Structural diversity of roots: The comparative analysis and modelling

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During 1985-2009, we compared morphological and anatomical specific features of underground organs in 900 plant species belonging to 6 divisions: Psilotophyta, Lycopodiophyta, Equisetophyta, Polypodiophyta, Pinophyta and Magnoliophyta. Root structure was compared in plant habitats in Ural mountains, in West, Central and East Siberia, and in Far East. In a number of russian botanical gardens, 767 introduced species were also investigated. To estimate common traits and the range of their variation in roots of these species, on cross sections under microscope we evaluated the variability of root anatomical traits, and then calculated variation coefficient (CV%).In roots with primary structure we measured the ratio of cortex to stele. In the case of secondary structure, we measured the sizes of periderm, phloem, wood and pith, and then calculated their proportions. Basing on root micro photos in computer, we have drawn their structural models. Their analysis permitted us to determine most stable, systematically important structural root features typical of plants belonging to the same taxons (divisions, classes), families and subfamilies. For example, for 4 species of the subfamily of Pyroloideae, a single common anatomical model of root structure was presented, although the plants were collected in 45 biocenoses located in european and asian regions of their areas. Due to quantitative evaluation of the variability of anatomical traits in species belonging to different taxons, we revealed the stability and systematic importance of the traits and constructed 137 structural models basing on microscopic examinations of root cross sections. Such modelling facilitates the insight into root structural commonness and diversity.

Keywords: roots, anatomy, intraspecific variability, structural model.

Research of a structural diversity of the roots of vascular plants is one of fundamental, but insufficiently known problems of botany.

Principal causes of backlog of researches in the given area were specified by a prominent American anatomist Sharles J. Carlquist (Carlquist, 1961, p.94) as early as in 60-es of XX century. These are: a poor knowledge of a variation of root structures within of a species and widespread among the taxonomists and anatomists opinion, that anatomic features of roots of plants are monotonous.

Therefore, the purpose of the given work was studying a structural diversity of roots of vascular plants and revealing on this basis of a complex of the anatomic traits describing specificity of root structure in representatives of taxa of various systematic rank.

Material and methods

The researches of root structure of the vascular plants have been put in a basis of the given work, lead by the author during 1985-2009. Features of the structural organization of root systems in 133 wild-growing species were studied in their natural coenopopulations, in the Ural Mountains, Altai, Western and Central Siberia, Transbaikalia and Far East. In each of characteristic habitats of a species the root systems of 10 single-aged individuals were extracted from the ground by dry digging method. Besides, the structural features of roots were studied in 767 introduced species grown in open air and green-house conditions in the Botanical gardens of

Russia. In total, morphological and anatomic traits of underground organs of 900 species of vascular plants from 6 divisions: Psilotophyta, Lycopodiophyta, Equisetophyta, Polypodiophyta, Pinophyta, Magnoliophyta, are investigated by the same method.

In comparative anatomic researches the traditional methods of light microscopy were used. Studying of structural features of roots was carried out on the cross-sections prepared for 10 individuals of each species in basal part of root of the one order of branching. By means of ocular micrometer one measured the sizes of anatomic-topographical zones and ones of separate anatomic structures. A level of intraspecific variability of anatomic traits was estimated by means of a coefficient of variation (CV%) and a scale of the levels of variability of traits of the plants developed by S. A. Mamayev (1973). All the results of microscopic analysis were subjected to statistical processing. The original technique of development of structural models of roots of plants (Tarshis, 2007) has been used. In graphical structural models there were presented the complexes of anatomic traits and topography of systems of tissues (integumentary, conducting, generating, etc.).

Results and discussion

As is known, all the modern vascular cryptogamic plants belonging to 3 divisions of the subkingdom of Higher Plants: Lycopodiophyta, Equisetophyta и Polypodiophyta, are capable, with rare exception, to develop the numerous additional cladogenous roots forming, by K.Goebel's (Goebel,1931) definition, homogenous root system. The comparative analysis has shown that development of only primary anatomic structures in additional roots is characteristic for all vascular cladogenous plants.

Two anatomic-topographic zones – a primary bark and stele – are precisely expressed on cross-sections of the additional roots in vascular cladogenous plants. Therefore, the ratios of a bark and stele developing in a basal zone of the additional roots were reflected in model schemes. Besides, the differentiation of the bark on zones and the order of arrangement of cells, presence of cavities in aerenchyma, symbionts, elements of mechanical tissues, as well as ectoderm and endoderm, were allocated in the models. The most important structural trait of roots is the type of stele organization. Therefore, in names of the models of roots we had used the standard in botany names of types of steles (Takhtajan, 1956, p.27-28). For example, the additional roots of wild-growing club-mosses from genera Lycopodium L. and Diphasiastrum Holub., possess characteristic for representatives of class Lycopodiopsida plectostele. On this basis, the structure of roots in Diphasiastrum complanatum (L.) Holub., Lycopodium annotinum L., L. clavatum L., L. dubium L. and some other species of club-mosses is described as "plectostelic" model.

In five species of horsetails from the division Equisetophyta: Equisetum arvense L., E. hyemale L., E. sylvaticum L., E. pratense L. и E. fluviatile L., the development of two morpho-types of additional roots in the root systems of cryptogamous individuals is revealed. These are single, thick, long, positive geotropic "growing" roots, and short, thin, numerous, ageotropic, formed in knots of the rhizomes, "sucking" roots. For the roots of horsetails haplostelic and actinostelic models are developed. First of them characterizes the structural features of ultra-thin sucking roots at which one tracheal element surrounded by phloem elements is located in the center of small stele. The second model differs by larger stele in which two-four radial protoxylem strands alternate with two-four groups of phloem elements.

The greatest structural diversity of roots among cryptogamic plants is revealed in representatives of the division Polypodiophyta. 14 structural models of additional roots are developed for 80 species of wild-growing and cultivated in the Botanical gardens ferns. In the class Ophioglossopsida the roots of ferns from genus Ophioglossum possess the most primitive haplostele. For example, the roots of wild-growing in the Urals Ophioglossum vulgatum L. and tropical fern O. petiolatum Hook. have identical anatomical traits. For the roots of these species the more powerful development of a primary bark, in 5 times surpassing the sizes of stele, is characteristic. The same ratio of bark and stele is noted in roots of three wild-growing in Western Siberia species from genus Botrychium L., but for them it is characteristic the actinostele with small amount of radial protoxylem strands (from 2 up to 4) and gifs of fungi in the bark cells. Unique in ferns siphonostelic model is developed by us on the basis of studying root structure of three tree-like tropical ferns from class Marattiopsida.

All angiosperms, unlike of cryptogamic vascular homorhizophytes, are, by V.Troll's definition (Troll, 1949), allorhizophytes. In the structure of root systems of angiosperms there can simultaneously function the main, or primary root, lateral roots of the first and subsequent orders, and also additional rhizogenous and cladogenous roots. Therefore, to the anatomical analysis and modeling of roots of angiosperms the detailed morphological analysis of root systems formed in generative individuals of species, belonging to divisions Pinophyta and Magnoliophyta, always preceded. In underground sphere of gymnosperms the main root and lateral roots of different orders and different spatial orientation are developed. Complexes of the structural traits describing specificity of anatomic structure of the roots of gymnosperms and dicotyledonous angiosperms included the following traits: features of an arrangement of phellogen layers and cambium; position and structure of conductive and non-conductive bast; presence and expressiveness of annual rings in wood, structure of its elements; presence of pitch courses, mucous channels, core, etc. Besides, in the single-aged roots of each species the ratios between width of cork, bast, wood and core have been determined. The comparative anatomic analysis of roots of the gymnosperms which are constituents of 4 classes: Cycadopsida, Ginkgopsida, Pinopsida, Gnetopsida, has allowed to develop 12 structural models. For the majority of studied species the so-called "cyclic" model is characteristic.

Comparative researches have shown, that the roots of plants belonging to division Magnoliophyta differ by the most significant structural diversity. It is necessary to emphasize, that at interpretation of the results of studies we were guided by a system of Magnoliophytes developed by A.L.Takhtajan (1987). The comparative analysis of the diversity of structural traits of roots of the angiosperms has been made in 476 species from 8 subclasses included in composition of the class Magnoliopsida and in 269 species from 3 subclasses of the class Liliopsida.

Roots of the dicotyledonous plants differ by the maximal originality of an anatomic structure. For example, the roots possessing ability to active secondary growth are found out in 42 species from subclass Asteridae. As a result of such growth, in the majority of species the typical ring arrangement of secondary integumentary and conducting tissues formed from phellogen and bast is generated. The originality of root structure is caused by the development in them of separate anatomic traits specific to closely related species, for example, - segmented lacticifers.

Roots of the monocotyledonous plants, as well as the roots of pteridophytes, consist only of primary tissues. Therefore, at the development of root models in 269 species of monocotyledonous plants belonging to 3 subclasses: Alismatidae, Liliidae, Arecidae, the traits describing specificity of structural features of single- layered rhizoderm or multilayered velamen, the primary bark and stele, were allocated. For example, in roots of the representatives of the subclass Alismatidae the wide primary bark (up to 82%) is usually differentiated on internal (with radial and concentric arrangement of cells) and external zones. The large cavities of aerenchyma are developed in the bark. There is presented a small stele (up to 18%) with tetrarch, but more often polyarh conducting bunch in which 10 radial xylem strands alternate with 10 groups of phloem elements. The greatest diversity of structural traits is revealed in the roots of species from the most large subclass Liliidae.

<u>The conclusion</u>

The topographical regularities in architectonics and differentiation of structural elements of a bark and stele of the roots characteristic for representatives of taxa of different rank have been defined in this work. They have laid down in a basis of development of 70 structural models of the roots of vascular plants. Use of structural models facilitates an identification of taxonomic belonging of plant roots and opens new prospects for profound understanding of principles of structuring of plants and inventorying of their diversity. Structural models of the roots are the convenient tool for comparative anatomic researches.

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