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PRIMARY AND ADDITIONAL LATERAL ROOTS IN SOME APIACEAE SPECIES: STRUCTURE AND DEVELOPMENT FEATURES

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The author highlights different aspects of root branching in some species of Apiaceae family. It is pointed out that Apiaceae can produce single and groups of multiple primary and additional laterals (adventitious branch roots) along the bearing parental axes. During the process of multiple roots formation, the primordia origin is usually confined to the callus-like protuberances («excrescences», in the author's terms). They consist of parenchymatic tissue emerged as a result of divisions of pericyclic or phellogen cells. In the perennial root system, the excrescence is more often the remainder of the previously died roots, and then primordia of fine additional lateral roots replaced them appearing in phellogen at their base. The connection of conductive elements of newly formed multiple fine roots occurs due to the trace complexes. The additional fine roots periodically die off and are replaced by new originated from the same excrescences several times per life of the parental root. Functions of additional lateral roots vary: increase of the surface area of absorption and taking up the water from the certain soil layer, replacement of deformed or stop-growing parental roots, and mycorrhizal symbiosis. The way of the lateral roots development in Apiaceae is an important mechanism of plants adaptation to specific environmental conditions. The ability for regular renewal of roots in the old parts of the underground axes is an important acquisition of plants during the structural evolution. The obtained results are also discussed in connection with some practical problems.

Key words: *apiaceae, lateral roots, adventitious roots on roots, multiple roots, branching, Chamaesciadium acaule, Conioselinum tataricum, Trinia multicaulis.*

Introduction

Many researchers mention special protuberances at the thick skeletal roots of some Apiaceae on which multiple fine roots emerge [9, 17]. The origin, development and functions of such outgrowths and roots are not fully understood. In the latest review on the development of laterals [1] there is no information about roots of this kind. The most complete analysis of the fine roots on the secondary thickened root axes (so called adventitious branch roots) in different plants is listed in the article by Paolillo and Zobel [14]. The authors reported that the formation of adventitious branch roots is a common occurrence for intact, unflooded, field grown dicotyledonous plants. The main focus in the article is placed on the anatomical features, while the morphological and developmental aspects are discussed rather poorly. Paolillo and Zobel have proposed a very detailed classification of the anatomical criteria of the adventitious branch roots origin. But among species studied by authors in this way there are no Apiaceae, except carrot and parsnip with reference to the classical work of Warning [20] and Esau [7].

The most information concerning Apiaceae is available only to *Daucus*. Esau [8] indicated that on the thick roots of carrot, additional lateral roots have pericyclic origin and appear at the base of the previously developed root when the latter dies. The yearly renewal of the groups of roots in carrot was also shown by other authors. According to Ignatieva [10], the initial root group of the first order on the carrot root develops from a massive dividing pericycle of the main root, further the base of this group expands already due to the activity of the pericycle of the newly formed multiple roots.

As for field grown plants, the existence of fine ephemeral roots on the secondary thickened taproot is known for many Apiaceae [9]. In *Astrodaucus orientalis* such roots are alive in early May, and at other times one could see only their dried parts [17]; early summer dying of ephemeral roots are revealed in *Conioselinum tataricum* [18]. In *Seseli libanotis* fine roots may appear under the good soil conditions [4]. However detailed information on the origin, morphology and anatomy of multiple roots on roots is extremely scarce.

It is obvious that the ability to yearly produce the new absorbing structures on the suberized old parts of the parental roots should play a crucial role in the life of perennial plants; thereby new information on this topic is actual. So in this article we try by the example of the model species roots to deal with the peculiarities of the origin and functioning of such roots. We also attempt to clarify the problem of root branching in non-agricultural Apiaceae species. The main aim of the article is to emphasize the presence of several ways of root branching in plants and to attract the attention to the difference between primary and additional laterals formation in Apiaceae and to investigate whether or not the phenomenon is widespread under conditions that do not involve flooding or artificial root pruning.

Material and methods

We studied three species of different ecological groups as a sample: *Chamaesciadium acaule* – a typical species of alpine flora of the Caucasus, *Conioselinum tataricum*, spread in the meadows, by the White Sea, in forests, and the steppe species *Trinia multicaulis*. The plants were analyzed in nature and grown in the botanical garden of the Moscow State University. We photographed the roots, fixed them in 75% ethanol and then investigated their macro- and microstructure. Many other Apiaceae species were also investigated in nature regarding mostly their root and underground shoot morphology.

The sections were produced by a safety razor and then the slides prepared. To examine anatomy and morphology using a scanning electron microscope (SEM), material was fixed in 70% ethanol, then dehydrated through 96% ethanol, 96% ethanol: acetone (1:1), acetone and critical-point dried. Dried material was mounted onto specimen stubs using a double-sided tape, coated with platinum and examined using a CamScan 4 DV (CamScan, UK) in the electron microscopy laboratory of the Faculty of Biology MSU.

Results

Our observations focused on all possible types of lateral root formation on the parental axes in individuals of different ages – juveniles and adults, both in morphological and anatomical aspects. Lateral roots emerged in the young root of the primary structure are called «primary lateral roots» or simply «laterals», those, formed in old secondary thickened axes – «additional lateral roots» or «adventitious roots on roots» [19, 14].

Morphology of the root system in the juvenile plant

The young primary root of the juvenile plant of studied Apiaceae actively branches up to the fourth order (Fig. 1, A). Externally, the branching is not strictly acropetally, in the sequence of the following parts of the root on the surface, there are lateral roots of different ages and asynchronous in time of appearance. Between the two well-developed lateral roots we observed primordia of roots which have not yet struck the surface tissue of the main axis.

Besides the normal single lateral roots (Fig. 1, B) there are also protuberances with special multiple lateral roots along the young taproot (Fig. 1, C).

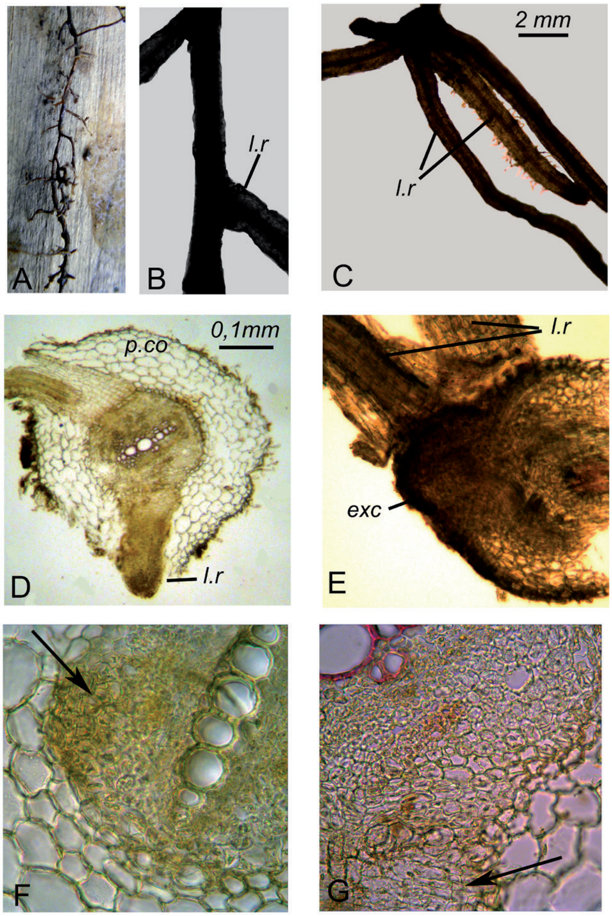

Fig. 1. A – young tap root system; B – single lateral roots on the young root of *Ch. acaule*; C – a group of multiple lateral roots on the excrescence of the young root of *Ch. acaule*; D – cross section of the young tap root of *Ch. acaule* with two opposite lateral roots; E – cross section of the young tap root of *Ch. acaule* with excrescence and a cluster of lateral roots; F – cross section of the young tap root stele of *Ch. acaule* on which the beginning of primary lateral root formation in pericycle is visible (arrow); G – cross section of the young tap root stele of *Ch. acaule* on which the beginning of excrescence formation in pericycle is visible (arrow). *l.r* – lateral root; *exc* – excrescence; *p.co* – primary cortex

An original way of multiple roots formation on the young tap root was observed in details on the plants of *Ch. acaule* cultivated in the botanical garden. It occurs as follows. In many young plants, apical growth of the tap root rapidly stops (reaching 50–60 mm) as a result of deformation or attenuation of the apical meristem. Its functions are passed on to the lateral roots (linear growth of the last also stopped soon) handing the baton over to the next order roots. More often several lateral roots simultaneously replace the tap root. At the same time, along the main axis of the root begins the formation of the callus-like large outgrowths – we called them «excrescences», on which the groups (including 2–3) of short lateral roots often appear. Sometimes excrescences are free from lateral roots (Fig. 1, C; Fig. 2, A, B). Such groups of roots on the excrescences can be observed on the single root branches of different orders. Some of roots are covered with root hairs, the others are smooth, with no hairs. In many plants, roots of different orders are swollen near the apex.

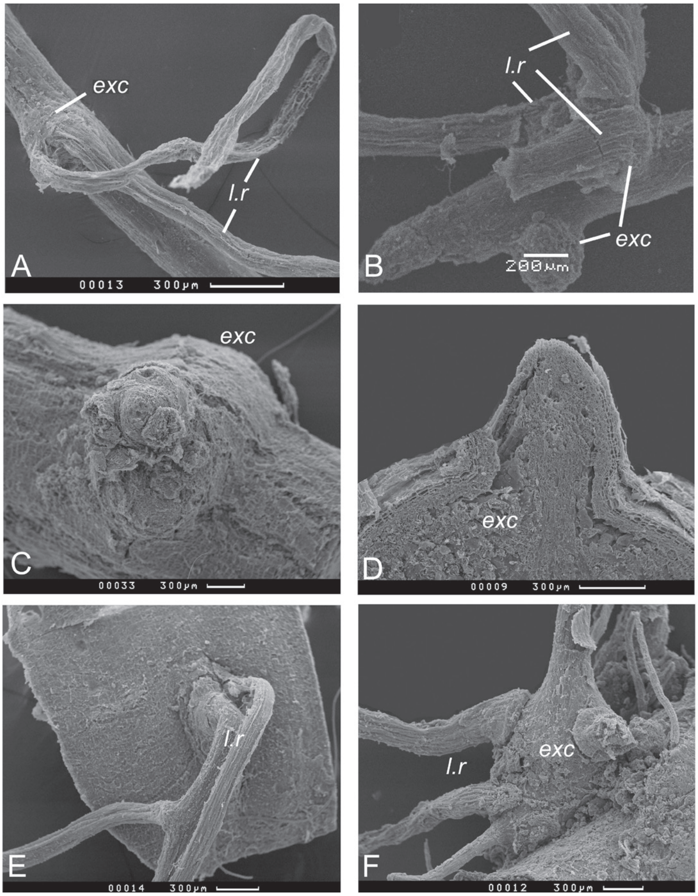

Fig. 2. A, B – groups of multiple lateral roots on the excrescences of the young root of *Ch. acaule* (SEM); C – the free excrescence on the secondary thickened mature root of *Ch. acaule* (SEM), D – cross section of the excrescence of *Ch. acaule* root (SEM); E, F – groups of multiple additional lateral roots on the excrescences of the thick mature root of *Ch. acaule* (SEM).
Symbols – look at Fig. 1

Anatomy of roots in the juvenile plant

The young tap root and a single lateral root of studied Apiaceae species has a primary structure typical for Apiaceae. The rhizodermis is usually with root hairs. The primary cortex is parenchymatous five or six-layered. The endodermis and pericycle are single-layered. The pericycle opposite the rays of the primary xylem can also be multi-layered because its cells divide and disperse to form secretory ducts. The primary xylem is diarch. Over time, the phellogen arises in pericycle, and it soon produces a multilayered cork.

The multiple roots have a structure similar to the young tap root.

Anatomical aspects of root branching in the juvenile plant

Single lateral root develops in such a way. At the branching zone the regular arrangement of the endodermal cells is interrupted. The pericyclic cells laying over the protophloem closer to the distal element of one of the diarch protoxylem ray are beginning to divide (Fig. 1, F). Then new cells form the root primordium, in which the apex and root cap are visible. The primordium continues to grow, and soon the lateral root reaches the surface, breaking through the overlaying cells of the primary cortex and rhizodermis. Sometimes two lateral roots emerge at the nearly same part of the tap root, in this case they appear opposite to each other between the ray of the primary xylem and protophloem (Fig. 1, D). In the case of multiple lateral roots the development proceeds in a bit another way. Thus an active proliferation of the pericycle can cover a large area (almost the entire circumference of the central cylinder) though it is usually localized at one side of the primary diarch xylem elements over the primary phloem (Fig. 1, G). The pericyclic initials elongate, divide and give rise to the outer layers of meristematic derivatives which later generate the primordia of several lateral roots. Then, the mass of cells of pericyclic origin shifts the primary cortex, strongly deforming cortex cells. Soon in this mass the groups of short annular and spiral conductive elements, connected to the primary xylem of the central cylinder, are differentiated from several rows of elongated meristematic cells. The conductive elements going from neighboring primordia can organize in separate traces or as a one complex trace branching at periphery. Cell divisions in the pericycle are activated by intensification of the secondary thickening. As a result, the excrescences look like callus burls on which several short lateral roots appear. Not all excrescences are involved in organogenesis of roots, some of them are free of any lateral structures, but save meristematic activity because they have a layer of lateral meristem – a newly formed phellogen originated from pericycle.

According to our data, the displacement of the tap root occurs as described above regarding the morphological aspect, also through the callus of the proliferating pericycle. In this area the elements of the primary xylem and phloem of the tap root are filled with yellow-brown content, much of them destroyed. At some distance from the primary elements several concentric layers of the meristematic tissue appear. In its periphery, the individual groups of xylem elements are emerging all over the root perimeter. Then, a strong unilateral growth of the pericycle and formation of vascular elements contacting with those laid back at the perimeter near the xylem of the central cylinder begin. At the same time in the periphery of this mass the primordia of several roots appear. As a result of this process one or more lateral roots replacing the tap one are formed (Fig. 1, E).

Morphology of root system in the adult plant

There are several types of lateral roots and their topography on parental axes (Fig. 4, A) in the root system of adult plants: 1 – single thick lateral roots (skeletal, perennial, long, dark, similar in structure to the tap root); 2 – groups of multiple fine roots (absorbing, ephemeral, short, whitish) in a cluster originating from excrescences (Fig. 2, E, F); 3 – groups of multiple fine roots placed below, above or around thick skeletal lateral roots. As for excrescences settling here and there along the parental axes, both single skeletal root and groups of fine ephemeral roots can locate on them.

Ch. acaule and *T. multicaulis* are perennial monocarpics and therefore their thick skeletal roots, as well as a whole plant, live 2–3 years and then die off. In perennial polycarpic *C. tataricum* the lifespan of skeletal perennial lateral roots can be up to 3–6 years. Multiple thin roots tend to live no more than one growing season. In *C. tataricum* multiple fine roots responsible for the absorbing water and nutrients, usually function only at the beginning of the summer. But the excrescences can be seen along the old parts of root axes all year round, the new fine roots appear annually on the same excrescences in spring or in a rainy season. *Ch. acaule* and *T. multicaulis* have more or less random arrangement of excrescences on the parental axes, in *C. tataricum* such excrescences are more regular and form a knotty structure of the underground organs (Fig. 4, C, D).

Interestingly, the lifespan and extinction of fine roots correlate with the functioning of the aerial sphere. So, in spring ephemeroid *T. multicaulis* multiple roots are short-lived as the plant itself. In *C. tataricum* summer extinction of multiple roots is closely connected with stopping of the growth processes in shoots and leaves and the beginning of the summer dormancy typical of this species.

As well as roots, rhizids (*Ch. acaule*), tubers (*T. multicaulis*) and rhizomes (*C. tataricum*) have callus-like protuberances on which the single thick perennial and groups of thin ephemeral roots are forming in a similar manner. The position of root-birth excrescences on rhizomes of *C. tataricum* as well as on the roots, forms some kind of regular ornament: they are arranged in more or less regular rings that occur regularly every growing season at the new rhizome growth.

Anatomy of roots in the adult plant

The mature secondary thickened tap root and thick lateral roots of studied species at the differentiation zone are covered by the cork, consisting of 3–6 layers of tabular cells with dark content. The secondary cortex is composed of large amount of parenchyma cells filled with starch and a small number of conductive phloem elements as well as the secretory ducts; the xylem includes tracheids, vessels and parenchyma cells. The thickness of the secondary cortex ring is 2–2,5 times more than the diameter of the secondary xylem. The primary parenchymal rays are broad; their cells are lysed and sometimes disrupted, forming cavities. The secretory system is represented by primary secrete ducts of pericyclic origin located under the periderm and large secondary secrete ducts caved by 5–8 epithelial cells and located in the secondary cortex.

Fine ephemeral secondary lateral roots preserve a primary structure. They are covered by rhizodermis under which there is a layer of exodermis cells with suberinized walls. The primary cortex consists of 3 to 4 layers of thick-walled parenchyma cells. In mid-summer, thin roots begin to break down, and next season are replaced by newly

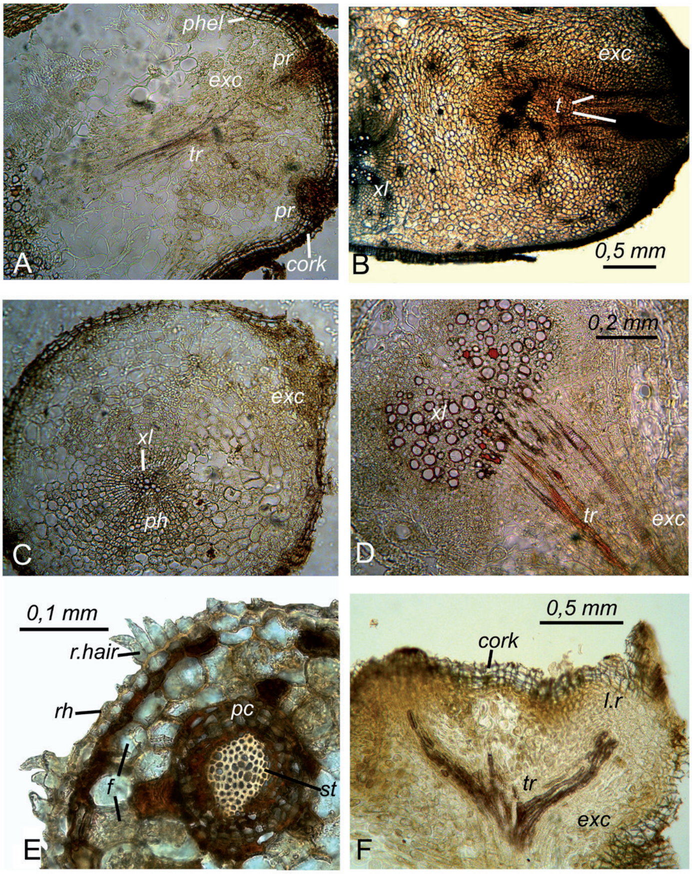

Fig. 3. A, B – cross section of the excrescence of C. *tataricum* root;
C – cross section of the C. *tataricum* root with the excrescence originated in phellogen; D – the trace connected the conductive elements of the additional lateral roots with the xylem of the parental root in C. *tataricum*;
E – cross section of the ephemeral additional lateral root of C. *tataricum*;
F – peripheral branching traces from additional lateral roots in C. *denudatum*.
cork – cork; *f* – hyphae of fungi; *pc* – pericycle, *ph* – phloem; *phel* – phellogen;
pr – root primordia; *r.hair* – root hair; *rh* – rhizodermis; *st* – stele;
t – trace of conductive elements; *tr* – tracheids; *xl* – xylem;
others – look at Fig. 1

formed roots. Anatomical structure of dying ephemeral roots is shown in Fig. 3, E. The walls of some cortex cells in them are lignifying, and the protoplasts are getting filled with dark secretion. All cells of the central cylinder are strongly lignifying. Often, the cells of the primary cortex of ephemeral roots are filled with hyphae of fungi. Their activities lead to disturbance of the intracellular processes. In the central cylinder only the multi-layered pericycle is clearly distinguishable. The phloem consists of a mass of small cells irregularly shaped. The conducting elements of the xylem are represented by the central strand of thick-walled cells.

Anatomical aspects of root branching in the adult plant

The single thick lateral roots in the mature plant are the result of secondary thickening and active linear growth of primary lateral roots, laid back early near the apical zone of the parental root with a primary structure. The process of the development of such roots has been described above.

In the case of formation of the multiple fine ephemeral roots on excrescences, the process is somewhat different from that observed in the young root system of juveniles.

In the old parts of the secondary thickened perennial parental root, the excrescences (Fig. 2, C, D) looking like protuberances outward the secondary cortex, are remainder of the previously developed and now dying roots. Repeated cycles of root formation and branching resulted in a spreading of the locus of root formation at the surface of the parental axis, which altered its morphology into recognizable excrescences. Sometimes the excrescences are overgrown meristematic active tissues of phellogenic origin. Rarely in the relatively young axes they are of pericyclic origin and formed at the very beginning of the secondary thickening of the tap root as described above (Fig. 3, C). The cells of the free excrescences usually accumulate starch. In roots of *C. tataricum* in some cases fungal hyphae can be found in cell protoplasts of excrescences especially near the dying fine roots. The new primordia of fine ephemeral additional lateral roots appear in phellogen of such excrescences (Fig. 3, A). After the differentiation of conductive elements in the tissue of excrescences (Fig. 3, A, B) a connection between the newly-formed vascular system of the fine root primordia and the secondary xylem of the central cylinder is established (Fig. 3, D) due to the specialized short tracheal elements with ladder perforation. When fine ephemeral roots appear near the thick perennial lateral root the vascular system of the former is connected to that of the latter. Many trace complexes develop from traces that served branch roots that formed in the pericycle and later became defunct. Conductive elements from common trace go to different parts of the xylem of the parental root: to the earliest elements of the primary xylem or to the late secondary xylem.

The fine roots can appear on the same excrescences several times per bearing root life. So after the death of lateral roots of the first vegetative season, the excrescences do not cease to function. The following year they produce new fine roots that form branched trace complexes on the periphery.

Additional lateral roots in some other Apiaceae species

A study of root systems in many Apiaceae species of different life forms, ecological groups and living in various communities showed that most of them also have excrescences and multiple fine roots on the old parts of the established parental organs as described above (Fig. 4). More often, these roots are short-lived and seasonally timed. In different plants such roots may develop on the old parts of the tap root (*Laserpitium hispidum* – Fig. 4, G) and laterals (*Laserpitium prutenicum* – Fig. 4, I) as well as on adventitious roots (*Ch. aureum*, *Aegopodium podagraria* – Fig. 4, H, J), tubers (*Ch. prescottii* – Fig. 4, E) and rhizomes (*Anthriscus sylvestris* – Fig. 4, F), often they replace the dead single root. The traces of not a one-time group of multiple fine roots in the form of the extensive conductive system in the outer parenchyma of the excrescence is distinguishably visible in bearing parental axes of many species, for example, on the cross section of the main root of *C. denudatum* (Fig. 3, F).

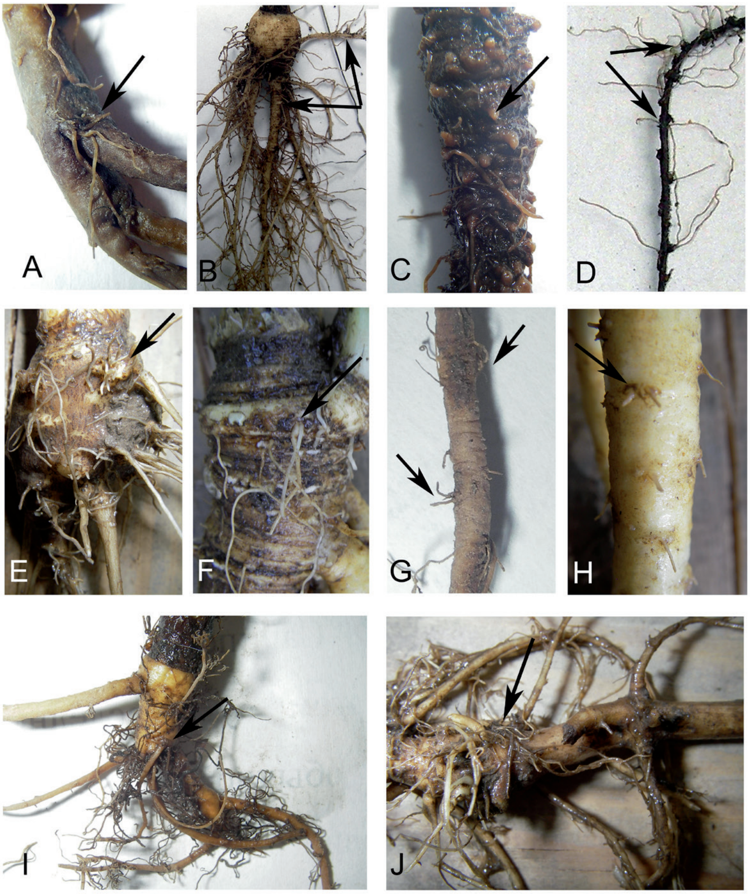

Fig. 4. A – the tap root of *Ch. acaule*; B – the hypocotyl-root tuber of T. *multicaulis*; C – the rhizome; D – the knotty established root of *Conioselinum tataricum* root; E – the hypocotyl tuber of *Chaerophyllum prescottii*; F – the rhizome of A. *sylvestris*; G – the thick skeletal root of L. *hispidum*; H – the thick skeletal lateral root of *Chaerophyllum aureum*; I – the branching tap root of L. *prutenicum*; J – lateral roots on the rhizome of *Aeg. podagraria*. The arrow indicates excrescences and groups of additional lateral roots

Discussion

As a result of our study we can give several conclusions.

1. Most Apiaceae can produce both single and groups of multiple roots along the bearing parental one.

2. In the first case, the process of branching is similar to that observed in most dicots [6]: lateral roots occur in the pericycle near the apices of the parental root with a primary structure.

3. In the second case, the callus-like parenchimatic tissue emerges at the young parental root as a result of divisions of pericyclic cells, forming the excrescences, in which

peripherally primordia of several lateral roots appear. Such roots can only conditionally be called laterals.

4. At the mature secondary thickened old parts of the perennial roots excrescences are often the base of the previously developed root when the latter die and the primordia of new additional roots laid here in phellogen.

5. The additional fine roots periodically die off and are replaced by new roots emerging at the same excrescences several times per parental root life.

6. The vascular system of the groups of multiple roots is connected to the xylem of the parental root by merging into the common trace or very rarely by separate traces due to the specialized short tracheal elements similar to the elements of the hydrocyte system emerged in the callus during regeneration [5]. Thus, in accordance with the classification of possible variants of the anatomical origin of newly formed vascular bundles proposed by Paolillo and Zobel [14], in Apiaceae «trace complexes» are found.

When try to understand the reasons of multiple lateral roots formation some similarities can be found. In a case of their production on the tap root of a primary structure the picture resembles the effect of infection by root-knot nematode, marked for many crops. As shown by many researchers in response to damage inflicted by the nematode intrusion, roots often form numerous swellings along the entire length and increase the lateral roots production. Very often, these lesions are characteristic of carrot that greatly reduces its marketability. There are several species of nematodes known to infect a wide range of plants, causing them symptoms described above [2, 15]. Many Apiaceae of wildlife are likely to be affected by nematodes. We have not observed nematodes in the roots of the studied species, but it is not excluded. Perhaps, some other external factors can also cause a similar picture of the root branching.

If the development of multiple roots at the primary parental root of young plants can sometimes be related to soil organisms, their annually occurrence on secondary thickened suberenized old parts of the perennial axes is a result of unknown internal mechanisms. To date, nothing is known about the genetic and physiological factors controlling adventitious branch roots formation on undisturbed root systems [13]. The overwhelming majority of the information on adventitious rooting has been obtained from shoots, and the control mechanisms that regulate adventitious rooting on roots and hypocotyls may differ from those that regulate adventitious rooting on shoots.

Functions of roots on excrescences vary. When young root system develops over a limited volume of soil (as it has been observed on the plants grown in containers in the botanical garden) multiple lateral roots are used to increase the surface area of absorption and to replace deformed or stop-growing parental roots. In the mature root system thin multiple lateral roots on excrescences are a seasonal phenomenon; they are ephemeral and can absorb water from the certain soil layer only for a short period of time before they die. Sometimes, mycorrhiza are found in excrescences and in ephemeral fine roots. The presence of fungi in such roots may be connected with destructive processes or it can be a normal mycorhizal symbiosis. Thus, the way of the lateral roots development in Apiaceae is an important mechanism of plants adaptation to the specific environmental conditions.

Our study shows that multiple roots can develop on different types of roots and rhizomes in plants of different life forms, different ecology and living in various habitats. The formation of additional laterals (adventitious roots on roots) and the stimulating effect of dead roots on the emergence of new roots in pericycle are described not only in Apiaceae, but also in plants from other families [16]. Bogar and Smith [3] reported that the removal of a branch lateral root at its base instigated the formation of new, adventitious roots directly above and directly below the excision scar on parental roots of *Pseudotsuga menziesii*. So it is a very widespread phenomenon among dicotyledonous angiosperms. However, the versatility of the mechanisms of additional lateral roots formation in all plants is controversial. For example, the periodic formation of roots which is superficially similar to Apiaceae described above is also observed in *Taraxacum kok-saghyz* (Asteraceae). In autumn it usually gets completely deprived of absorption system, but its tap root contains an abundance of dormant primordia of lateral roots, the top of which sit outside the bumps. On the other side *Taraxacum officinalis*, which does not lose the absorbing roots in autumn has no dormant root primordia [12]. This fact indicates that in each individual species the origin and functioning of additional laterals may vary, therefore it is necessary to study the largest possible number of species regarding to ecology and anatomy of root systems. An important problem is also the topography of adventitious branch roots on roots, which apparently can vary depending on the type and age of the parental root in different species.

In conclusion, it should be noted that the ability for regular renewal of roots on the old parts of the underground axes is one of the most important acquisition of plants during the structural evolution, it is a matter of life or death, as it allows not only to absorb water from the remote areas of the soil, where are the apexes of the young lateral segregate roots, but also from near-surface layers. It also make possible the continuous functioning of the root system when apexes are disturbed. The ability of adventitious roots to emerge repeatedly from the same area of the surface of a parental root creates a scenario where adventitious roots can enter and re-enter the same volume of soil. The phenomenon provides an ideal situation for the formation of «opportunistic» roots that take advantage of water and nutrients in parts of the soil that are not populated with the root apical meristems of primary root tissues [14]. This is especially important for plants from areas with unstable humidity. On the other hand cores of meristematic activity and starch reservation in the roots in the form of excrescences are important for regeneration when the roots are damaged. The obtained additional information on the root branching in Apiaceae is not only of theoretical significance, it is also directly related to the methodology of roots transplantation and vegetative propagation by root cuttings. If one chooses the wrong time for the transplantation, when thin roots are not able to develop, rooting will not be successful. We also suppose the active long-lived callus-like protuberances (excrescences) on the roots of Apiaceae are the favorable parts for the rapid formation of a tissue culture of some Apiaceae that should be kept in mind by plant physiologists, agronomists and introducers.

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