, Juglans, Cornus mas* (KUBÍKOVÁ in lit.). KRÖMER (1903, p. 71—74) gave a very long list of plants possessing some type of exodermis. It would, however, be necessary to reexamine some data of older authors.

It is clear from this uncomplete review that different forms of protective layers on the primary root surface are a very frequent phenomenon in higher plants. Plants so equipped are always the hosts of only endotrophic (endophytic) mycorhizae. One exception known to me is *Salix herbacea*, which regardless of the impregnated exodermis has a mycorhizal mantle (JENÍK et KUBÍKOVÁ 1963). Maples are sometimes reported to have an epiphytic mycorhiza (KELLEY 1960); according to my samples they have only significant infection of the endophyte.

Exodermis or other impregnations of the surface layers do not occur for instance in *Quercus* (JENÍK 1957), *Fagus* (HARLEY 1959), *Corylus* (BELICOVÁ 1963), *Tilia* (SEN (1962), *Araucariaceae, Picea. Tsuga, Pseudotsuga, Abies, Larix, Pinus* (NOELLE 1909), *Dryas octopetala* (LUHAN 1952). All above species are characterized by the formation of epiphytic mycorhizae which clearly coincides with the easy penetration of rhizodermis and cortex.

Büsgen (1905) was the first to use terms intensive and extensive root system. These systems differ, according to him, as follows: 1. in the diameter of single root branches, 2. in the relation between the length and width of ultimate laterals to the length and width of their mother roots, 3. in the richness and character of branching at the periphery of root system. The ecological significance of these two types lays in complete exploitation of small space by the intensive root system (viz. *Fagus silvatica*) or in using salts and water at a great distance from the trunk by an extensive root system (*Fraxinus excelsior*). According to Büsgen there are numerous transients between the end types, the maple species laying in the middle.

A comparison and combination of all these aspects is shown in the following table:

root system	
intensive	extensive
typical heterorhizis	atypical heterorhizis
presence of epiphytic (ectotrophic) mycorhizae	presence of endophytic (endotrophic) mycorhizae
protective layers are not developed	protective layers on the primary root surface (impregnation of rhizodermis, exodermis etc.) very distinct

I would like to conclude with the following hypotheses: it is possible that one of the reasons enabling the present dominant and pioneer woody plants (*Quercus*, *Fagus*, *Abies*, *Picea*, *Pinus*, *Carpinus*, *Betula*) to acquire this ecological and coenological significance — in the course of historical evolution of plant communities — was the anatomical structure of their roots. The unprotected layers of the cortex facilitated their symbiotic relations with soil fungi; these in turn mediated better exploitation of nutrient reserves of the habitat and thus the woody plant was better equipped for competition with other plant species.

Souhrn

Kořenové systémy všech dřevin se vyznačují tzv. heterorhizií — kvalitativním rozrůzněním koncových kořenů na makrorhizy a brachyrhizy. Makrorhizy (růstové prodlužovací kořeny) a brachyrhizy (drobné kořeny omezeného růstu) jsou podrobně charakterizovány. Za hlavní rozdíl, mimo řadu dalších, považuji schopnost druhotného tloustnutí makrorhiz. Brachyrhizy druhotně netloustnou vůbec, nebo jen velmi omezeně.

Dřeviny lze podle jejich kořenových systémů dělit na dvě velké skupiny: 1. dřeviny s intenzívním kořenovým systémem, s vyhraněnou heterorhizií a ektotrofními (epifytickými) mykorhizami, bez ochranných vrstev na obvodu primárního kořene; 2. dřeviny s extenzivním kořenovým systémem; s nevyhraněnou heterorhizií a endotrofními (endofytickými) mykorhizami, s různými typy ochranných pletiv na obvodu primárního kořene (ztluštění nebo impregnace rhizodermis, tvorba impregnované exodermis, korkové vrstvy ve vnější kůře atd.).

Práce upozorňuje na souvislost anatomické stavby určité dřeviny s tvorbou mykorhiz (epifytické mykorhizy se vyskytují většinou jen u dřevin bez ochranných vrstev na povrchu primárního kořene) a dále na ekologický význam výskytu epifytických mykorhiz většinou u dominantních a pionýrských druhů dřevin.

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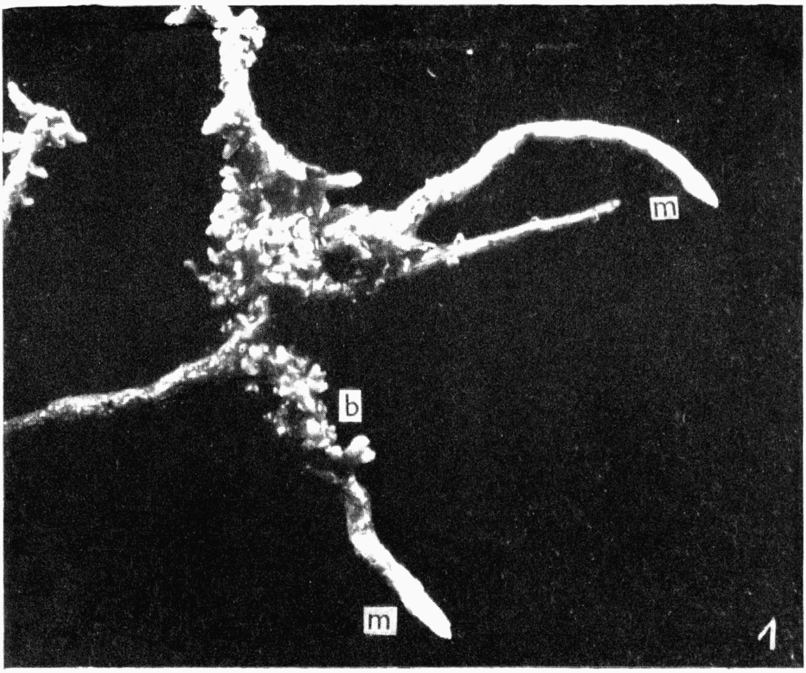
See also plates XIX and XX in the appendix.



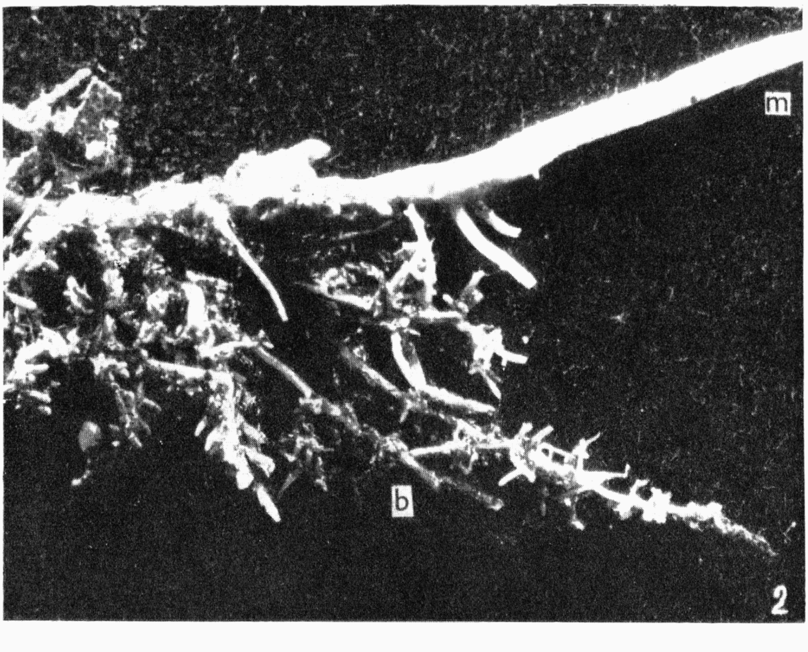
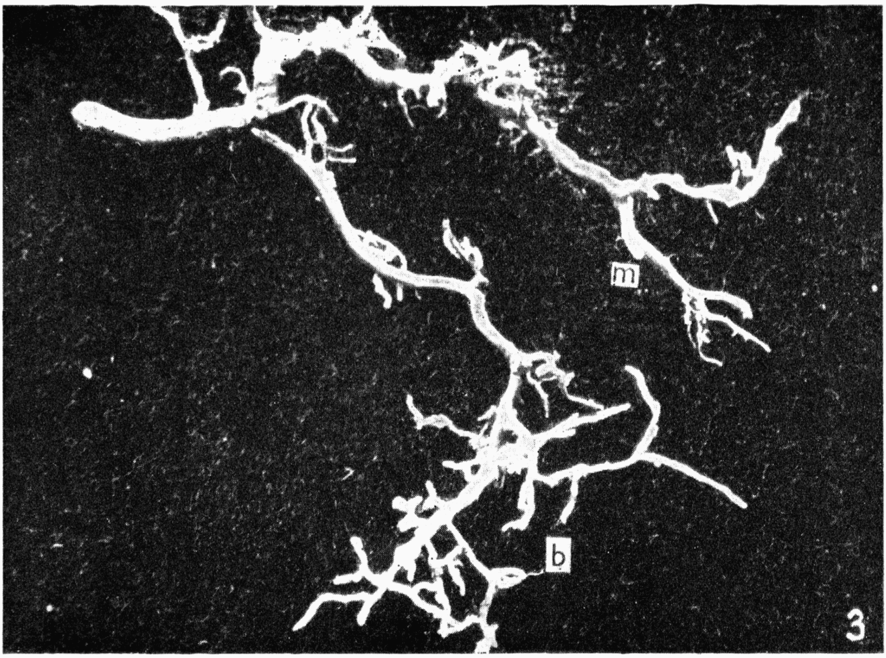


Photo 1. — Typical heterorhizis in pine. (Natural pine forest on sand dunes near Kozly, Central Bohemia, 20. 9. 1966) b — brachyrhizae, m — macrorhizae
Photo 2. — Typical heterorhizis in lime. (Natural oak-hornbeam forest, Lovoš, České Středohoří, 20. 9. 1966)



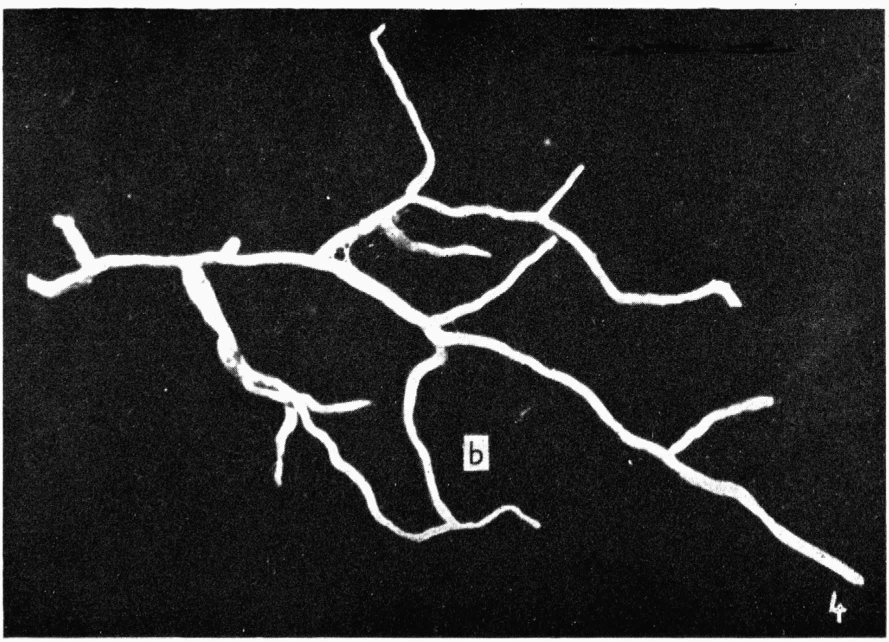


Photo 3. — Atypical heterorhizis in Acer platanoides. (Natural flood-plain forest, Doksany, Central Bohemia, 20. 9. 1966) b — brachyrhizae, m — macrorhizae
Photo 4. — Atypical heterorhizis in Acer campestre. (Forest nursery, Kunratice near Praha, 15. 11. 1966)