

Chapter 1

Higher Plants: Structural Diversity of Roots

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Abstract At the present time, the necessity of accumulating information about structure diversity of roots and root systems of the species existing on Earth has occurred, due to development both of theoretical basis and methods of preservation of plant biodiversity. There are few publications on structural features of plant roots in botanical literature. Moreover, comparative anatomical studies of roots of higher plants are far behind the researches on structure of shoots. Due to this fact, so far there is an opinion among botanists about the structure uniformity of roots of higher plants, and root systems. We are not going to consider all the causes for lag of comparative anatomical studies on higher plant roots in botany. This was done as long ago as in 1960s by (Comparative plant anatomy, Chapter 7. Root. Holt, Rinehart and Winston, NY. pp 94–101), American anatomist. Let us remind just of the main causes:

- Weak knowledge about intraspecific variation of root structure
- Technical difficulties in collecting root samples, the same as shoot samples, etc.
- Deficiency of monographs on rhizology, with comparative anatomical studies of roots, similar to those of other plant organs

We had taken into account these causes in our long-standing rhizological researches from 1974 to 2010.

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1.1 Rhizological Research: Material, Methods, and General Principles

Base material for the analysis of structure diversity of roots of rhizophytes was collected in natural populations of species during our expeditions to the Baltics, Ukraine, Russia (Ural, Siberia, Altai, and Far East). Along with wild-growing plants, we examined root structural features of introducents, which grow in the Russian botanic gardens. We have analyzed a total of 1,200 species of higher plants, which belong to various taxa and biomorphs.

We extracted root systems from substrate using the method of dry excavation along the trench walls. Trench depth varied from 15 cm to 3 m, depending on the mechanical soil characteristics. We excavated roots of ten mature blossoming or sporificating plants of each species. The samples were described according to the biomorphological characteristics by Serebryakov's (1962). We washed the roots, sketched them or photographed them. After that we fixed them in 73% *ethanol* for further anatomical examination. Every new root sample was included into the collection of rhizomes.

In laboratory by microtome, or manually by razor, we made cross-sections of ten roots of each species through the basal zone, middle zone, and apical zone. We examined and prepared microslides under the optical microscope according to anatomy standards (Kivenheimo 1947; Voronin et al. 1972). We used the ocular micrometer to measure root microstructures. To evaluate microstructure variation we applied the variation coefficient CV%. This value helped to compare features with different characteristics. Along with that, we developed structure models of roots in a form of graphical schemes. We used map symbols to mark topographic zones, systems of tissues, and some specific root structures, which had been found during microscope examination of the cross-sections. To create schemes we used computational microscope and the "Paint" program. A brief description of anatomic features was provided for each scheme.

1.2 Root System of a Plant: Specifics of Root Variability Manifestation

All higher plants, rhizophytes, are characterized by structure variability of roots, though to a different degree. To a less degree structure variability manifests itself among primary homorhizic plants, which belong to the following divisions: Lycopodiophyta, Equisetophyta, and Pteridophyta. Conventionally, we named this form of intraspecific variability of root structures as endogenous variability. It means variation of structure features among the cognate roots of a specimen.

Among present-day spore-bearing plants the endogenous variability is most pronounced in the representatives of the division Equisetophyta. We have studied five species of horsetails from natural populations of various geographical areas of

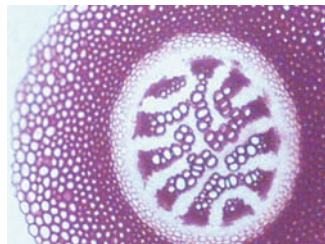
Russia (*Equisetum arvense* L., *E. pratense* L., *E. sylvaticum* L., *E. hyemale* L., *E. fluviatile* L.), and have found a distinct dimorphism of adventitious roots. In all these species, the so-called extension roots and sucking roots can be distinguished in root systems of each specimen. These roots are conspicuous. Extension roots are thick, look longer, and have positive geotropism. They are few in number and vegetate one by one from plagiotropic rhizomes. *Sucking* roots are very thin and short; they vegetate in groups from rhizome nodes, and form small fibrils. Comparative anatomical analysis allowed to reveal at them characteristic structural features similar structure features, typical for these types of roots in all examined horsetails. Comparison of cross-sections of the extension roots showed that they are 3.5–3.7 times thicker than the sucking roots. This occurs due to the growth of wider multilayered primary cortex. It has external and internal zones with large aerenchyma cavities. For example, primary cortex in extension roots of *E. arvense* is 4.3–4.6 times wider than the sucking roots cortex (Fig. 1.1). The stele size is only 1.8–2 times bigger in the extension roots. That is why the number of xylem and phloem strands is 5–6 in steles of the extension roots, while it is not exceeding 4 in sucking roots. General amount of the tracheary elements reaches 12–14 in extension roots, and it is only 4–5 in sucking roots. Together with the distinctions between roots of two morphotypes, there are a number of similar identities among different species of horsetails. For example, all these roots develop the single-layered rhizodermis, whose cells have reddish membranes, and are divided into trichoblasts and atrichoblasts. All the horsetails roots have sparse, though long, root hairs. Their paucity seems to compensate by means of absorbing hairs, which appear on the epidermis cells of rhizomes. For example, in *E. arvense* a number of such tubular hairs varies from 15 to 22 (CV% = 11.7) along the perimeter of cross-section of the plagiotropic rhizome.

The representatives of Lycopodiophyta demonstrate root dimorphism less distinctly than horsetails. Root differentiation in a specimen root system has been found among species of the following genera: *Lycopodium* L. and *Diphasiastrum* Holub. (Tarshis 2007). The most specific anatomical features of roots of club moss are presented in the basal zone, where plagiotropic shoot produces the root. Here a root has a wide, multilayered cortex, differentiated into three zones, and



Fig. 1.1 Dimorphism roots in primarily homorhizophytic root system of a *Equisetum fluviatile* L.

Fig. 1.2 A cross-section cut of an adventitious root of *Lycopodium clavatum* L



relatively small plectostele, which is similar in its structure to stele of shoot (Fig. 1.2).

We have registered two types of different by origin adventitious roots, in a root system of specimens, growing in the introduction conditions, which belong to the genus *Selaginella* Beauv.: *S. apoda* (L.) Fern., *S. emmeliniana* Van Geert., *S. kraussiana* (G.Kunze) A.Br., *S. vogelii* Spring. These two types are shoot-borne roots, which occur on the lower side of plagiotropic shoots, and rhizophore-borne roots, which occur on the apical tips of the orthotropous rhizophores. It must be emphasized that, notwithstanding the different origin, rhizophore- and shoot-borne roots are anatomically identical and have specific structures: protostele, tertiary structure of endodermis cells with wide Casparian strips, and long root hairs on the thin-walled cells of rhizodermis.

Among the representatives of the division Pteridophyta, in general, endogenous variability of roots manifests itself only in small variations of organs' thickness and length, and in dimensions of certain microstructures. Hardly ever can we find more significant differences in specimens of some species, which occur between thick aerial roots and thin roots, which grow in substrate. We can observe this among tropical epiphytic ferns, belonging to the genus *Platyserium* Desv.

The seed plants, allorhizophytes, as W. Troll called them (1949), show endogenous variability in the most distinct way. Representatives of the divisions Pinophyta and Magnoliophyta are known to undergo various underground root metamorphoses extremely frequently. Their roots greatly differ in their exterior and microstructure. As a rule, structure diversity of such roots is coming from their functions. For example, aerial roots of many representatives of the families Orchidaceae and Bromeliaceae are being developed in environment different than soil, and have quite specific structure. Contractile roots, which grow from the perennial bulb stem of *Lilium martagon* L., and draw it into substrate, differ as well. We will not recite various metamorphoses of roots of seed plants, which are resulting from their long adaptation to the certain environment. This problem was fully considered by many morphologists before (Serebryakov 1962; Tarshis 1975). But it must be emphasized that as well as root metamorphoses, seed plants undergo various shoot metamorphoses: rhizomes, stolons, tuber, and bulb. There are also metamorphoses of mixed shoot-root nature in seed plants, e.g., caudices. Many of these organs greatly resemble roots. That is why in the process of study of structure diversity of roots we identified the morphology of underground organs, which comprise the root system of each generative specimen, beforehand. For this purpose, we used method

of anatomical diagnostics. We also took into account that roots may vary themselves within a species' group of plants. Due to such a careful approach, we established the root system structure of two types in species belonging to the division Magnoliophyta: isomorphic and heteromorphic (Tarshis and Tarshis 1998).

For example, species of the subfamily Pyroloideae are found to have isomorphic type of root system structure, while species of the various taxa of the division Magnoliophyta are found to have heteromorphic type of root system structure.

Isomorphic type manifests itself most distinctly in four species: *Pyrola rotundifolia* L., *Orthilia secunda* (L.) House, *Moneses uniflora* (L.) A.Gray, and *Chimaphila umbellata* (L.) W. Barton. Isomorphic type was found in all the specimens from 35 populations under study, located in various regions of Russia. We found that four species, which grow in wide range of environmental conditions, develop the uniform secondary homorhizic root system, which consists of numerous adventitious roots, growing from the plagiotropic stolon-like rhizomes (Fig. 1.3). Structure features of both roots and rhizomes in these Pyroloideae are alike and unique. Anatomical features of the underground organs show great stability and low level of variation. Roots and rhizomes of this taxon species do not change their specific anatomical features, although demonstrate the miniaturization of structures, even in the Far North, on the Yamal Peninsula, in extreme environmental conditions. Due to this characteristic, it is possible to describe features of these roots, using just one single structure model. The uniformity of the inner structure of the stolon-like rhizomes is represented on the second structure model.

Another type of structure of root systems, heteromorphic, was found in natural populations among many Magnoliophyta species. For example, great structural diversity of root systems was registered in generative specimens in the populations of *Lupinaster pentaphyllus* Moench and *Sanguisorba officinalis* L. (Fig. 1.4).

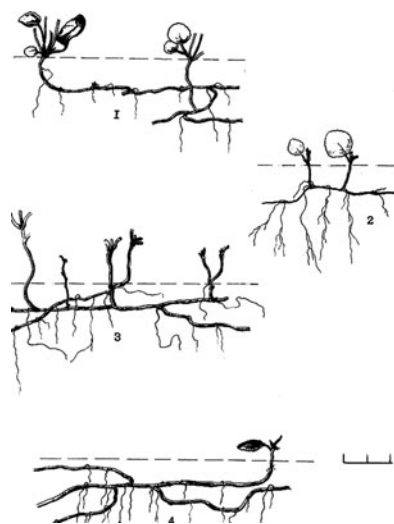


Fig. 1.3 Isomorphic type structural organization root system at species: (1) *Pyrola rotundifolia* L., (2) *Moneses uniflora* (L.) A.Gray, (3) *Orthilia secunda* (L.) House, (4) *Chimaphila umbellata* (L.) W. Barton



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