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GENERAL BIOLOGY

Rapid Use of Resources as a Basis of the *Heracleum sosnowskyi* Invasive Syndrome

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Abstract—The functional properties of the invasive *Heracleum sosnowskyi* were compared with those of the native *Heracleum sibiricum*. The leaf and root traits, as well as those of a whole plant and of the mycorrhiza formation, were studied. *H. sosnowskyi* can fulfill the high-productivity potential only under the optimum availability of resources (especially water), while it is poorly adapted to maintain a high physiological activity under the unfavorable soil conditions. An important component of the *H. sosnowskyi* invasiveness is an ability to utilize rapidly resources in both the above- and underground areas at the optimum conditions.

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By 2015, 13 168 plant species of Earth (3.9%) have naturalized in regions that are new for them [1]. Because of global biotic mixing, it is important to study the invasive organisms, some of which become fixed in the autochthonic communities and block a regional changes of species and communities [2]. The hogweed *Heracleum sosnowskyi* Manden. is an actively invasive transformer species in Europe and Russia [3, 4]. The autecology, demography, and physiology of *H. sosnowskyi* and of the close species *Heracleum mantegazzianum* Somm. et Lev have been described [5, 6]. In the center of the secondary area, in middle taiga, *H. sosnowskyi* is known to use effectively light and water [6], but the structural, physiological and ecological mechanisms of this phenomenon are still unclear.

We studied the structure and function of *H. sosnowskyi* in the above- and underground areas and aimed at comparing of its features with those of *Heracleum sibiricum* L., an native species of the same genus. The material was collected in 2014–2015 in the vicinity of Yekaterinburg (a subzone of southern taiga), where *H. sosnowskyi* has been naturalized and widely distributed. In plants collected from two to four sample plots, different traits were studied. In the selected plots, *H. sosnowskyi* and *H. sibiricum* individuals were growing simultaneously. The functional traits of 20–48 individuals of the reproductive stage were studied using standard techniques. The traits were grouped as indicated in the table.

The invasive and native species did not differ significantly in the content of photosynthetic pigments in leaves or in photosynthetic activity of chloroplasts. The distinctions were found at higher levels of plant organization: at the cell, tissue and whole plant levels. In the invasive *H. sosnowskyi,* the larger spongy mesophyll cells were found with a great amount of chloroplasts in them. In addition, mesophyll cells of this species were more tightly packed because a unit of leaf area contained the higher number of cells. Despite a lower leaf thickness in *H. sosnowskyi,* the dry mass per unit of leaf area did not differ in the species compared. The mesophyll structure and the gas exchange rate differed by a factor of 1.5 between the two species. The linear dimensions of *H. sosnowskyi* plants exceeded by a factor of 1.4–2.7 those of *H. sibiricum*, while their absolute biomass was at least 5 times higher.

An increase in the integrated mesophyll parameters in leaves (total surface area of cells and chloroplasts per unit leaf area) due to increase of surface area of spongy mesophyll was the most substantial feature of the invasive species when compared to the native one. These parameters are positively correlated with the rate of CO_2 and water vapor diffusion within a leaf at high light and in the absence of a water deficit [7]. The complication of cell structure in the deeper layers of spongy mesophyll provides an advantage only at the high light, since up to 80% of the photosynthetically active radiation tends to be absorbed in the upper layers of the palisade tissue [8]. Therefore under optimum light and water conditions, the invasive species has a higher rate of gas exchange in leaves related to both photosynthesis and transpiration. However, the

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Functional traits of *Heracleum sosnowskyi* and *Heracleum sibiricum*

Trait	*H. sosnowskyi*	*H. sibiricum*	*n*	Statistical processing	*p*
Biochemical features					
Content per unit of leaf area, mg/dm^2:					
chlorophylls	3.29 ± 0.40	3.17 ± 0.32	20	2A	>0.05
carotinoides	0.63 ± 0.04	0.66 ± 0.04	20	2A	>0.05
Chloroplast features					
Volume, μm^3	32.5 ± 2.3	32.0 ± 1.4	20	2A	>0.05
Photosynthetic activity, 10^{-10} μmol/s	5.71 ± 0.54	5.58 ± 0.39	20	2A	>0.05
Mesophyll cell traits					
Mesophyll cell volume, 10^3 μm^3					
palisade	10.22 ± 0.64	9.33 ± 0.50	20	2A	>0.05
spongy	6.34 ± 0.57	4.38 ± 0.42	20	2A	<0.01
The number of chloroplasts per mesophyll cell:					
palisade	23.8 ± 1.1	24.2 ± 1.6	20	2A	>0.05
spongy	19.8 ± 1.6	15.7 ± 1.4	20	2A	<0.05
The leaf traits					
Leaf thickness, μm	179 ± 5	197 ± 4	20	2A	<0.01
Leaf mass area, mg/dm^2	367 ± 18	369 ± 23	20	2A	>0.05
The number per leaf area of					
mesophyll cells, $10^3/cm^2$	1150 ± 38	984 ± 31	20	2A	<0.01
chloroplasts, $10^6/cm^2$	25.7 ± 2.0	20.3 ± 1.6	20	2A	<0.01
Total mesophyll cell surface per unit of leaf area, rel. un.	30.9 ± 0.99	22.8 ± 1.3	20	2A	<0.001
Physiological traits					
Maximum rate of:					
photosynthesis , μmol/(m^2 s)	13.9 ± 0.5	10.8 ± 0.4	20	2A	<0.001
transpiration, mmol/(m^2 s)	4.04 ± 1.23	3.15 ± 0.71	20	2A	<0.01
Water use efficiency, μmol CO_2/mmol H_2O	3.79 ± 0.43	3.60 ± 0.27	20	2A	>0.05
The underground organ traits					
The number of branching orders	5–6	4–5	20	M–W	<0.001
The last-order root diameter, μm*	232 ± 12	206 ± 9	20	2A	>0.05
Frequency of occurrence:					
root hairs, %	0.4 ± 0.2	18.1 ± 3.7	48	2A	<0.0001
arbuscular mycorrhiza, %	38.9 ± 5.5	52.2 ± 5.4	48	2A	<0.01
ephemeral roots, %	63	15	39	χ^2	<0.01
Whole plant traits					
Height of the aboveground part, cm	245 ± 13	179 ± 7	20	2A	<0.001
The leaf crown diameter, cm	253 ± 28	94 ± 9	20	2A	<0.0001
Total mass, g	903 ± 162	158 ± 29	27	2A	<0.001

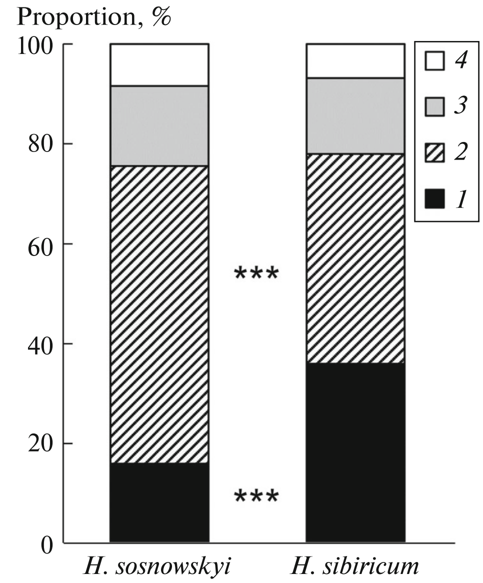
$M \pm m$, n is the number of individuals studied. * Diameter of the primary-structure non-ephemeral roots without any signs of degradation. 2A, two-way analysis of variance; M–W, Wilcoxon–Mann–Whitney test; χ^2, χ^2 test; *p,* significance of differences between *Heracleum* species.

water use efficiency (the ratio of photosynthesis to transpiration) was not species-specific. Therefore, to provide a higher level of photosynthesis, *H. sosnowskyi* needs more of available water source. In general, under the optimum conditions, the functional properties of *H. sosnowskyi* in the aboveground part of plant enable this species to use resources more rapidly than those of the native species.

We have found that, in all habitats, *H. sosnowskyi* had lower of roots and higher contribution of stems into total biomass as compared to the native species (figure). The roots of *H. sosnowskyi* had many branching orders, while occurrence of the root hairs and arbuscular mycorrhiza was lower. In some habitats, the roots of *H. sosnowskyi* contained no arbuscles, which are the main symbiotic structures of the arbuscular mycorrhizae. The mean diameter of the last-order roots was similar in both species. The fine root state varied significantly, because of strongly varying combinations of the degradation signs. During the vegetative period of *H. sosnowskyi,* the proportion of the last-order roots with the signs of degradation reached sometimes 83%. Frequent occurrence of the ephemeral roots shows to a plasticity of *H. sosnowskyi* root system. The bundles of ephemeral roots were usually located on the II- to IV-order roots at the place of the lateral roots that died earlier. The ephemeral roots were not branching, they never had secondary structure, and mycorrhiza or the root hairs were not frequently observed. The ephemeral roots were thicker than the typical last-order roots. Their vessel diameter was larger and the aerenchyma cavities were more frequent than in typical hairs.

The functional properties of underground organs *H. sosnowskyi* were well correlated and indicative of a low ability to maintain absorption activity under unfavorable soil conditions. Unlike *H. sibiricum*, *H. sosnowskyi* had poorly developed arbuscular mycorrhiza and root hairs, which were the adaptation tools enabling a plant to absorb soil resources at low concentration. However, their development and maintenance require large consumption of matter and energy. Since the fine root dying was readily possible in *H. sosnowskyi*, formation of the ephemeral roots is probably a compensatory mechanism that promoted the water and mineral nutrient flow restoration under the favorable conditions. Similar adaptation to use of cyclic resources by means of the rapid absorption root formation at the beginning and end of the vegetative season has been described for the invasive trees [9, 10].

To generalize various ideas of the mechanisms underlying biological invasions, the concept of the invasive syndrome has been proposed [11]. Our study provides some evidence for the invasive syndrome of *H. sosnowskyi*. Because of the leaf and root specific structure and specific features of mycorrhiza formation and biomass allocation to different organs, *H. sosnowskyi* can have high photosynthetic activity and productivity only when the optimum resources are available (water, first of all). Like in other plants [12], the vital processes in roots of *H. sosnowskyi* are probably reduced under water deficit. When soil conditions are optimized, *H. sosnowskyi* can readily compensate a reduced power of the root system by means of the ephemeral root formation, which grow intensely and are adapted to water absorption under the optimum water availability.



Biomass allocation to (*1*) roots, (*2*) stems, (*3*) leaves and (*4*) reproductive organs of *Heracleum sosnowskyi* and *Heracleum sibiricum*. $^{***}p < 0.0001$ in the two-way analysis of variance when (*1*) and (*2*) were compared, $n = 27$.

Thus, we have found consistency of functioning of the above- and underground organs of *H. sosnowskyi*. Specific combination of the plant functional traits suggests that an ability to the fast use of resources is an important component of the invasive syndrome. A complex of *H. sosnowskyi* traits corresponds to a common, physiologically interpretable syndrome of a fast-growing species both in the aboveground [13, 14] and underground [15] parts of plant. The described *H. sosnowskyi* properties well explain the fact that the secondary area of this plant is mostly confined to the regions with cool humid climate and the plant populations occupy preferentially the low-relief elements under the drier conditions of the continental southern taiga and forest–steppe.

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