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BOTANY

Root Structure Indicates the Ability of *Heracleum sosnowskyi* To Absorb Resources Quickly under Optimum Soil Conditions

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Abstract—The structure of the root systems and roots of the invasive plant *Heracleum sosnowskyi* and the local species *H. sibiricum* have been compared in three habitats of the southern taiga subzone by the standard methods of plant morphology and anatomy. Differences in the structure of the root systems and roots of *H. sosnowskyi* and *H. sibiricum* ensuring the ability of the invasive species to absorb resources under optimum soil conditions have been revealed. These are the occurrence frequency of ephemeral roots, the number of orders of root branching, the size of absorbing roots, and the development of xylem elements.

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INTRODUCTION

More than 13000 plant species, or 3.9% of the Earth's flora species, had become naturalized in new regions by 2015 (van Kleunen et al., 2015). This global mixing of biota calls for study of invasive organisms and invasion mechanisms (Mirkin and Naumova, 2002; Kumschick et al., 2015).

A meta-analysis of the structural traits of 125 invasive and 196 native plant species has shown that the invasive status is positively correlated with a high relative growth rate, a high intensity of physiological processes, and high biomass allocation to leaves and shoots (van Kleunen et al., 2010). Another meta-analysis has revealed an elevated phenotypic plasticity of invasive plants compared to local species (Davidson et al., 2011). Both these reviews considered the most general parameters of underground organs (underground biomass and the under-to-aboveground biomass ratio), and the range of characteristics of aboveground organs was significantly wider (van Kleunen et al., 2010; Davidson et al., 2011). It was determined that the underground features of invasive plants had been studied less than their aboveground features (Smith et al., 2014). However, more information is available about the underground organs of invasive trees (Hodge, 2004; Craine et al., 2011; Jo et al., 2014; Smith et al., 2014; Keser et al., 2015; Veselkin and Prokina, 2016) than about those of grasses.

Heracleum sosnowskyi Manden is an important invasive type in Europe and Russia (Vinogradova et al., 2010; Delivering ..., 2016). Different aspects of its autecology, demography, and physiology were studied earlier (Satsyperova, 1984; Dalke et al., 2015), as well as the physiological and morphological characteristics of the related species *H. mantegazzianum* Somm. et Lev. (Cock et al., 2007). The structure of underground organs was described for some Apiaceae species (Petrova, 2007, 2012; Salpagarova et al., 2012), but no information is available about hogweeds. *H. sosnowskyi* forms arbuscular mycorrhiza with a lower intensity than the local species (Betekhtina and Veselkin, 2015; Majewska et al., 2015).

It was substantiated that the high biomass of giant hogweeds, the large area of their actively transpiring leaves (Dalke et al., 2015), and the high growth rate should correlate with some features of the absorbing underground organs.

The aim of this work was to reveal the morphological and anatomical features of the root systems and roots of invasive *H. sosnowskyi,* which could be considered as components of its invasive syndrome. For this purpose, the structures of root systems and roots of invasive *H. sosnowskyi* and local *H. sibiricum* L. were compared with consideration of their environmental variability.

MATERIALS AND METHODS

Sampling was performed in June 2014 and July 2015 in Yekaterinburg, the southern part of the Middle Ural boreal zone with a temperate continental climate. The intensive growth of plants continues from May to August. The mean duration of the period with temperatures above 10°C is 127 days. The mean temperature of July is 17.6°C, and the mean temperature of January is –12.6°C. The mean annual precipitation is

537 mm with a maximum in July. Pine forests prevail on the surrounding areas; soddy-podzolic soils and burozmes are the prevalent soil types. *H. sosnowskyi* has been recorded in Sverdlovskaya oblast since 1994 (*Opredelitel'*..., 1994). In Yekaterinburg, the sites of its possible naturalization and potential distribution centers included the Botanical Garden of the Ural Branch, Russian Academy of Sciences (RAS UB BG) and the Botanical Garden of Ural Federal University (UFU BG). At present, *H. sosnowskyi* is sporadically distributed in Yekaterinburg and its environs along the bottoms of small streams, roadsides, and wastelands.

Sampling was performed afrom three areas where *H. sosnowskyi* and *H. sibiricum* grow together or in the vicinity of each other.

On plot 1, hogweed beds are noted on heavy loamy soddy-podzolic soil in the RAS UB BG (56°47′56″ N, 60°36′37″ E; 2014–2015); the total projective cover of plants is 50%; isolated *Salix* sp. and *Padus avium* Mill. are observed; *H. sosnowskyi*, *Urtica dioica* L., *Leonurus quinquelobatus* Gilib., and *Arctium tomentosum* Mill. are the dominants of the grass cover.

On plot 2, self-restoring hogweed monostands are revealed on loamy soddy-podzolic soil in the UFU BG (56°35′06.6″ N, 60°19′15.7″ E; 2015); the total projective cover of plants is 100%; isolated *Salix* sp. and *Padus avium* are observed; *Dactylis glomerata* L., *Deschampsia caespitosa* (L.) Beauv., and *H. sibiricum* are found.

On plot 3, *H. sosnowskyi* stands on construction-site soil are observed on a slope of 25°–30° of the Yekaterinburg ring road (56°53′13.5″ N, 60°46′59.8″ E; 2015); the total projective cover of plants is 50%; the upper layer includes *H. sosnowskyi, Pinus sylvestris* L., and *Populus tremula* L.; the ground cover consists of meadow, edge, and ruderal species; *H. sibiricum* was sampled on the side of the same road.

On each plot, four–five generative plants of each hogweed species with whole root systems were dug up, purified, photographed, and described; some roots were fixed in 70% ethanol. In the general analysis of the root structure, root orders were determined. The primary or secondary root on the rhizome was taken as a root of order I, and their lateral roots, as roots of order II, etc. (Serebryakov, 1952). This is the centrifugal method of ordering (Berntson, 1997). It reflects the order of root appearance. Ephemeral roots—absorbing rhizogenic roots arranged in clusters along the main and lateral roots of the secondary structure (Petrova, 2011)—were recorded separately. We did not follow the definition of ephemeral roots as any roots of 1–2 years old (Xia et al., 2010).

The diameters of roots of orders I–III were measured in the fresh state with callipers to within 0.05 mm. The main root thickness was determined at the root collar. The diameters of roots of orders II and III were measured in five replicates at the base of the corresponding roots. The diameters of roots of orders IV–VI were determined on fixed material in 15 replicates on cross sections in the middle of the corresponding roots.

The anatomical parameters were studied only on absorbing roots: all roots of the primary structure with apices and meristem (Berntson, 1997). For the anatomical analysis, 15–20 absorbing roots were randomly taken from each individual. Several cross sections of 12–15 μm were prepared for each root, and only one of them was analyzed. The sections were examined and photographed with a DM 5000 microscope (Leica, Germany) at a magnification of 200–400×. The conventional parameters of fine roots (Cornelissen et al., 2003) were recorded on the photos of sections of primary-structure roots using the Simagis Mesoplant software (SIAMS, Russia).

Differences between parameters were estimated using the χ^2 test for shares, ANOVA and MANOVA analysis for quantitative parameters, and the Mann–Whitney test for parameters measured on an ordinal scale. Factor analysis was performed by the principal component method with the threshold minimum eigenvalue of components equal to 1. The standard error (SE) is given after the ± symbol.

RESULTS

Root system structure. H. sosnowskyi and *H. sibiricum* are taproot hemicryptophytes; the former is a monocarpic plant, and the latter is a polycarpic plant. The root system of each species consists of primary and secondary roots. In the generative *H. sosnowskyi* plants, the root system contains a short epigeogenic rhizome and a taproot (Fig. 1a). The rhizome is formed by basal metamers of the leading shoot (annual increment) embedded in the soil; secondary roots of various thicknesses branch from it. The maximum number of root orders per individual is V–VI. The root system of *H. sibiricum* consists of a short epigeogenic rhizome with the system of primary and secondary roots (Fig. 1b). The rhizome consists of horizontal annual growths of the leading shoot. The primary root can be oriented horizontally and vertically. The maximum number of root orders per plant is IV–V.

Comparison of *H. sosnowskyi* with *H. sibiricum* shows that the former has, first, a reliably higher absolute weight of underground organs (but their share in the total biomass is lower); second, a reliably higher number of orders of root branching; third, generally thicker roots of the same order (by 2–2.5 times); and, fourth, ephemeral roots in a higher number of individuals.

Structure of the absorbing roots. The fine features of the internal structure were studied on living root sections without signs of ontogenetic transformations ($n = 169$). Roots were placed into this category by the following criteria: the presence of an undeformed round stele and cortex with marked rhizodermis

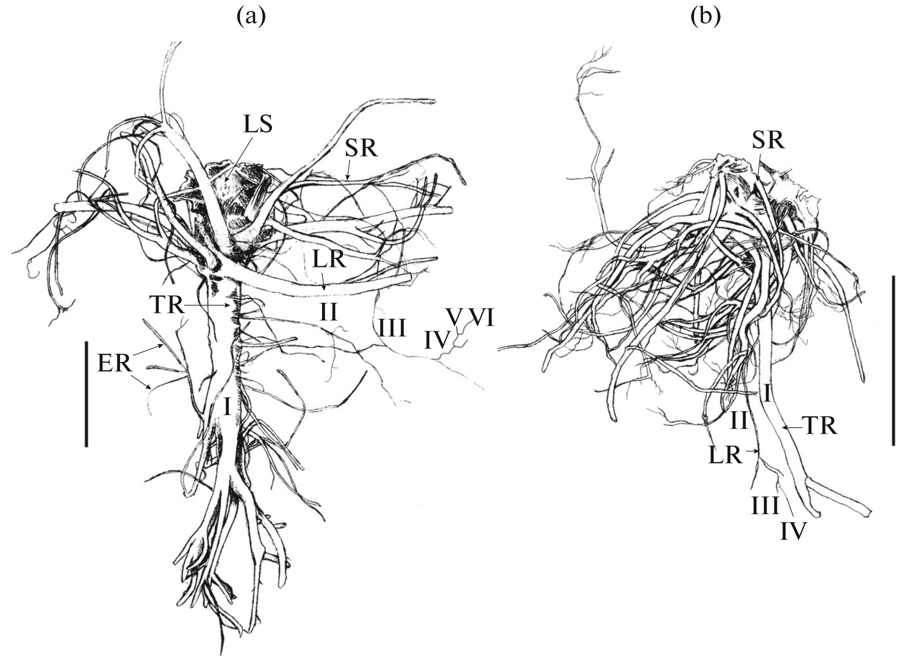

Fig. 1. Root systems of (a) *Heracleum sosnowskyi* and (b) *H. sibiricum*: (TR) taproot; (LR) lateral root; (SR) secondary root; (LS) leaf scar; (ER) ephemeral root. Roman numerals denote the orders determined by the centrifugal method. Scale is 15 cm.

and/or exodermis layers and the maintenance of turgor in cortex cells. The structures of absorbing roots in two hogweed species were compared by single and two-factor ANOVA and MANOVA. The ecological variability due to the variation in root structure among habitats was not analyzed in the single-factor scheme and was analyzed in the two-factor schemes. Samples collected in the RAS UB BG in 2014 and 2015 were analyzed as samples from different places.

From the complete set of parameters, living roots of the last order of *H. sosnowskyi* and *H. sibiricum* differ in structure. This is indicated by reliable values of the Wilks λ test. In the single-factor MANOVA, $\lambda = 0.79$, $F_{(7;\,161)} = 5.96$, $P < 0.0001$ (λ is the Wilks test; F is the Fisher test with specific numbers of degrees of freedom for the factor and the error; P is the significance of difference). In the two-factor MANOVA for species differences, $\lambda = 0.88$,

Table 1. Parameters of *Heracleum sosnowskyi* and *H. sibiricum* root systems (mean ± SE, or range)

Parameter	Number of		*Heracleum*		Significance of difference	
	sites	individuals	*sosnowskyi*	*sibiricum*	test	*P*
Weight of underground organs, g	3	27	130 ± 19	57 ± 12	ANOVA	0.0043
Share of underground organs in the plant weight, %	3	27	16 ± 2	36 ± 4	ANOVA	<0.0001
Number of root branching orders	2	20	5–6	4–5	MW	0.0009
Diameters of roots of different orders, mm						
I	1	10	67.50 ± 3.16	27.60 ± 3.7	ANOVA	<0.0001
II	1	10	17.28 ± 2.36	9.10 ± 0.86	ANOVA	0.0115
III	1	10	5.22 ± 1.24	2.28 ± 0.35	ANOVA	0.0533
IV	1	10	0.38 ± 0.04	0.20 ± 0.03	ANOVA	0.0044
V	1	10	0.18 ± 0.03	0.10 ± 0.01	ANOVA	0.0242
VI	1	5	0.08 ± 0.01	–	–	–
Share of plants with ephemeral roots, %	4	36	84	24	χ^2	0.0009

(–) No roots of order VI are found in *H. sibiricum*; (MW) Mann–Whitney test.

Table 2. Structural parameters of *Heracleum sosnowskyi* and *H. sibiricum* absorbing roots (mean ± SE)

Parameter	*Heracleum*		Difference significance (*P*) in ANOVA	
	sosnowskyi (*n* = 108)	*sibiricum* (*n* = 61)	single-factor	two-factor
Original parameters				
Diameter, μm				
root	255 ± 10	207 ± 8	0.0013	0.0042
Stele	86 ± 3	74 ± 3	0.0041	0.1390
the largest metaxylem vessel	14.3 ± 0.5	10.7 ± 0.4	<0.0001	0.0022
Xylem ray length, μm	57 ± 2	48 ± 2	0.0016	0.0216
Number of xylem vessels	5.0 ± 0.2	4.5 ± 0.2	0.0565	0.1939
Primary cortex thickness, μm	84 ± 4	67 ± 3	0.0056	0.0071
Number of primary cortex layers	5.2 ± 0.2	5.0 ± 0.1	0.3823	0.8509
Partial cortex volume, %	85 ± 1	85 ± 1	0.7189	0.9788
Principal component estimates				
Component 1, cortex	0.06 ± 0.11	–0.10 ± 0.08	0.3071	0.3543
Component 2, stele and xylem	0.23 ± 0.10	–0.41 ± 0.1	<0.0001	0.0147

$F_{(7;\,155)} = 3.13$, $P = 0.0041$. Partial differences between the species (Table 2) include, first, the thicker roots and cortex and, second, the better developed xylem of *H. sosnowskyi* than that of *H. sibiricum*, which is manifested by longer xylem rays and a higher maximum diameter of the metaxylem vessel. Reliable differences in these parameters were found in single and two-factor ANOVA. Only the single-factor ANOVA revealed differences in the stele diameter between the *Heracleum* species. Therefore, the statement that *H. sosnowskyi* and *H. sibiricum* differ in this parameter is less reliable.

Ecological diversity is an important reason for the variation in the hogweed root structure. This is indicated by the reliable values of the Wilks' λ test for the factor of habitat in the two-factor MANOVA: $\lambda = 0.4$, $F_{(21;\,445.6)} = 8.06$, $P < 0.0001$. However, large differences between habitats do not radically change the direction and manifestation of the species features of the root structure.

From the factor analysis results (Table 3), the parameter range of the internal root structure is excessive. All parameters were combined in two principal components accounting for 73% of the total variance. The first component includes all of the characteristics of the cortex size and the root diameter; the second component includes the stele size and the length of xylem rays. The second principal component also correlates closely with the diameter of the largest metaxylem vessel (0.68) and the number of xylem vessels (0.635). This allows interpreting the first principal component as a characteristic of cortex development and the second principal component as a characteristic of the development of stele conductivity. The analysis of the values of these new variables shows (Table 2) that the main difference between the roots of the last order in *H. sosnowskyi* and *H. sibiricum* is the better development of the stele and xylem in the invasive species.

A hypothesis explaining the internal structural features of the last-order roots in two hogweed species is that they can be related to the structure of ephemeral roots, which are more abundant in *H. sosnowskyi* than in *H. sibiricum*.

Structure of ephemeral roots. In both hogweed species, ephemeral roots are arranged by two–three on scars after dead roots on the roots of orders II and III. Ephemeral roots are usually 1–3 cm in length. Ephemeral roots do not branch and form no secondary structure. By these parameters, these are typical absorbing roots (Fig. 2). By the complete set of quantitative parameters of the internal structure, ephemeral roots reliably differ from nonephemeral roots. In two-factor MANOVA with the factors of species and root type, $\lambda = 0.89$, $F_{(7;\,159)} = 2.87$, $P = 0.0076$. In ephemeral roots, almost all dimensional and quantitative parameters are higher than in nonephemeral roots. Therefore, the comparison of the estimates of principal components shows that ephemeral and nonephemeral roots differ reliably in the cortex size and total diameter (Table 4).

As for other features, it may be noted that ephemeral roots are sparser and contain mycorrhiza. The occurrence frequency of mycorrhizal structures is 57% in nonephemeral roots ($n = 120$) and 20% in ephemeral roots ($n = 49$). These differences are reliable: $\chi^2 = 18.41$, $df = 1$, $P < 0.0001$ (χ^2 is the Chi-square test; *df* is the number of degrees of freedom). Aerenchyma is also more common in ephemeral roots. It is noted in 53% of ephemeral roots and in 19% of nonephemeral roots: $\chi^2 = 19.42$; $df = 1$; $P < 0.0001$.

Table 3. Correlations between the parameters of anatomical structure of *Heracleum sosnowskyi* and *H. sibiricum* absorbing roots after varimax rotation

Parameter	Factor loads of principal components	
	1, cortex	2, stele and xylem
Diameter of		
root	+0.843	+0.458
stele	+0.116	+0.872
largest metaxylem vessel	–0.163	+0.680
Xylem ray length	+0.438	+0.758
Number of xylem vessels	+0.356	+0.635
Primary cortex thickness	+0.935	+0.245
Number of primary cortex layers	+0.769	+0.162
Partial cortex volume	+0.818	–0.377
Explained variance share	0.4	0.33

Ontogenetic transformations of roots. A reason for root variability is ontogenetic transformation, which is manifested in the accumulation of tissues with signs of degradation with age. The above-analyzed roots with a round-section stele and cortex and turgor of all tissue cells are living or functioning (Bagniewska-Zadworna et al., 2014) (Figs. 3a, 3b). The initial stage of root degradation is identified by changes in the cortex (except endoderm), but it does not touch the central cylinder. The cellular walls become tortuous; cells acquire a stellate shape and anomalously increase or radially retract; the protoplast darkens in some cells (Figs. 3c, 3d). At the next stage, creasing of tissues is recorded in the stele, except xylem vessels (Figs. 3e, 3f). Thus, the main vector of ontogenetic changes in the roots consists of three stages: untransformed cortex and stele (C+S+); transformed cortex and stele without degradation signs (C–S+); and transformed cortex and stele (C–S–).

The root age ratios in both hogweed species vary widely among habitats. In *H. sosnowskyi*, the occurrence ranges of roots with different combinations of parameters are as follows: C+S+, 17–73%; C–S+, 14–68%; and C–S–, 13–55%. The analogous ranges for *H. sibiricum* are as follows: C+S+, 15–71%; C–S+, 12–40%; and C–S–, 17–50%. In both species, roots in any state can prevail depending on the habitat; the share of roots with C+S+ can be <20% in the vegetation period.

DISCUSSION

The structural features of the *H. sosnowskyi* root system agree well with the large size of the plant (generative individuals reach 2.5 m in height in the Middle Urals). *H. sosnowskyi* differs from the local species *H. sibiricum* by thicker primary and secondary roots, which serve for the fixation of the plant in the soil and fulfill storing functions. Therefore, a larger number of orders should be used for *H. sosnowskyi*. The diameters of thick roots of the same order differ between the species by 2–2.5 times, and the diameters of roots of the last order differ by no more than 25%. Therefore, in *H. sosnowskyi*, the transition from thick to thin roots involves 4–5 successive branchings accompanied by reduction in size, which result in the formation of roots of orders V–VI; in *H. sibiricum*, such a transition includes 3–4 branchings. In other species from the family Apiaceae (*Aegopodium podagraria* L., *Anethum graveolens* L., *Angelica sylvestris* L., *Carum carvi* L., *Daucus carota* L., and *Pimpinella saxifraga* L. (Betekhtina and Veselkin, 2014)), the number of root orders varied from III to IV. Thus, *H. sosnowskyi*, for which the number of root orders reaches VI, differs

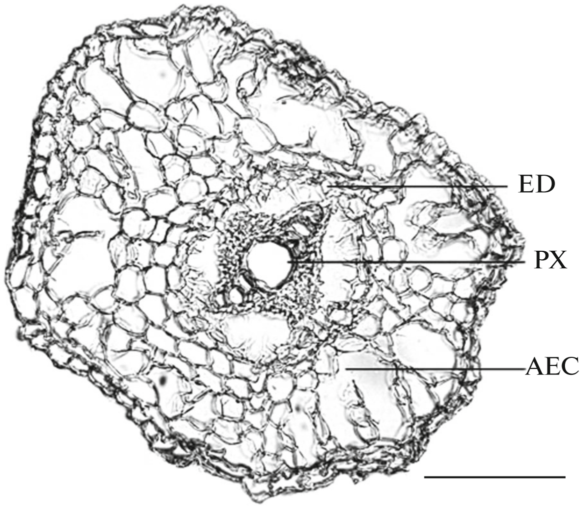

Fig. 2. Structure of the *Heracleum sosnowskyi* ephemeral root. In Figs. 2 and 3, (ED) endodermis; (PX) primary xylem vessel; (AEC) aerenchyma; scale is 100 μm.

Table 4. Structural parameters of ephemeral and nonephemeral roots (mean ± SE)

Parameter	Root type		Difference significance (P) in ANOVA		
	ephemeral ($n = 49$)	nonephemeral ($n = 120$)	species (1)	root type (2)	(1) × (2)
Original parameters					
Diameter of					
root, μm	268 ± 15	225 ± 8	0.9039	0.0175	0.0818
stele, μm	87 ± 4	80 ± 2	0.7342	0.0415	0.0424
metaxylem largest vessel, μm	14.2 ± 0.9	12.5 ± 0.4	0.0021	0.6689	0.4577
Xylem ray length, μm	66 ± 3	49 ± 2	0.9689	0.0006	0.4491
Number of xylem vessels	5.5 ± 0.2	4.5 ± 0.1	1	0.0284	0.7315
Primary cortex thickness, μm	90 ± 6	73 ± 3	0.978	0.0399	0.1843
Number of primary cortex layers	5.6 ± 0.2	4.9 ± 0.1	0.2243	0.0107	0.1811
Partial cortex volume, %	87 ± 1	84 ± 1	0.5317	0.2634	0.9730
Estimates of principal components					
Component 1, cortex	0.31 ± 0.15	–0.13 ± 0.09	0.3365	0.0188	0.2511
Component 2, stele and xylem	0.23 ± 0.10	–0.41 ± 0.11	0.2908	0.0730	0.3861

significantly from other species of the same family by the increased branching of the root system.

The living absorbing roots of the invasive *H. sosnowskyi* are larger (the mean diameter is 255 μm) than the roots of the local *H. sibiricum* (207 μm) and other species from the family Apiaceae (156–207 μm). The higher total size of the root is due to the proportional increase in the cortex and stele. Therefore, their ratio characterized by the partial volume of the cortex is similar for both hogweed species (85%), as well as for other species from the family Apiaceae (81–91%).

Of importance is the difference in the maximum diameter of vessels, which is higher in *H. sosnowskyi*. The relationship between the lumens of xylem elements and their conductive properties is universal (Gamalei, 2006; Kirdyanov and Vaganov, 2006), because the conducting capacity of the vessel is directly proportional to its radius to the fourth power. It was shown that large quick-growing grasses have thicker roots with larger stele, xylem, and vessels than slowly growing plants (Wahl and Ryser, 2000). Therefore, it may be stated that *H. sosnowskyi* conducts water more rapidly and productively than *H. sibiricum*. However, we found no special anatomic features of *H. sosnowskyi* for activating the uptake of water and other resources. Thus, *H. sosnowskyi* apparently fulfills its high-water conduction potential only under optimum water supply.

The ability of *H. sosnowskyi* to uptake resources rapidly under optimum soil conditions is also confirmed by the active formation of ephemeral roots. The ephemeral roots of hogweed are similar to those of other Apiaceae species, where they occur as temporary replacing roots under variable water supply (Petrova, 2012). According to the development of the xylem and cortex, ephemeral roots are active in the uptake and conduction of substances. The differences between the nonephemeral roots of *H. sosnowskyi* and *H. sibiricum* are manifested by a single, although important, parameter: the diameter of the largest vessel (Table 4). Consequently, the high frequency of ephemeral roots in the invasive *H. sosnowskyi* can satisfactorily explain the differences in most of the internal structural parameters of fine roots between the species. Thus, most of the anatomical features of fine roots revealed in *H. sosnowskyi* are due to the active formation of ephemeral roots.

The high variability in the share of absorbing roots of different ages is a common tendency for *H. sosnowskyi* and *H. sibiricum*. The examples of cortex degradation analyzed were not due to the transition of roots to the secondary structure, because these roots were excluded from anatomical analysis. The absorbing roots of hogweeds are apparently short lived, as are those of woody species (Eissenstat and Yanai, 1997; Eissenstat and Volder, 2005), and their ontogenetic transformations primarily affect the cortex. The increase in the share of roots with a degraded cortex is usually caused by unfavorable soil conditions (Spaeth and Cortes, 1995; Visser et al., 1996). After the optimization of soil conditions, *H. sosnowskyi* can be capable of rapidly developing the root system and forming ephemeral roots, which grow rapidly and specialize in water uptake under optimum water supply. The formation and functioning of ephemeral roots under optimum and probably excessive wetting conditions is confirmed by the active formation of their aerenchym. An analogous adaptation to the uptake of ephemeral resources due to the peak formation of absorbing roots at the beginning and end of the vegetation period was revealed for invasive woody species (Jo et al., 2014; Smith et al., 2014). Another analogue of ephemeral roots is specialized snow roots of the mountain *Corydalis conorhiza* Ledeb. adapted to the

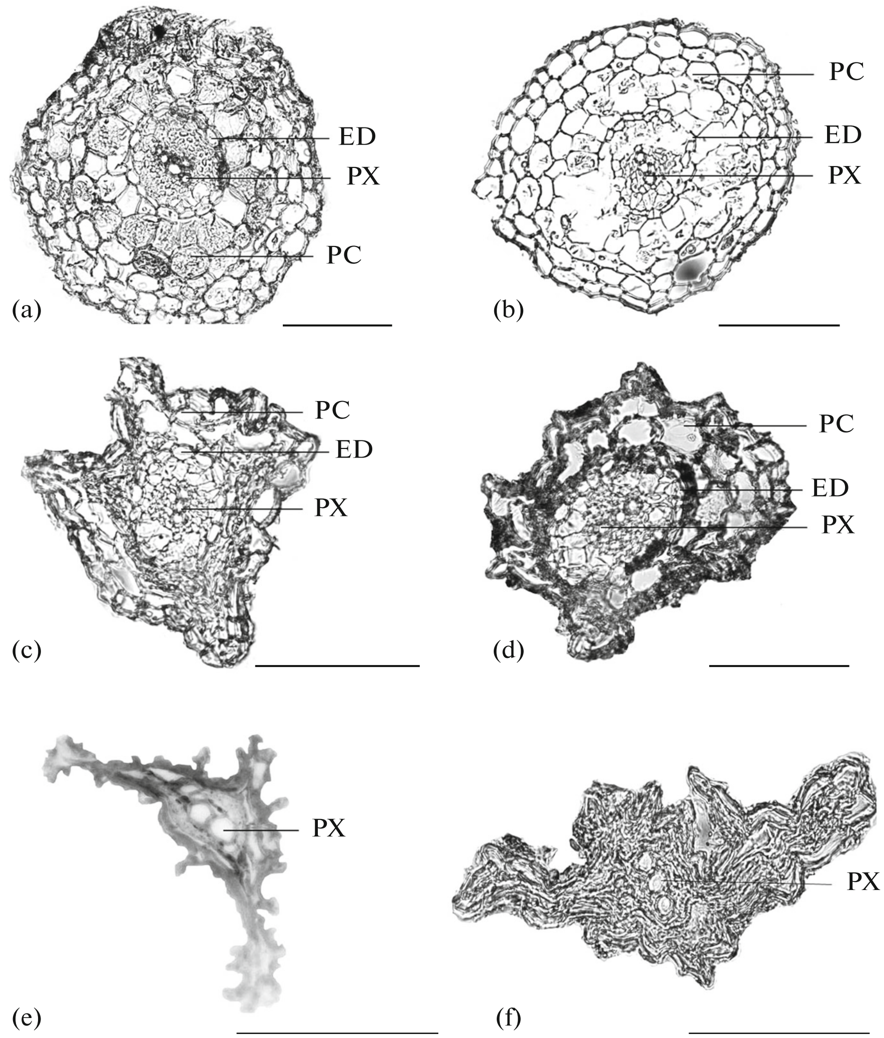

Fig. 3. Age stages of absorbing roots of the last order in (a, c, e) *Heracleum sosnowskyi* and (b, d, f) *Heracleum sibiricum*: (a, b) roots without aging signs, C+S+; (c, d) roots with a degraded cortex but untransformed stele, C–S+; (e, f) roots with degraded cortex and stele, C–S–; (PC) primary cortex.

uptake of mineral nutrients from melting snow (Onipchenko et al., 2009).

Thus, the underground features of *H. sosnowskyi* agree well and with the properties of its aboveground organs. The internal consistency is that the features of root systems and roots of *H. sosnowskyi* indicate its capacity of rapid uptake of resources under optimum soil conditions. This is confirmed by the better development of the xylem in fine roots of the invasive species and the active transformation of ephemeral roots.

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REFERENCES

Bagniewska-Zadworna, A., Stelmasik, A., and Minicka, J., From birth to death—*Populus trichocarpa* fibrous roots functional anatomy, *Biol. Plant.*, 2014, vol. 58, no. 3, pp. 551–560.

Berntson, G.M., Topological scaling and plant root system architecture: developmental and functional hierarchies, *New Phytol.*, 1997, vol. 135, no. 4, pp. 621–634.

Betekhtina, A.A. and Veselkin, D.V., Relationship between root structure of herbaceous dicotyledonous plants and their mycorrhizal status, *Dokl. Biol. Sci.*, 2014, vol. 459, pp. 348–350.

Betekhtina, A.A. and Veselkin, D.V., According to the results of indirect comparisons invasive plants form mycorrhiza with a less intensity than aboriginal ones, *Vestn. Orenburg. Gos. Univ.*, 2015, no. 10(185), pp. 7–9.

Cock, M., Nentwig, W., Ravn, H.P., and Wade, M., *Ecology and Management of Giant Hogweed (Heracleum mantegazziannum),* Wallingford: CABI, 2007.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H., Morgan, H.D., van der Heiden, PausasJ.G., and Poorter, H., A handbook of protocols for standardised and easy measurement of plant functional traits worldwide, *Aust. J. Botany*, 2003, vol. 51, no. 4, pp. 335–380.

Craine, J.M., Wolkovich, E.M., Towne, E.G., and Kembel, S.W., Flowering phenology as a functional trait in a tallgrass prairie, *New Phytol.*, 2011, vol. 193, no. 3, pp. 673–682.

Dalke, I.V., Chadin, I.F., Zakhozhiy, I.G., Malyshev, R.V., Maslova, S.P., Tabalenkova, G.N., and Golovko, T.K., Traits of *Heracleum sosnowskyi* plants in monostand on invaded area, *PLoS One*, 2015, vol. 10, no. 11, pp. 1–17.

Davidson, M., Jennions, M., and Nicotra, A., Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis, *Ecol. Lett.*, 2011, vol. 14, no. 4, pp. 419–431.

Delivering Alien Invasive Species Inventories for Europe (DAISIE). http://www.europe-aliens.org/ (accessed September 1, 2016).

Eissenstat, D.M. and Yanai, R.D., The ecology of root lifespan, *Adv. Ecol. Res.*, 1997, vol. 27, pp. 1–60.

Eissenstat, D.M. and Volder, A., The efficiency of nutrient acquisition over the life of a root, *Ecological Studies. Nutrient Acquisition by Plants an Ecological Perspective,* Bassirirad, H., Heidelberg: Springer-Verlag, 2005.

Gamaley, Yu.V., Structural and functional basis of decryption of meteorological information of plants, *Bot. Zh.*, 2006, vol. 91, no. 3, pp. 361–374.

Hodge, A., The plastic plant: root responses to heterogeneous supplies of nutrients, *New Phytol.*, 2004, vol. 162, no. 1, pp. 9–24.

Jo, I., Fridley, J.D., and Frank, D.A., Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests, *Biol. Invas.*, 2014, vol. 17, no. 5, pp. 1545–1554.

Keser, L.H., Visser, E.J.W., Dawson, W., Song, Y.B., Yu, F.H., Fischer, M., Dong, M., and van Kleunen, M., Herbaceous plant species invading natural areas tend to have stronger adaptive root foraging than other naturalized species, *Front. Plant Sci.*, 2015, vol. 6, no. 273, pp. 1–9.

Kirdyanov, A.V. and Vaganov, E.A., Separation of the climatic signal contained in the variability of the width and density of annual rings of wood, *Lesovedenie*, 2006, no. 6, pp. 71–75.

van Kleunen, M., Weber, E., and Fischer, M., A metaanalysis of trait differences between invasive and noninvasive plant species, *Ecol. Lett*, 2010, vol. 13, no. 2, pp. 235–245.

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, J., Antonova, L.A., Barcelona, J.F., Cabezas, F.J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A.L., Figueiredo, E., Fuentes, N., Groom, Q.J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S., Meerman, J., Morozova, O., Mose, D., Nickrent, D., Patzelt, A., Pelser, P.B., Baptiste, M.P., Poopath, M., Schulze, M., Seebens, H., Shu, W., Thomas, J., Velayos, M., Wieringa, J.J., and Pyšek, P., Global exchange and accumulation of non-native plants, *Nature*, 2015, vol. 525, no. 7567, pp. 100–103.

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A., and Winter, M., Ecological impacts of alien species: quantification, scope, caveats and recommendations, *BioScience*, 2015, vol. 65, no. 1, pp. 55–63.

Majewska, M.L., Błaszkowski, J., Nobis, M., Rola, K., Nobis, A., Łakomiec, D., Czachura, P., and Zubek, S., Root-inhabiting fungi in alien plant species in relation to invasion status and soil chemical properties, *Symbiosis*, 2015, vol. 65, no. 3, pp. 101–115.

Mirkin, B.M. and Naumova, L.G., Adventization of vegetation in the prism of the ideas of modern ecology, *Zh. Obshch. Biol.*, 2002, vol. 63, no. 6, pp. 500–508.

Onipchenko, V.G., Makarov, M.I., Van Logtestijn, R.S.P., Ivanov, V.B., Akhmetzhanova, A.A., Tekeev, D.K., Ermak, A.A., Salpagarova, F.S., Kozhevnikova, A.D., and Cornelissen, J.H.C., New nitrogen uptake strategy: specialized snow roots, *Ecol. Lett.*, 2009, vol. 12, no. 8, pp. 758–764.

Opredelitel' sosudistykh rastenii Srednego Urala (Identification Guide to the Vascular Plants of the Middle Urals), Moscow: Nauka, 1994.

Petrova, S.E., Morphological study of the underground organs of some members of the family Umbelliferae of Central Russia, *Bot. Zh.*, 2007, vol. 92, no. 7, pp. 986–997.

Petrova, S.E., Features of structural adaptation of *Chamaesciadium acaule* (Apiaceae) to high-altitude conditions, *Bot. Zh.*, 2012, vol. 97, no. 7, pp. 884–901.

Salpagarova, F.S., Onipchenko, V.G., Agafonov, V.A., and Adzhiev, R.K., The specific length of roots of alpine plants of the Northwest Caucasus, *Byul. MOIP. Otd. Biol.*, 2012, vol. 117, no. 4, pp. 69–76.

Satsyperova, I.F., *Borshcheviki flory SSSR – novye kormovye rasteniya* (Hogweeds of the Flora of the USSR—New Fodder Plants), Leningrad: Nauka, 1984.

Serebryakov, I.G., *Morfologiya vegetativnykh organov vysshikh rastenii* (The Morphology of the Vegetative Organs of Higher Plants), Moscow: Sov. Nauka, 1952.

Smith, M.S., Fridley, J.D., Goebel, M., and Bauerle, T., Links between belowground and aboveground resource-related traits reveal species growth strategies that promote invasive advantages, *PLoS One*, 2014, vol. 9, no. 8, pp. 1–11.

Spaeth, S.C. and Cortes, P.M., Root cortex death and subsequent initiation and growth of lateral roots from bare steles of chickpeas, *Can. J. Bot.*, 1995, vol. 73, no. 2, pp. 253–261.

Veselkin, D.V. and Prokina, N.E., Mycorrhiza formation in ash-leaved maple (*Acer negundo* L.) within the urbanization gradient, *Russ. J. Biol. Invas.*, 2016, vol. 7, no. 2, pp. 123–128.

Vinogradova, Yu.K., Maiorov, S.R., and Khorun, L.V., *Chernaya kniga flory Srednei Rossii: chuzherodnye vidy rastenii v ekosistemakh Srednei Rossii* (The Black Data Book of the Flora of Central Russia: Alien Plant Species in the Ecosystems of Central Russia), Moscow: GEOS, 2010.

Visser, E.J.W., Blom, C.W.P.M., and Voesenek, L.A.C.J., Flooding-induced adventitious rooting in *Rumex*: morphology and development in an ecological perspective, *Acta Bot. Neerl.*, 1996, vol. 45, no. 1, pp. 17–28.

Wahl, S. and Ryser, P., Root tissue structure is linked to ecological strategies of grasses, *New Phytol.*, 2000, vol. 148, no. 3, pp. 459–471.

Xia, M., Guo, D., and Pregizer, K.S., Ephemeral root modules in *Fraxinus mandshurica, New Phytol.*, 2010, vol. 188, no. 4, pp. 1065–1074.

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