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A Study of the Root Systems and Root Ecology of Perennial Herbs in the Undergrowth of Deciduous Forests

Studie o kořenových systémech a kořenové ekologii vytrvalých bylin v podrostu listnatých lesů

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Abstract — The morphology, seasonal development and environmental relationships of the root systems of perennial herbs was investigated in the undergrowth of deciduous forests in the České středohoří, NW Bohemia. With regard to the root systems, the caulophytes represent approx. 90 per cent of the herbaceous species; the rhizocaulophytes and rhizophytes are represented in limited numbers. The period of intensive growth of roots and rhizomes follows after the flowering stage in most of the species studied. No strictly pronounced growth period of the root systems could be determined. The majority of species develop roots, rhizomes, tubers and bulbs within the surface layer down to 15 cm; the maximum concentration occurs in the surface 5 cm layer. The horizontal spread of the roots exceeds the vertical size, 20 to 60 cm being the usual range of the horizontal distribution. No distinct stratification of the entire mass of herbaceous roots could be detected. However, both the root accumulation and the ratios of herbaceous and tree roots allow the definition of the herbaceous underground layer and the tree underground layer.

Introduction

In the study of plant communities the phytosociology deals predominantly with aboveground organs of plants; the study of underground structure of communities is, in most cases, omitted as it consumes much time and labour. In synecological relations, not only the study of root systems of individual plants is important, but also the research of root systems of the whole phytocoenosis and all participant species.

As regards the synusia of perennial herbs in temperate zones, it is always advisable to consider the root forms, as these perennial underground organs may provide a „clue“ to the competitive capacity of the whole plant.

A survey of works dealing with root systems from the point of view of plant communities is given by Wilmanns (1959). Thorough studies of root systems of forest herbs in relation to soil have been carried out by Kievenheimo (1947) and Lisiewska (1960).

In this paper, the term „root system“ is understood in the broader sense of the word as a set of all underground organs both of root and stem origin (cf. Metsävaínio 1931, Jeník 1957). The term „rhizome“ and „runner“ are used in the meaning of Serebrjakov et Serebrjakova (1965).

Methods

The observations of seasonal rhythm of root systems were carried out at two or three weekly intervals during 1964 and 1965, in oak and beech forests. Each observation included root systems of 3 to 5 specimens of the same species, which were excavated with a small spade. Plants with

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normally developed aboveground organs were selected for these observations. The following quantitative and qualitative changes were examined:

1) beginning of the growth of new parts of the rhizome,
2) beginning of the formation of new adventitious roots,
3) period of formation of underground shoots,
4) period of intensive growth of adventitious roots,
5) period of formation of lateral roots.

A similar investigation of phenological stages of aboveground and underground organs was also repeated in the year 1967.

The forms and distribution of the root systems in soil were examined by the usual methods of transect and horizontal excavation (Jeník 1954, Šalyt 1960), which were variously combined according to actual requirements. The depth of the transect was limited to 20—30 cm in most cases, in single cases down to 60 cm. These observations were carried out at the peak of the growing season and 5 to 10 specimens of the same species were studied on each site.

Specific gravity, volume of aerial spaces, moisture content, field capacity, minimum aerial capacity, texture and pH of the soil were determined by the usual methods described in the handbook by Klika, Novák, Gregor (1954).

All the names of plants in the present study are given according to Rothmaler (1966).

Description of the sites of excavations

The study was carried out in three forest stands on slopes of the hills of the České středohoří, NW Bohemia, in the vicinity of Velemín and Milešov. The climate of this territory is classed, within Czechoslovakia, as a moderate and warm climate: the average annual temperature being 7° C, the average temperature during the growing season (April to September) 12° C, the average annual amount of precipitation 550 mm, and the average amount of precipitation during the growing season 350 mm (see Vesecký 1958). However, the macroclimate of this area is considerably modified by the dissected relief. The course of temperatures and precipitation during the year of continuous phenological observations (1965) is presented in Table 1.

1. Hornbeam-oak forest. — A stand at the foot of the Milešovka Hill, 490 m above sea level, inclination approx. 3° to South, geological substratum is oberturon marl. The stand belongs to the association *Galio-Carpinetum primuletosum veris* Klika (1928) 1932, within the alliance *Carpinion betuli* (Mayer 1937) Oberdorfer 1953.

In the tree layer, *Quercus petraea* predominates; in the shrub layer (30%), *Acer campestre*, *Crataegus oxyacantha* and *Cornus sanguinea* are represented. To the most frequent species in the luxuriant herb layer (95%) belong: *Galium odoratum*, *Fragaria moschata*, *Convallaria majalis*, *Lathyrus niger*, *Melica nutans*, *Pulmonaria officinalis* subsp. *officinalis*, *Stellaria holostea*, *Poa nemoralis*, *Festuca heterophylla*, *Carex montana*, *Chrysanthemum corymbosum*, *Anemone nemorosa*, etc.

Soil profile (depth 120 cm): A_{00} (0—1 cm) — litter; A_0 — almost missing; A_1 (1—10 cm) — dark brown, humous, fresh clay, crumbly structure, penetration by roots plentiful, pH 6.4; A_2 (10—20 cm) — brown, humous clay without distinct structure, gradually passing down to next horizon, frequent roots, pH 5.7; B (20—65 cm) — ochre-brown, firm clay, penetrated by roots, pH 6.0; C (65—120 cm) — light grey marl, pH 7.0. Phonolite stones are sporadically distributed in the soil profile. Roots of the trees spread in the whole profile. Soil texture in the profile (according to the classification of Novák 1949 in Klika, Novák, Gregor l.c.) is prevailingly clay.

Physical characteristics of the surface soil layer (0—10 cm) where maximum concentration of plant roots occurs ("rhizosphere") are given in the Table 2.

2. Beech forest. — A stand on the northern slope of the Ostrý Hill; 420 m above sea level, inclination approx. 15° to North. The stand belongs to the alliance *Fagion silvaticae* Tüxen et Diemont 1936, suballiance *Eu-Fagion* Oberdorfer 1957 em.

In the tree layer (90%), *Fagus sylvatica* predominates; *Quercus petraea* and *Tilia cordata* are also represented. The herb layer is very rich (the total number of species is 46). *Galium odoratum* is dominating species. The following species are also plentiful: *Ranunculus lanuginosus*, *Lamium galeobdolon*, *Hepatica nobilis*, *Hordelymus europaeus*, *Aegopodium podagraria*, *Lathyrus vernus*, *Mercurialis perennis*, *Prenanthes purpurea*, *Senecio nemorensis* subsp. *fuchsii*, *Anemone nemorosa*, *Melica nutans*, etc.

Soil profile (depth 110 cm): A_{00} (2 cm) — litter; A_0 (0—0.5 cm) — compact, half-decomposed litter; A_1 (0.5—8 cm) — dark brown, fresh, clayey, humous, crumbly soil, richly penetrated by roots, pH 5.9; A_2 (8—20 cm) — dark brown, fresh, humous, structureless soil, penetrated by roots, gradually passing into lower horizon, frequent small basalt stones, pH 5.8; B (20—60 cm) — light brown, fresh, clayey, firm soil, regularly penetrated by roots, pH 5.7; C (60—110 cm) —

Table 1. — Annual march of temperatures and rainfall at the station Milešovka, 835 m above sea level (according to the data of the Hydrometeorologický ústav in Prague)

Month		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Average temperature	Annual amount of precipitation
Temperature	1965	−2.7	−6.3	−1.7	3.9	7.8	12.7	12.9	13.0	10.5	6.2	−2.4	−1.5	4.4	—
	1900 to 1950	−4.3	−3.5	0.0	4.3	9.8	12.7	14.6	14.0	10.7	5.5	0.0	−3.0	5.1	—
Precipitation	1965	38.0	43.0	58.1	64.9	133.9	68.4	67.9	24.5	89.0	8.5	61.0	67.6	—	724.8
	1900 to 1950	40	34	36	42	58	64	71	60	44	40	38	37	—	564

Table 2. — Physical characteristics of rhizosphere

Site	Pure clay < 0.01	Fine silt $0.01-0.05$	Fine sand $0.05-0.1$	Course sand $0.1-2.0$	pH	Specific wt.	Volume of aerial spaces	Moisture content	Field capacity	Minimum aerial capacity
Oak forest	84.68	6.07	3.61	5.64	6.4	2.48	66.53	47.85	57.45	9.08
Beech forest	78.11	9.58	5.13	7.19	5.9	2.52	68.77	53.12	57.96	10.81
Calciphilous beech forest	85.62	5.20	3.64	5.55	6.9	2.44	68.43	50.88	58.90	9.53

light grey-brown marl, basalt stones occur in the profile from 75 cm, pH 6.3. Roots of the tree species pass through the whole soil profile. Prevailing soil texture is clay, the soil type is eutrophic brown soil (KUBIENA 1953). For physical characteristic of the soil of the rhizosphere see Table 2.

3. Calciphilous beech forest. — The stand is located in the vicinity of the previous site; inclination is 10° to North. The stand is formed by the association *Cephalanthero-Fagetum* OBERDORFER 1957 from the alliance *Fagion silvaticae* TÜXEN et DIEMONT 1936, suballiance *Cephalanthero-Fagion* TÜXEN 1955.

In the tree layer (90%), the dominant *Fagus sylvatica* is accompanied by *Tilia platyphyllos*. Compared with previous communities, the herb layer is poorer in the number of species (35 species); abundant *Mercurialis perennis*, due to its great coverage, restricts the distribution of other species.

Soil profile (depth 120 cm): A_{00} (2 cm) — litter; A_0 — missing; A_1 (0—18 cm) — brown-black, fresh, clayey, humous, crumbly soil, with plentiful roots, pH 7.0; C (18—120 cm) — grey marl, pH 7.2. Roots of the tree species spread in the whole profile. The soil texture is clay, the soil type is marl rendzina (LAATSCH 1957). For physical characteristics of the soil of the rhizosphere see Table 2.

Forms of root systems

There are various criteria according to which the root systems can be classified: morphological, anatomical, physiological, physiognomical, ecological and developmental criteria, or their various combinations (FREIDENFELT 1902, METSÄVAINIO 1931, LINKOLA et TIIRIKKA 1936, KIVENHEIMO 1947, NAUMANN 1932, SEREBRJAKOV 1962).

LUKASIEWICZ (1962) divided the perennial herbs into three basic types according to morphological and developmental qualities of their perennial organs, i.e. their root systems. Each of the three types, i.e. rhizophytes, rhizocaulophytes and caulophytes, is further divided into groups. On the basis of our investigation, we could divide the groups of the caulophytes into smaller subdivisions. The main emphasis, as regards these subdivisions, is laid on the morphology of the rhizome, which, to a certain extent, determines the pattern of the whole root system.

In the following survey, we present only the plant species whose root systems were actually studied in the forests of the České středohoří; a number of other types of root systems which do not appear in the studied area are omitted.

A. Rhizophytes (species with a perennial main root):

Phyteuma spicatum.

B. Rhizocaulophytes (species with a perennial main root and with perennial underground organs of stem origin bearing adventitious roots):

BA. Typical rhizocaulophytes:

Astragalus glycyphyllos, Campanula trachelium, Lathyrus niger.

BB. Rhizome rhizocaulophytes (underground organs of stem origin are similar to rhizomes):

Campanula persicifolia, Campanula rapunculoides, Vicia sylvatica.

C. Caulophytes (species with perennial organs of stem origin and with adventitious roots as perennial organs):

CA. Typical caulophytes:

CAA. Cylindrical, thin, long, horizontal rhizome — *Hepatica nobilis, Viola mirabilis, Viola reichenbachiana, Viola riviniana.*

CAB. Short, almost perpendicular rhizome bearing a bunch of adventitious roots — *Ranunculus auricomus, Ranunculus lanuginosus.*

CAC. Mostly short, horizontal rhizome — *Primula veris, Geum urbanum, Chrysanthemum corymbosum, Mycelis muralis, Lathyrus vernus, Melittis melissophyllum, Serratula tinctoria, Sanicula europaea, Solidago virgaurea, Hieracium sabaudum, Hieracium sylvaticum, Hieracium lachenalii.*

CAD. Short, thick rhizome from which very thick adventitious roots grow up — *Heracleum sphondylium.*

CAE. Mostly very short rhizomes — *Epilobium montanum, Galium silvaticum, Senecio nemorensis* subsp. *fuchsii.*

CAF. Thick, cylindrical, sometimes ramified rhizomes from which thick adventitious roots grow out — *Astrantia major, Betonica officinalis.*

CAG. Multiple-headed sympodial rhizome with thick adventitious roots — *Actaea spicata.*

CAH. Mostly long, sympodial rhizomes — *Bupleurum longifolium, Prenanthes purpurea.*

CAI. Thick rhizome of the sedge — *Carex montana.*

CAJ. Bunchy rhizome — *Carex sylvatica, Agropyron caninum, Brachypodium sylvaticum, Dactylis glomerata, Deschampsia cespitosa, Hordelymus europaeus, Festuca heterophylla, Hierochloë australis, Calamagrostis arundinacea, Poa nemoralis.*

CAK. Short rhizome of grasses — *Bromus ramosus* subsp. *benekenii.*

CB. Tuberous caulophytes:

Platanthera bifolia, Scrophularia nodosa.

CC. Rhizome caulophytes:

CCA. Cylindrical, relatively short horizontal rhizomes — *Asarum europaeum, Pulmonaria officinalis* subsp. *officinalis.*

CCB. Vertical rhizome with thick unramifed roots — *Epipactis helleborine.*

CCC. Thick, fleshy rhizomes with apparent annual additions — *Anemone nemorosa, Anemone ranunculoides, Polygonatum multiflorum, Polygonatum verticillatum.*

CCD. Ramified rhizomes creeping in the upper layer of the humus horizon — *Calamintha clinopodium, Veronica chamaedrys, Stachys sylvatica.*

CCE. Richly ramified rhizomes creeping most frequently in the depth of 2–6 cm — *Aegopodium podagraria, Convallaria majalis, Maianthemum bifolium, Mercurialis perennis.*

CCF. Richly ramified rhizomes creeping mostly in the soil surface — *Galium odoratum, Stellaria holostea.*

CCG. Long, ramified rhizomes with rare adventitious roots — *Vicia sepium.*

CCH. Rhizome of grasses, sedge and wood-rush — *Luzula albida, Melica nutans, Milium effusum, Carex digitata.*

CD. Stoloniferous caulophytes:

CDA. With runners — *Fragaria moschata, Fragaria vesca, Ajuga reptans.*

CDB. With creeping stems — *Lamium galeobdolon, Lysimachia nummularia.*

CE. Bulbous caulophytes:

Lilium martagon.

The quantitative distribution of main root forms follows from Fig. 1. Caulophytes are the leading type in the studied forests. Among them the typical caulophytes and rhizome caulophytes are most numerous. Rhizophytes and rhizocaulophytes represent only an insignificant portion (altogether about 10%), whereas in the case of steppe vegetation

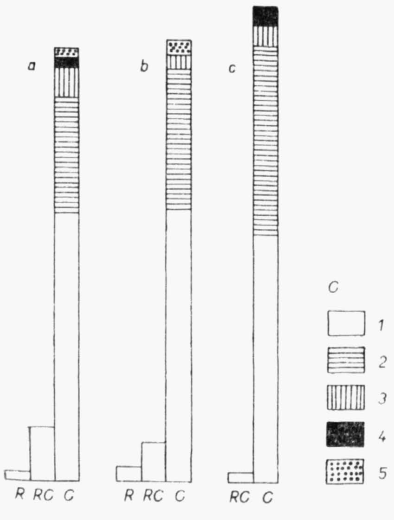

Fig. 1. — Distribution of various types of root systems of herbs in studied forest communities: *R* — rhizophytes, *RC* — rhizocaulophytes, *C* — caulophytes, 1 — typical caulophytes, 2 — rhizome caulophytes, 3 — stoloniferous caulophytes, 4 — tuberous caulophytes, 5 — bulbous caulophytes, *a* — hornbeam-oak forest, *b* — beech forest, *c* — calciphilous beech forest.

in the same area (alliance *Festucion valesiaceae* Braun-Blanquet 1936), rhizophytes and rhizocaulophytes, i.e. the types with the perennial main root, form a substantial part (47.4%). This is in connection with the general fact that rhizophytes are numerous in desert and steppe environments, and that rhizocaulophytes develop strong main roots in dry soils (Lukasiewicz 1962).

We can conclude that in the undergrowth of fresh soils with shallow humous layer in the central European deciduous forests, caulophytes are the best adjusted life-form.

Phenology of root systems

During the growing season, plants undergo successive changes in phenological phases which are well marked on the aboveground organs. The seasonal development of root systems of forest herbs is not yet known. Šalyt (1960) deals at length with the methods of phenological observations of root systems; due to their complexity, however, the given methods are suitable only for autoecological studies. Šulc (1966) emphasizes the necessity for the investigation od seasonal development of underground organs of geophytes. As the present work has been directed above all to cover the entire synusia of perennial herbs in forests, the method described in the introduction was used.

Observation of seasonal rhythm of root systems with regard to the seasonal rhythm of aboveground organs was carried out at two sites: in hornbeam-oak forest and in beech forest. Yet, individual phenological phases of the species found on both sites were identical. Though the year 1965, in which phenological observations were carried out, possessed abnormal precipitation (cf. Tab. 1), similar relations between the seasonal development of aboveground organs and root systems was found in 1967.

The illustration of phenological phases of the aboveground organs was prepared according to the diagrams of Ellenberg (1939). For illustration of the phenological phases of root systems, these diagrams were completed with arrows that are attached to the bottom of the graphs. The succession of phenological phases for 15 species in hornbeam-oak forest is presented in Fig. 2. The main result seems to be that in most species the formation of new adventitious roots and the regrowth of rhizome take place simultaneously with the flower period and, chiefly, after this period of flowering.

The fact of intensive growth of the root systems in the period following the flowering, was first shown by Lukasiewicz (1962). Also, Smelov (1966) finds an intensive growth of roots of meadow grasses in the period after the flowering phase, i.e. in the period of fruit ripening and the gradual dying off in aboveground parts. Smelov (l.c.) also claims that the period of intensive growth of root systems is connected with the storage of reserves in roots, as the amount of reserves increases when flowering is finished.

In the case of typical caulophytes, the formation of adventitious roots takes place in the youngest part of the rhizome (*Bupleurum longifolium, Chrysanthemum corymbosum, Serratula tinctoria, Sanicula europaea, Fragaria moschata, Viola riviniana, Ranunculus auricomus, Primula veris* and others).

In most cases, the rhizome caulophytes form first a new annual increase of the rhizome which is followed by the growth of roots (*Convallaria majalis, Maianthemum bifolium, Galium odoratum, Stellaria holostea, Veronica chamaedrys, Stachys sylvatica* and others). On the contrary, in *Mercurialis perennis*, new adventitious roots are formed first, arising on the nodes of the

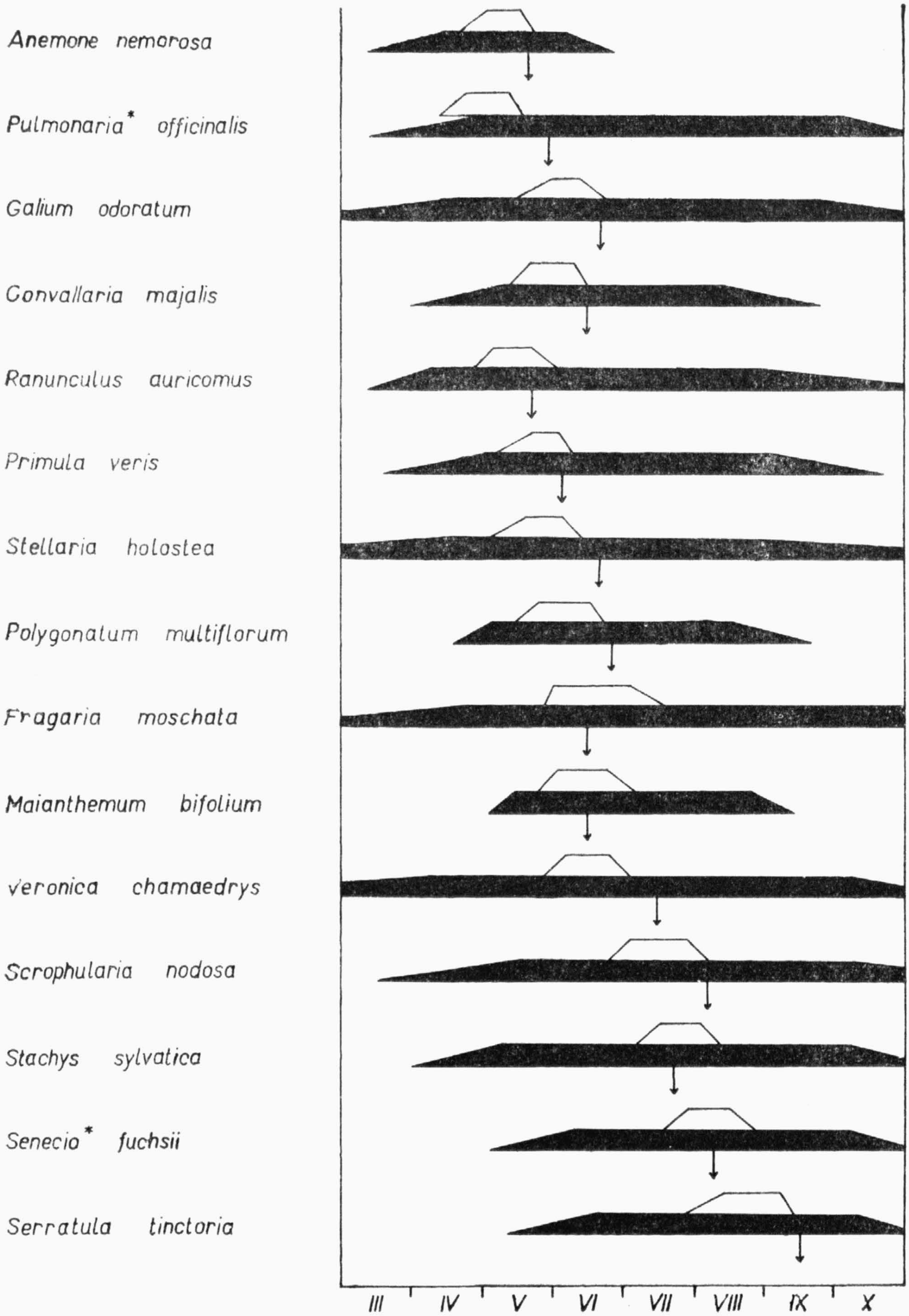

Fig. 2. — The seasonal succession of phenological phases of herbs in oak forest. Black — assimilating phase with leaves; white — flowering phase; ↓ — period of the growth of new parts of rhizomes and new adventitious roots, or only period of the appearance of the underground shoots (*Senecio nemorensis subsp. fuchsii*).

youngest part of the rhizome, in the second half of May; only later, in the middle of July, the plagiotropous underground shoots grow off from the youngest part of the rhizome.

Attempts to estimate the period of intensive longitudinal growth and ramification of roots has further been made. For this purpose, however, only estimates of the rate of longitudinal growth of roots could be used. In some species the newly created roots do not grow in length in the same growing season: *Serratula tinctoria*, *Chrysanthemum corymbosum*, *Bupleurum longifolium* and others. In most of the species, however, intensive growth in length of adventitious roots takes place in the same growing season after which they cease extending for good (*Stachys sylvatica*, *Maianthemum bifolium*, *Ranunculus auricomus*, *Ranunculus lanuginosus* and others).

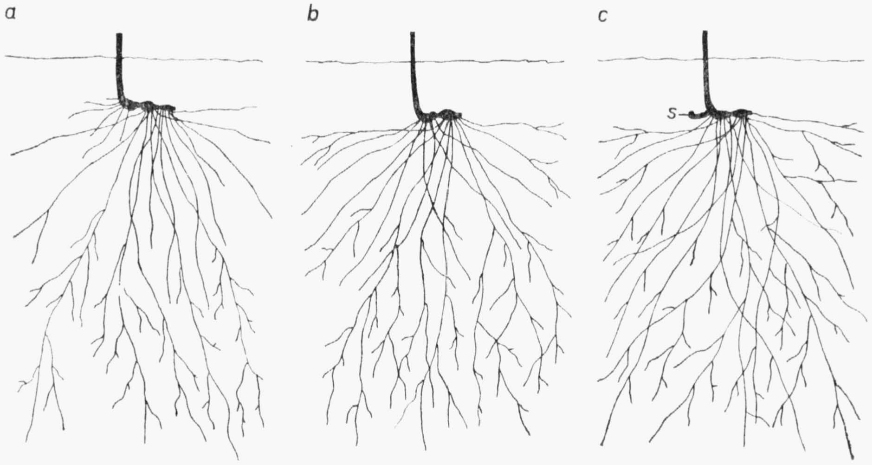

Fig. 3. — Seasonal changes of the root systems of the species *Senecio nemorensis* subsp. *fuchsii*: *a* — first half of March, plant approx. 20 cm height, white adventitious roots began to grow from the youngest part of the rhizome, the oldest part of rhizome is completely decayed, but still connected with the other part of the rhizome; *b* — beginning of July, the plant is in advanced stage of vegetative development, height 40 to 60 cm, adventitious roots reach about 3/4 of the usual length, not yet ramified; *c* — the second half of August, the plant shortly after the end of flowering stage, height 70 to 90 cm, adventitious roots reach the usual length, they start ramifying, and from the youngest part of the rhizome the underground shoots (s) start growing.

The creation of lateral branches in these species takes place mainly in the following spring. As regards the first named group of species, their adventitious roots elongate always in the following spring, while the creation of new laterals also occurs.

Senecio nemorensis subsp. *fuchsii* has an interesting underground phenology. Only white and slightly violet underground shoots were observed during the flowering phase in August. Creation of new adventitious roots of this species does not occur in the same year, but it takes place in spring of the following year, at the end of April; these roots reach their final length by the middle of August. This fact is probably connected with the relatively late flowering. For changes of phenological phases of the root system of *Senecio nemorensis* subsp. *fuchsii* see also Fig. 3.

As it is evident from Fig. 2, the formation of new adventitious roots of different species of herbs within the same plant community takes place in different periods of the growing season. In the species found in hornbeam-oak forests, the period of formation of new adventitious roots, and the period of new annual increases of the rhizomes extends from the beginning of May till the middle of September. Therefore, we cannot distinguish a defined period of the year as a season of general active root growth, comparable with the flushing of leaves in aboveground parts. SEREBRJAKOV (1952) points out that the different period of growth of roots contributed to better utilization of the limited space occupied by the phytocoenosis. Examples of the period of the initial growth of adventitious roots of some species is given also by SEREBRJAKOV (1952) and LUKASIEWICZ (l.c.).

Distribution of root systems in soil

An important characteristic of root systems is their spatial distribution in soil, both in vertical and horizontal direction. The character of a root system is dependent on the genotype as well as on the environmental factors of the site. As the sites studied in the present paper were very similar in soil properties, no substantial differences in root systems within the same species have been distinguished.

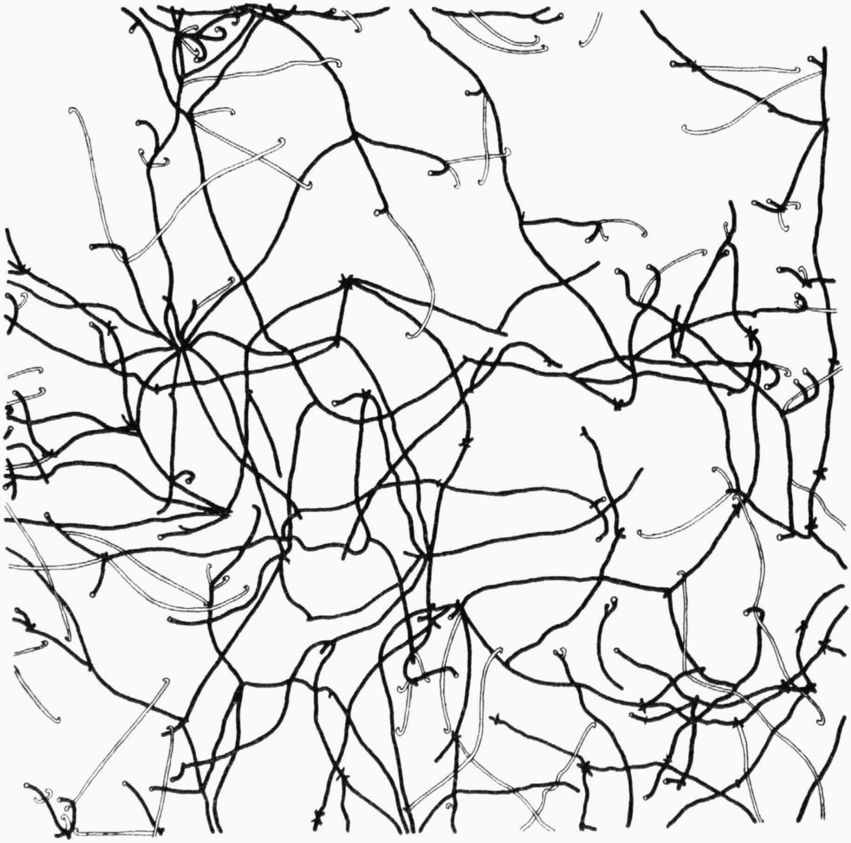

Fig. 4. — The rhizome system of *Mercurialis perennis* on a sample plot 75 by 75 cm. Black — rhizomes; white — underground shoots. Blank disk — the place of outgrowing aboveground shoots.

In most of the studied species, the horizontal spread of the root system exceeds the vertical one.

The rhizophytes and, partly, the rhizocaulophytes show a very small horizontal spread of the root system: *Astragalus glycyphyllos, Campanula trachelium, Phyteuma spicatum* and *Lathyrus niger*. In the last named species, the horizontal spread only exceptionally exceeded 15 cm.

In most of the forest herbs, the horizontal spread of the root system exceeds 20 cm. Among the species whose horizontal spread is approx. 20 to 60 cm belong: *Hepatica nobilis, Sanicula europaea, Bromus ramosus* subsp. *benekenii, Mycelis muralis, Galium silvaticum, Fragaria moschata, Festuca heterophylla, Viola mirabilis, Viola reichenbachiana, Viola riviniana, Primula veris, Bupleurum longifolium, Geum urbanum, Hordelymus europaeus, Ranunculus auricomus, Poa nemoralis, Pulmonaria officinalis* subsp. *officinalis*.

Fig. 5. — Detail of the horizontal excavation of the root system of *Mercurialis perennis*. Black disk marks the place of outgrowing aboveground shoot. Underground shoots — marked as *s*.

Another group is formed by species the horizontal spread of whose root system is greater than 60 cm: *Ranunculus lanuginosus, Betonica officinalis, Scrophularia nodosa, Dactylis glomerata*.

Horizontal spread of the root system of the species *Actaea spicata, Astrantia major, Chrysanthemum corymbosum* and *Lathyrus vernus* often exceeds 100 cm.

The study of the horizontal spread of root systems is very important in species that form polycormons, i.e. in species growing in vegetatively reproduced clumps (PENZÉS 1960). Root studies enable us to get a more detailed picture about the structure and size of large polycormons which cannot be identified according to aboveground shoots which generally intermingle. Horizontal spread of these species (*Aegopodium podagraria, Galium odoratum, Convallaria majalis, Maianthemum bifolium, Stellaria holostea* and others) very often exceeds 100 cm. Considerable, though smaller horizontal spread is also reached by the species with richly ramified rhizome: *Asarum europaeum, Lamium galeobdolon, Melica nutans, Polygonatum multiflorum, Polygonatum verticillatum, Stachys sylvatica*.

The actual horizontal spread of species forming large polycormons is very interesting. As an example a study of the horizontal spread of the root system of *Mercurialis perennis* has been made. This species was particularly excavated both in the beech forest and in the calciphilous beech forest.

In the beech forest where *Mercurialis perennis* occurs in small polycormons, one polycormon covering an area of irregular shape and about 1 sq. m size was chosen for a complete horizontal excavation down to 10 cm depth. Over this area there were 77 aboveground shoots of the predominating *Mercurialis perennis*. Other species present: *Galium odoratum* (39 shoots), *Lamium galeobdolon* (30) and *Hepatica nobilis* (2). Several rhizomes of *Anemone nemorosa* were also found in the soil. The rhizome system of *Mercurialis perennis* forms a kind of irregular grid (Fig. 4). The majority of roots of this species grows in the depth of about 5 cm and forms there a very dense network (see Fig. 5). In the layer above the 5 cm depth, the root systems of *Galium odoratum* and *Lamium galeobdolon* predominate.

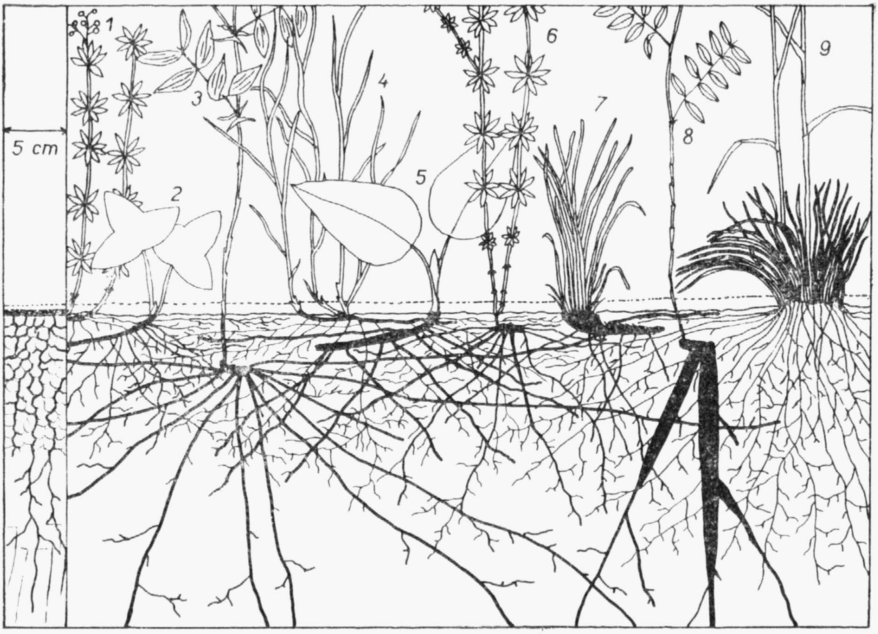

Fig. 6. — Bisect showing the root systems of herbs in the undergrowth of the oak forest: 1 — *Galium odoratum*, 2 — *Hepatica nobilis*, 3 — *Lathyrus vernus*, 4 — *Melica nutans*, 5 — *Pulmonaria officinalis* subsp. *officinalis*, 6 — *Galium silvaticum*, 7 — *Carex montana*, 8 — *Lathyrus niger*, 9 — *Festuca heterophylla*.

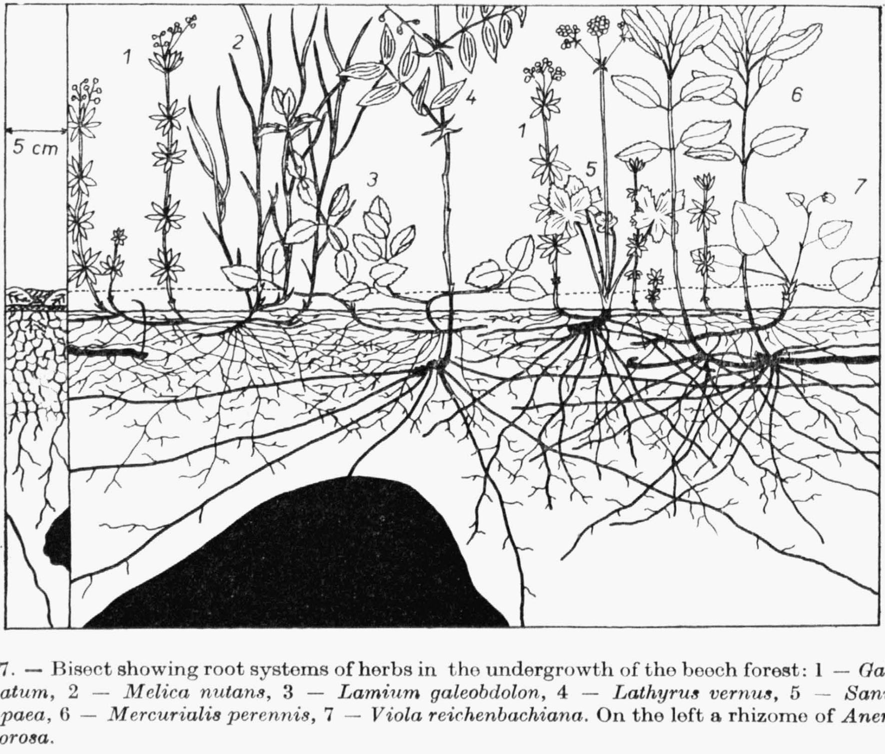

Fig. 7. — Bisect showing root systems of herbs in the undergrowth of the beech forest: 1 — *Galium odoratum*, 2 — *Melica nutans*, 3 — *Lamium galeobdolon*, 4 — *Lathyrus vernus*, 5 — *Sanicula europaea*, 6 — *Mercurialis perennis*, 7 — *Viola reichenbachiana*. On the left a rhizome of *Anemone nemorosa*.

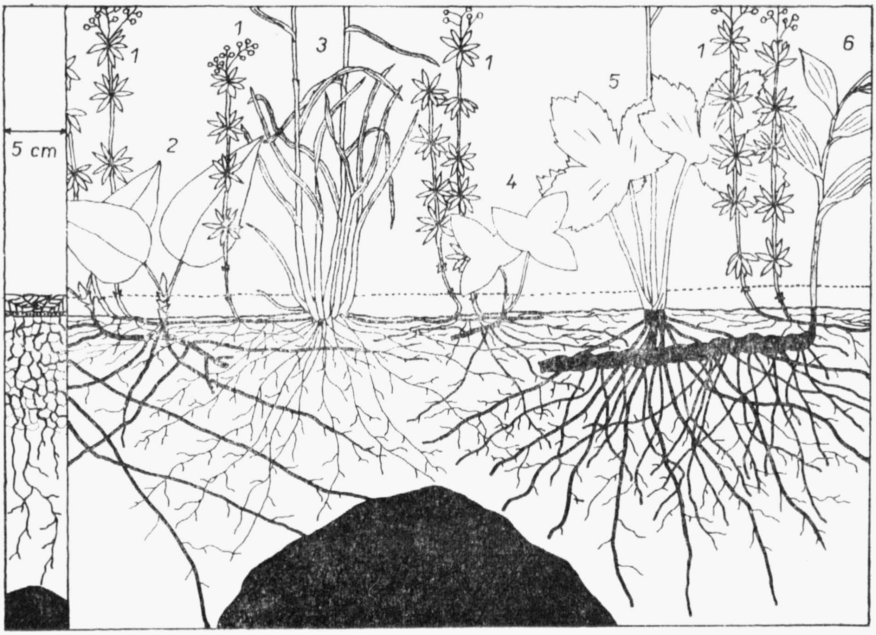

Fig. 8. — Bisect showing root systems of herbs in the undergrowth of the beech-forest: 1 — *Galium odoratum*, 2 — *Pulmonaria officinalis* subsp. *officinalis*, 3 — *Hordelymus europaeus*, 4 — *Hepatica nobilis*, 5 — *Ranunculus lanuginosus*, 6 — *Polygonatum multiflorum*.

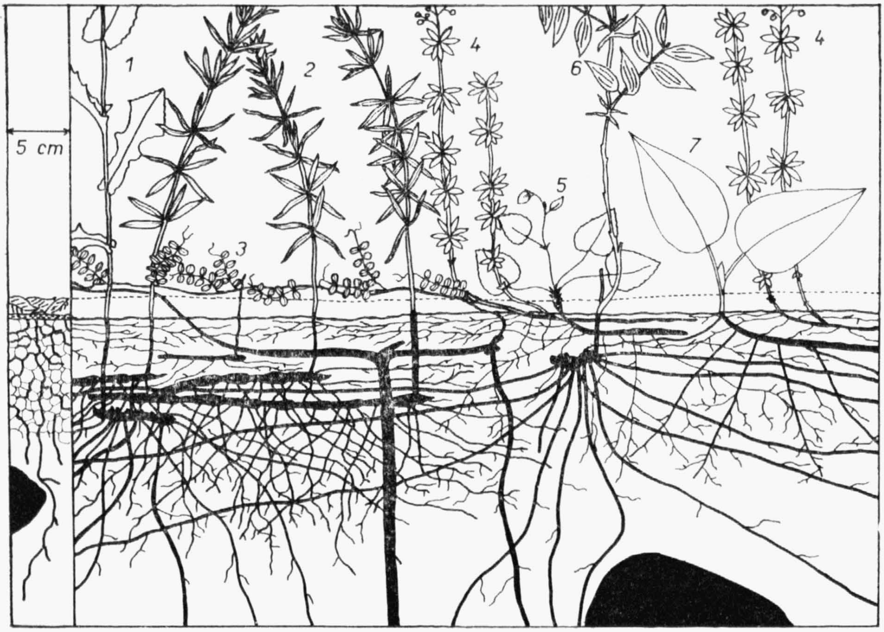

Fig. 9. — Bisect showing root systems of herbs in the undergrowth in the beech forest: 1 — *Prenanthes purpurea*, 2 — *Polygonatum verticillatum*, 3 — *Vicia sylvatica*, 4 — *Galium odoratum*, 5 — *Viola reichenbachiana*, 6 — *Lathyrus vernus*, 7 — *Pulmonaria officinalis* subsp. *officinalis*. On the left — rhizome of *Anemone nemorosa*.

In the calciphilous beech-forest, *Mercurialis perennis* absolutely predominates (134 shoots); only four shoots of other species were present. In the rhizosphere, besides the roots of tree species, there is an almost exclusive ocurrence of the roots and rhizomes of *Mercurialis perennis* (see Fig. 11).

Various criteria are employed for the evaluation of the vertical distribution of the root system. Maximum depth reached by the roots of individual species does not provide the best information. In most of the forest herbs this feature is very difficult to assess. More significant is the average depth which is generally reached by the vertical roots; this depth, however, is not identical with lower reaches of the maximum concentration of roots in the humous horizon. It is on this average depth that Linkola et Tiirikka (1936) divides the root systems of plants. On a similar basis, Ellenberg (1939) divided the root systems into three groups which I use — to some extent — in the following division of herbs in the deciduous forests of České středohoří.

1. Shallow rooted species, i.e. those with the majority of roots in the layer down to 5 cm. Within this group, many small herbaceous species with shallow situated or superficious rhizome can be classed, e.g. *Anemone nemorosa, Galium odoratum, Stellaria holostea, Maianthemum bifolium, Veronica chamaedrys* etc.

2. Middle-deep rooted species, i.e. plants with most of their roots down to 15 cm depth. The majority of the species examined in our work appears in this group: *Melica nutans, Poa nemoralis, Sanicula europaea, Ranunculus auricomus, Galium silvaticum, Pulmonaria officinalis* subsp. *officinalis, Hordelymus europaeus, Geum urbanum, Mycelis muralis, Bupleurum longifolium, Primula veris, Aegopodium podagraria, Campanula rapunculoides, Stachys sylvatica, Polygonatum multiflorum, Polygonatum verticillatum, Viola riviniana, Viola reichenbachiana, Carex montana, Carex sylvatica, Mercurialis perennis, Fragaria moschata, Hepatica nobilis, Lamium galeobdolon, Convallaria majalis.*

Table 3. — Representation of the groups of the root systems classed according their vertical distribution in soil

Groups	Oak forest	Beech forest
Shallow rooted species	**14.6**	**13.5**
Middle-deep rooted species	**52.1**	**48.7**
Deep rooted species	**33.3**	**37.8**

3. Deep rooted species, i.e. herbs with many vertical roots exceeding the depth of 15 cm. Above all tall herbs belong into this group: *Senecio nemorensis* subsp. *fuchsii, Dactylis glomerata, Bromus ramosus* subsp. *benekenii, Chrysanthemum corymbosum, Ranunculus lanuginosus, Lathyrus niger, Lathyrus vernus, Lilium martagon, Phyteuma spicatum, Prenanthes purpurea, Serratula tinctoria, Actaea spicata, Astrantia major, Epipactis helleborine, Vicia sylvatica, Campanula trachelium, Heracleum sphondylium, Festuca heterophylla, Hierochloë australis, Agropyron caninum.*

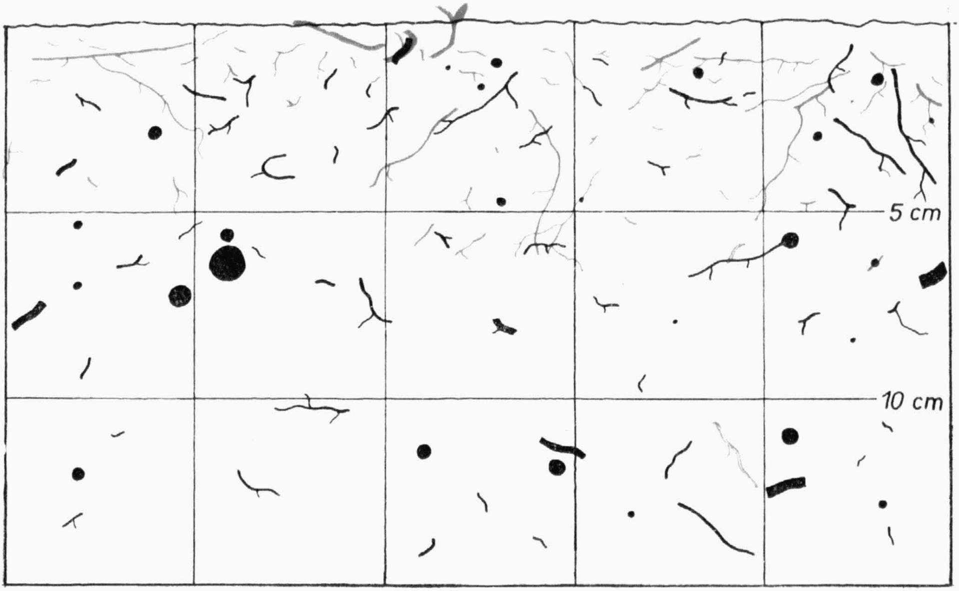

Fig. 10. — Vertical section of the rhizosphere in the beech forest: roots and rhizomes of herbs in red, roots of trees in black.

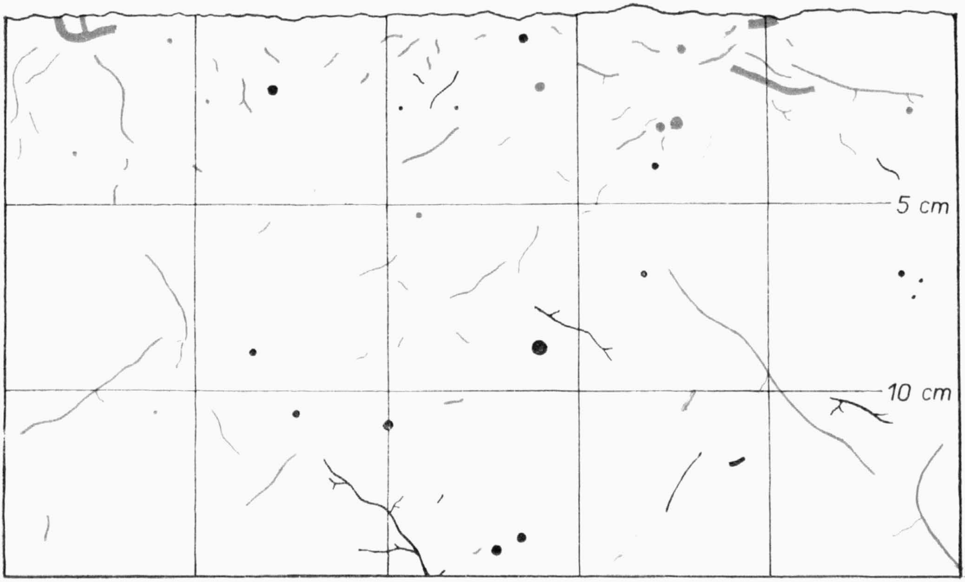

Fig. 11. — Vertical section of the rhizosphere in the calciphilous beech forest: roots and rhizomes of *Mercurialis perennis* in red, roots of tree species in black.

Altogether species of group 2 and 3 greatly predominate in the forest communities studied (cf. Tab. 3).

The deepest penetrating root systems are those of the rhizophytes and rhizocaulophytes (*Phyteuma spicatum, Lathyrus niger, Astragalus glycyphyllos*) and those of the caulophytes with mighty vertical roots, e.g. *Lathyrus vernus, Chrysanthemum corymbosum*, etc. As has been found in the oak forest, many roots of *Lathyrus niger* reach a depth of about 50 cm. As regards *Astragalus glycyphyllos*, ZIMNY (1964) states that specimens of this species develop main roots reaching a depth of 80 to 120 cm.

Both the vertical and the horizontal distribution of root systems examined is apparent from the diagrammatic bisects (Fig. 6—9) which were compiled on the basis of numerous drafts sketched during the field studies in the České středohoří.

The vertical distribution of the rhizomes deserves some comments. Rhizomes of a number of species creep on the soil surface or in the upper layer of the humous horizon down to the 5 cm depth, e.g. *Galium odoratum, Stellaria holostea, Maianthemum bifolium*. Only a few species develop their rhizomes deeper: *Prenanthes purpurea, Epipactis helleborine*.

A very important structural feature of plant communities is the stratification into more or less expressive layers (strata). In the underground space these strata arise as a result of accumulation of roots in a particular soil horizon (JENÍK 1964).

Whereas the stratification in semideserts and steppes is well known (MARKLE 1917; WEAWER 1919, 1920; ŠALYT 1950, 1952), there is lack of information as regards the forest communities.

The above mentioned groups according to the vertical distribution of root systems could awake a misleading opinion that even in the whole plant community well differentiated strata could be distinguished. This is, however, not the case as most of the deep rooted species develop a considerable portion of their roots in the upper soil layers. Thus, the stratification of the roots of the herbaceous synusia cannot be defined.

Moreover, roots of the tree species must be taken into consideration. The majority of the little end-roots is also distributed in the upper soil layer. However, the proportion of the herbaceous roots and rhizomes, under the conditions studied in the České středohoří, was most prominent.

On the grounds of this fact, we can distinguish in the studied stands two underground layers: the herbaceous underground layer and tree underground layer (see Fig. 10, 11). In the absence of any quantitative assessments in soil monoliths, we can characterize these two strata as follows:

The herbaceous underground layer contains almost all roots of herbs and the majority of thin end-roots of trees together with bigger horizontal skeleton roots bearing the end-roots. This root layer coincides well with the dark humus horizon of the soil.

The tree underground layer contains few of the vertical roots of herbs (together with their laterals) and is dominated by bigger tap-roots and sinkers of the trees bearing less numerous end-roots.

The above conclusion is in good accord with the results published by ELLENBERG (1939), KIVENHEIMO (1947), and LISIEWSKA (1960).

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Souhrn

V podrostu listnatých lesů v Českém středohoří (SZ Čechy) byla sledována morfologie, sezónní vývoj a vzájemné vztahy kořenových systémů vytrvalých bylin. Z hlediska typů kořenových systémů představují kaulofyty asi 90 procent bylinných druhů. Další typy (rhizofyty a rhizokaulofyty) jsou zastoupeny v nepatrné míře. Období intensivního růstu kořenů a oddenků u většiny druhů následuje po květní fázi. Nebylo zjištěno vyhraněné období simultánního plného růstu kořenových systémů všech bylin. Kořeny, oddenky, hlízy a cibule většiny druhů prorůstají povrchovou vrstvu do hloubky 15 cm, maximální koncentrace jejich výskytu je ve vrstvě 0—5 cm. Horizontální rozměr kořenového systému převažuje nad vertikálním. Časté horizontální rozložení kořenového systému zabírá 20 až 60 cm šířky. O vyhraněné patrovitosti kořenů bylinné synusie nelze hovořit, avšak podle koncentrace a vzájemného poměru kořenů bylin a kořenů stromů lze vylišit podzemní patro bylinné a podzemní patro dřevinné.

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Recensent: J. Slavíková

B. Boulard:

Les Mycorrhizes

Masson et Cie, Paris 1968, 135 str., 34 obr., cena 40 Fr. (Kniha je v knihovně ČSBS.)

Tato útlá, bezvadně technicky vypravená knížka vychází jako 2. svazek řady botanických monografií vydávaných prof. P. Champagnatem. Uvedená řada je míněna jako zdroj zasvěcených informací o současném stavu bádání v určitých úzkých oborech a je určena mladým vědeckým pracovníkům, studentům a učitelům biologie na středních školách. Recenzovaná knížka tento záměr velmi dobře splňuje. Autor, který sám publikoval řadu originálních prací o mykorhizách, velmi fundovaně vybral z obsáhlé literatury podstatné práce, na jejichž základě podává přehled o současných znalostech a směrech výzkumu v problematice mykorhiz.

Studie je logicky členěna na kapitoly o historii výzkumu, morfologii a anatomii mykorhiz, rozšíření mykorhiz v rostlinné říši, o technice studia mykorhiz, o fyziologii, ekologii a významu mykorhiz pro vyšší rostliny. Nejcennější a nejpodrobnější kapitoly se týkají morfologie a anatomie a techniky studia mykorhiz. Prozrazují velké osobní zkušenosti autora. Kapitola o rozšíření a výskytu mykorhiz u jednotlivých taxonů vyšších rostlin je velmi stručná a postrádám zde seznamy rostlin s jedním nebo druhým typem mykorhiz. Další kapitola, fyziologická, představuje výběr poznatků z literatury, hlavně prací Melinovy a Harleyovy školy. Zajímavá je poslední kapitola, která se zabývá praktickým uplatněním znalostí o mykorhizách v zemědělství, lesnictví a zahradnictví.

Kniha je doplněna francouzsko-německo-anglickým slovníčkem termínů užívaných při popisu mykorhiz. Ke každé kapitole je uveden výběr hlavní literatury. Tato úprava literárních pramenů se mi nezdá být výhodná, některé citace se zbytečně opakují, byl by přehlednější jeden celkový soupis literatury. Pro přehled je připojen rejstřík. Z této práce B. Boullarda plyne též zajímavé poučení, kteří autoři — z velmi mnoha — přinesli nové podstatné poznatky ve výzkumu mykorhiz. Jako klasiky tohoto oboru je možno jmenovat Melina, Harleye, Burgeffa, Bernarda, Dominika, Hatche, Stahla a Mosseovou.

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