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Accumulation of ^{137}Cs and ^{40}K by Plants of Forest Ecosystems: The Estimation of Plant Species Factor. Case Study: Mixed Forests of the East European Plain.

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ABSTRACT

This paper is devoted to the problem of ^{137}Cs и K accumulation by plants of forest ecosystems in the center of the East European Plain. It has been found that shoots and roots' phytomass has the maximum difference in the accumulation of these elements depending on the K-selective transport systems of plants. The increased accumulation of ^{137}Cs in green moss and aboveground organs of *Pterídium aquilínum* bracken fern, as well as in the leaves and thin branches of oak, aspen, and birch and in the shoots of cranberries has been revealed. Analysis of the physiological aspects of nitrogen and potassium nutrition allows supposing possible explanation of the mechanism of ^{137}Cs hyperaccumulation by aboveground phytomass of some species.

Keywords: forest ecosystems, radiocaesium, potassium, plant nitrogen nutrition, hyperaccumulation, K-selective transport systems.

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INTRODUCTION

Cesium (Cs) is a Group I alkali metal. Natural soil concentration of Cs is 0.3-25 µg/g, which is non-toxic to plants (Wiesel, 2010) since plants tend to absorb less than 3% of the Cs total content in the soil (in the form of monovalent cations Cs^+) (Sahr et al., 2005). Manifestation of the toxic effects is associated with increased levels of radioactive cesium ^{137}Cs accumulation in vegetation over large areas contaminated by the Chernobyl accident in April 1986.

Chemical properties of Cs are similar to those of the most important biophile element of Group I – potassium (K). In this connection, it was suggested that the Cs^+ ion enters the plant through the same transfer mechanisms as K^+ ion does (Hampton et al., 2005). The chemical similarity of these elements contributed to the widespread perception of the similarity in the behavior of ^{137}Cs and K in the plant body, and therefore, of the possibility of using quantitative information about the K content in order to explain the ^{137}Cs dynamics mechanisms in the biotic ecosystems (Mamikhin et al., 2014). However, as a result of detailed studies, it was found that the concept of similarity in behavior of these elements in plants is an oversimplification (Kobayashi et al., 2016). Nevertheless, a comparison of the behavior of ^{137}Cs and K is very useful, allowing identifying the specifics of ^{137}Cs uptake by plants and its distribution in their tissues and organs.

According to Calmon et al. (2009), the current stage of the radioactive contamination of forest ecosystems resulting from the Chernobyl accident can be characterized as a period of quasi-equilibrium state. For this stage, the slow changes in the bioavailability of ^{137}Cs and relatively stable distribution of this radionuclide in the phytomass are typical. At this, the degree of contamination of the plants is completely determined by the root absorption of ^{137}Cs.

There is a considerable amount of literature discussing factors influencing the ^{137}Cs accumulation by phytomass. At the same time, influence of the biological features of plants is significantly less, according to the tentative hierarchy of factors regulating the ^{137}Cs accumulation by forest ecosystems vegetation (Calmon et al., 2009). A similar conclusion about the insignificant role of the plant species specificity in the accumulation of elements is made in the work of Kovalevsky (2010). At the same time, as stated by Nimis (1996), the value of information on ^{137}Cs soil levels for forecasting its accumulation rate in the phytomass is limited because of the species differences in the ^{137}Cs absorption rate.

It must be emphasized that the evaluation of the role of the plants' biological characteristics in the ^{137}Cs accumulation is often given without a proper explanation. As a result, mechanisms that determine different levels of the radionuclide accumulation by different species remain unclear. When trying to explain the observed patterns, the researcher faces the fact that many aspects of plant physiology are underexplored, in particular those of the forest ecosystems' plants.

The purpose of this work is to study the influence of specific features of the forest ecosystems' plants on ^{137}Cs and K accumulation at the stage of quasi-equilibrium radioactive contamination, as well as to offer a possible explanation for the ^{137}Cs hyperaccumulation mechanism.

METHOD

The study area is located in the south-west of Mescherskaya lowland within the Ryazan Region (the center of the East European Plain) and belongs to the zone of mixed coniferous-deciduous forests (Krivtsov, 2008).

According to current estimates of radiation contamination for agricultural land (Romantsova, 2012), the Ryazan Region belongs to the group of the Russian Federation's regions where the average content of ^{137}Cs in the soil is above the lower limit of the permissible level.

A characteristic feature of the South Meshchera is a low-contrast terrain of wet, damp, and swamp sandy plains. Difficult hydrodynamics and peat low content substrates, which are the legacy of the Quaternary glaciations, define the specifics of soil and vegetation conditions of the study area. According to Krivtsov (2008), sod-podzolic soils of plakors (watershed heights with smooth or slightly elevated ridges and very gentle slopes) in drainage attenuation conditions are replaced by bog-podzolic and bog soils. In this case, since the

bioavailability of ^{137}Cs is inversely proportional to the content of clay soil (Nimis, 1996), a very low content of clay minerals in sandy and loamy sod-podzolic soils and peat soils of Meshchera leads to the increase in intensity of ^{137}Cs transfer into plants.

Pine (*Pinus sylvestris*), small-leaved species like birch (*Betula pendula*) and aspen (*Populus tremula*) are qualified as edificators of plant communities. And, in conditions of high trophic substrate, oak (*Quercus robur*), spruce (*Picea abies*) and alder (*Alnus glutinosa*) are as well regarded as edificators.

To study the patterns of ^{137}Cs accumulation in plants of forest ecosystems, we selected 20 key soil and biogeochemical sampling areas with different degree of hydromorphism and species composition of communities. Within these areas there has been carried out seasonal sampling (April, May, July, September, November) of soils, litter and various structural components of phytocenosis: all factions of tree (canopy and understory), shrub and herbaceous layer's and forest floor's phytomass.

Phytomass' samples were ground and dried to air-dry weight. Roots were thoroughly washed and dried.

Determination of the ^{137}Cs and ^{40}K specific activity in the selected samples was performed using a scintillation gamma-spectrometer "USK Gamma-Plus" and software "Progress" (measurements are repeated five times, background measurement control each time). ^{40}K is a long-live radionuclide, which is a part of the natural K in the amount of 0.012% (Alsaffar et al., 2015). ^{40}K, as well as its stable isotopes, is an integral part of plants and is necessary for their normal development (Romantsova, 2012). This explains the widespread use of the ^{40}K content data to identify the specifics of the ^{137}Cs behavior.

In this paper we analyzed specifics of ^{137}Cs and ^{40}K content in phytomass during the first half of the growing season (early June 2013), when the growth processes of plants are most active.

On the basis of the obtained data and the Zhu and Smolders (2000) method, for each biological object (a phytomass fraction) a K/Cs discrimination factor (DF) has been calculated:

$$DF = \frac{K_{plant}/Cs_{plant}}{K_{soil}/Cs_{soil}}, \tag{1}$$

where K_{plant} and K_{soil} – specific activity of ^{40}K (Bq/kg) in a fraction of phytomass and soil respectively; Cs_{plant} and Cs_{soil} – specific activity of ^{137}Cs (Bq/kg) in a fraction of phytomass and soil respectively.

DF gives an indication in what way and how much the soil ratio K/Cs in the plant organism changes. The value of DF > 1 is indicative of active selective absorption of K by the plant and cesium barrier for this fraction. By concentrating K, the plant changes the soil K/Cs relation in favor of K.

The DF value close to 1 is indicative of passive absorption of K and ^{137}Cs. The lack of selectivity in membrane transport results in preserving the soil K/Cs ratio in plant tissues.

Plants are capable of not only increasing the relation K/Cs in favor of K, but also of reducing it. This situation is described by DF < 1 and is the most typical of the plant bodies providing the barrier function, for example, the root systems.

RESULTS

Value of K/Cs DF is considered an indicator of the selectivity of biological absorption of K in comparison with ^{137}Cs. Table 1 represents the K/Cs DF values calculated for biological objects of the study area; the table includes the most representative data for 56 of the 92 analyzed biological objects.

Table 1. K/Cs DF for biological objects of the South Meshchera's mixed forest communities

Tree species	Phytomass fraction	DF
Mineral (sod-podzolic sandy and sandy loam) soils		
Oak (81 years)	Wood	4.397
	Bark	*0.289*
	Thin branches	*1.877*
	Leaves	*1.926*
Oak (20 years)	Wood	4.672
	Bark	*1.824*
	Thin branches	*1.956*
	Leaves	*1.532*
Oak (80 and 20 years – average)	Wood of thick roots	*1.139*
	Bark of thick roots	*0.070*
	Tender roots	*0.719*
Aspen (45 years)	Wood	3.013
	Bark	*0.679*
	Thin branches	*1.529*
	Leaves	*1.853*
Aspen (8-20 years)	Thin branches	*2.398*
	Leaves	*1.740*
	Wood of thick roots	*0.808*
	Bark of thick roots	*1.911*
	Tender roots	*1.190*
Spruce (55 years)	Wood	9.369
	Bark	*2.912*
	Thin branches	3.097
	Needles	3.138
Pine (88 years)	Wood	10.193
	Bark	3.070
	Thin branches	6.313
	Needles	3.159
Peat soils		
Pine (40 years)	Wood	22.190
	Bark	23.479
	Thin branches	6.630
	Needles	12.841
Birch (40 years)	Wood	38.807
	Bark	21.316
	Thin branches	8.578
	Leaves	*2.662*
Pine (63 yeras)	Wood	69.232
	Bark	27.948
	Thin branches	24.388
	Needles	29.827
Alder (45 years)	Wood	165.402
	Bark	9.947
	Thin branches	18.242
	Needles	9.048
	Roots	*0.073*
Herb-shrub layer		
Miscellaneous herbs of fire-damaged forest*	Aboveground organs	*0.893*
	Roots	*1.900*
Pterídium aquilínum	Aboveground organs	*0.388*
	Roots	*0.029*
Cowberry	Aboveground organs	*2.134*
	Roots	*2.467*
Green moss	Gametophyte	*0.418*
Lily of the valley	Aboveground organs	33.222
	Roots	3.059
Sedge, wet grasses	Aboveground organs	12.400
	Roots	4.321

DF values < 1 are underlined and given in italics, DF values of 1-3 are given in bold italics.
* The community is dominated by: bracken, willow-herb, bromegrass.

For clarity, the DF values from Table 1 are given in the form of a distribution curve (Figure 1). The curve has a complicated shape and, in fact, consists of two separate parts – notional boundary between them can be marked at the class interval with the maximum value of 8. The branch of the distribution curve to the right is in the range of high DF values: its modal class corresponds to the DF values of 20-30. Its phytocenosis' structural components represent a variety of phytomass fractions that selectively accumulate K. Despite the diversity of biological objects, it is possible, however, to note two features of the sample. Firstly, it is in the area of high DF values where the majority (75%) of all biological objects growing in peat soils are grouped. Secondly, this sample consists mainly of structural components of the aboveground phytomass, and the fraction of the underground organs accounts for only 11%..
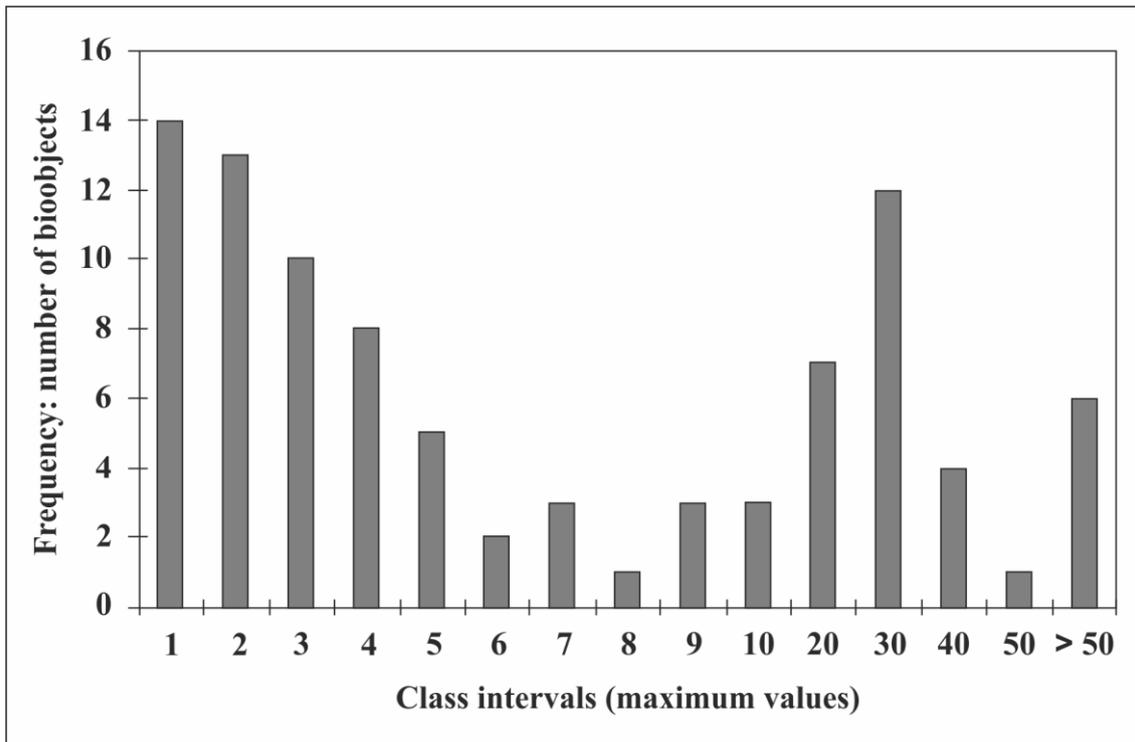

Figure 1. Distribution curve of K/Cs discrimination factor (DF) values for structural components of the South Meshchera phytocenosises

The first of these features – accumulating of K by plants of peat soils, which leads to a significant shift in the soil K/Cs ratio in favor of K in plant tissues – is quite natural. It is due to the ability of plants to ensure the homeostasis of the organism in conditions of the required nutrient deficiency. According to Alekhina et al. (2005), the degree of concentrating ions in the plant is particularly high when they are deficient in a nutrient medium. In this case, the plants are adapted to the growing conditions through changing not only the morphology of growing roots, but also the kinetic characteristics of ion transport systems (ion affinity and transfer rate).

It should be noted that in peat soils the accumulation by plants is increased not only when it comes to biophile K, but also toxic ^{137}Cs, which is associated with considerable mobility of these elements as a result of the lack of the exchange immobilization in the clay minerals (Scheglov, 2000). However, due to the selectivity of the membrane transport systems, ^{137}Cs is accumulated mainly passively due to its increased bioavailability in a peat soil, while K, along with the passive absorption, is also characterized by a strongly marked active concentrating by vegetation.

The second of the abovementioned features – a trend to preferential accumulation of K by the aboveground phytomass – can be traced quite clearly even in the most superficial consideration of Table 1. To identify the characteristics of the elements distribution in a plant body we have constructed the generalized series of ^{137}Cs and K distribution for the structural components of the tree species (Table 2). According to the data in Table 2, the fundamental difference in the nature of ^{137}Cs and K accumulation is the contrasting

distribution of the given elements between the phytomass of the aboveground and underground organs. Biophile K actively passes to the offshoots, while the translocation of the toxic ^{137}Cs is limited by the root barrier.

Table 2. ^{137}Cs and ^{40}K relative distribution series for the structural components of the South Meshchera mixed forest communities

Radionuclide	The contrast ratio for aboveground phytomass*	Relative distribution series
^{137}Cs	11.47	roots > photosynthetic organs > thin branches > bark (trunk) > wood (trunk)
^{40}K	3.90	photosynthetic organs > thin branches > bark (trunk) > wood (trunk) > roots

* The contrast ratio for the aboveground phytomass has been calculated as the ratio of the radionuclide specific activity for a fraction of aboveground biomass with the maximum activity to the same index for a fraction of aboveground biomass with the minimum activity.

It is obvious that the root barrier, preventing ^{137}Cs transfer to the aboveground phytomass, has nothing to do with the plant's exo- and endodermal barriers, limiting transfer of a number of heavy metals to the central cylinder of the root. ^{137}Cs, as well as its geochemical analogue K, is characterized mainly by symplastic radial root transport (Baxter et al., 2009), while the phenolic and lipophilic biopolymers of the endoderm's cell walls (the so-called Casparian strips) slow down the apoplastic diffusion current of water and dissolved substances (Chen et al., 2001). The reason for the preferential accumulation of ^{137}Cs in the roots should be sought in the specific nature of the transport mechanisms ensuring elements' loading into the xylem. Studies conducted on barley roots (*Hordeum vulgare*) (Alekhina et al., 2005) suggest that due to the selectivity of output and input cells' ion channels surrounding xylem vessels, on the one hand, a limited flow of ^{137}Cs from the root to aboveground organs is provided, and, on the other hand, its effective translocation backwards is ensured, together preventing the accumulation of toxic ions in the shoots.

Despite the difference in the ^{137}Cs and K accumulation by the phytomass' roots and shoots, the distribution of these elements in fractions of the aboveground phytomass on the whole is similar. According to Table 2, the maximum content of ^{137}Cs and K is characteristic of photosynthetic organs of trees, the minimum – of trunk's wood. The ability of ^{137}Cs and K to be accumulated in the most physiologically active bodies has been demonstrated in a number of studies (Scheglov, 2000; Hornik et al, 2007; Nobori et al., 2014). It should be noted that this ability cannot be considered as favorable because it is responsible for quite active participation of ^{137}Cs in cyclic migration.

At the same time, despite the similarity of ^{137}Cs and K relative distribution series in the aboveground phytomass, it is necessary to highlight one characteristic feature in the localization of these elements. As shown in Table 2, ^{137}Cs contrast ratio is almost 3 times greater compared to K. Thus, the most important biophile element K is distributed more evenly in the aboveground phytomass and is largely accumulated in trunk's wood, in contrast to ^{137}Cs. We also would like to note that our findings are fully consistent with the research results of Zhu and Smolders (2000). According to Zhu and Smolders (2000), ^{134}Cs concentration differences between various tissues of a willow reached 10-20 times, while for K the differences were less than 5 times. At that, as in our case, the general nature of the ^{134}Cs and K distribution in the aboveground organs' phytomass was similar.

The left branch of the distribution curve in Figure 1 lies in the area of reduced DF values. It is this sample that accounts for 83% of all studied fractions of underground organs and only 25% of biological objects growing on peat soils, which, according to the abovementioned statements, is quite natural. The modal class of sampling is the class interval with DF values < 1. Soil ratio K/Cs in biological objects of this class is shifted in favor of Cs, which is typical for the plant tissues that perform a barrier function, for example, for the root systems. In addition to the underground organs (they account for 57% of the biological objects of the modal class), the DF values < 1 are also obtained for the aboveground phytomass of *Pteridium aquilinum*, herbal phytocenosises with prevalence of *Pteridium aquilinum* and green moss.

Increased accumulation of ^{137}Cs by mosses was expected. According to Kovalevsky (2010), mosses and lichens, as the most ancient and primitive organisms, are characterized by simplified anatomical differentiation. They lack the organs and tissues that act as anti-concentration physiological barriers. Therefore, mosses and lichens are characterized by barrier-free accumulation not only of ^{137}Cs, but also, as pointed out by Kovalevsky, of a number of other elements: uranium, molybdenum, lead, silver, gold, selenium, zirconium, tin.

Our results, demonstrating the ultra-high accumulation of ^{137}Cs by bracken's fronds, were expected too. Excessive accumulation of this radionuclide by aboveground organs of ferns is quite a universal pattern, which manifests itself in a wide range of environmental conditions of near and far impact zones of the Chernobyl accident (Scheglov, 2000). At the same time, in spite of special works devoted to the subject, there is still no an adequate explanation of this phenomenon. Thus, Shura (2007), after analyzing the results of own studies and the literature data, concluded on the existence of a fern root cesium barrier. However, the author says nothing about the nature of this barrier and the reasons of excessive accumulation of ^{137}Cs in aboveground organs of bracken. According to Butkus and Konstantinova (2005), high specific activity of ^{137}Cs in fronds of male shield fern (*Dryopteris fílix-mas*) in the forest ecosystems of Lithuania are due to the peculiarities of fern root system. It is located close to the soil surface and in the litter, that is in the layer with the maximum ^{137}Cs activity that, according to the authors, determines the intensity of radionuclide absorption. Similar explanations concerning several other species are also provided in the works by Nimis (1996), Vinichuk et al. (2010).

We do not deny the importance of this factor, but would like to note, however, that, in our opinion, the cause of the excessive accumulation of ^{137}Cs by fern is due to the peculiarities of its physiology. Apparently, the absorption and transport of ^{137}Cs by bracken and other types of vascular plants is made by the K-transport systems, but due to the fern's simpler organization there is no discrimination (differentiation) between these elements. Thus, it can be assumed that while K and ^{137}Cs are freely transferred to the aboveground organs of bracken by means of xylem transport, the role of phloem transport for K and ^{137}Cs is low, whereby these elements are accumulated in the fronds. Probably, potassium-deficient sandy soils and "attempt" of plants to replace biophile K by toxic ^{137}Cs play a certain role in this accumulation (for example, Zhu and Smolders (2000) mentioned the increased accumulation of ^{137}Cs in K-deficient conditions). Nevertheless, the success of possible explanations of ultra-high specific activity of ^{137}Cs in the aboveground organs of *Pteridium aquilinum* we associate with the success in the study of ion transport systems of ferns. It should be stressed that so far there has been received the most valuable information on the mechanisms of ^{137}Cs and K absorption and transfer for thale cress (*Arabidopsis thaliana*) (Hampton et al., 2005) and a number of agricultural crops (Kobayashi et al., 2016). However, the transport systems of different plant species (and in particular of the more ancient and low-organized representatives of *Pteroid*) are highly specific and require independent study.

Back on Figure 1, particular attention should be paid to the structural components of phytocenosises with DF values close to 1 (approx. 1-3). These DF values are common for Meshchera communities (Figure 1). We emphasize that the underground organs account for only 34.8% of biological objects of these classes. The remaining fraction of a phytomass with DF of 1-3 are leaves and thin branches of oak (regardless of age) and aspen (from different sampling points), oak bark, birch leaves growing on highmoor bogs, and cranberries shoots. Thus, for these bioobjects, passive absorption with relatively low bioconcentration of K, hence with preserved values of K/Cs ratio close to that of soil, is typical. Consequently, the abovementioned phytomass fractions are ^{137}Cs-enriched, though do not function as a barrier in a plant organism.

DISCUSSION

Our findings raise a question about the causes of poor absorption selectivity for elements that are geochemical analogues fundamentally different in their biophile properties. As has been mentioned above, the excessive accumulation of ^{137}Cs is characteristic of the underground organs and is anomalous for aboveground phytomass' fractions. In this connection, it is advisable to refer to the species-hyperaccumulators of [137]Cs. According to Maestri et al. (2010), hyperaccumulation involves the ability of plants to accumulate elements in the aboveground phytomass in concentrations exceeding those in the soil. Despite the intensive study of various aspects of radiation contamination in recent years, including quite successful search for species-hyperaccumulators of ^{137}Cs for phytoremediation purposes, the mechanisms of this radionuclide's hyperaccumulation, as far as we know, remain unknown. Nevertheless, some attempts in this direction have

been undertaken. The most frequently, the plants' ability to accumulate ^{137}Cs in excess is associated with K-philic properties. Thus, Calmon et al. (2009) provide a hierarchical series of ^{137}Cs accumulation by different species of trees, which is as follows: Aspen > Oak > Birch > Pine > Linden > Spruce. According to the authors, this series is very close to a series of nutrient absorption by tree species, primarily K. Thus, K-philic species as well accumulate ^{137}Cs, K element analogue, more actively.

In a number of studies this issue is considered from a more general standpoint due to the nature of the mineral nutrition of plants. Willey and Tang (2005) studied the effect of nitrogen nutrition on the ^{137}Cs uptake and found that this radionuclide's accumulation depends on the nitrogen source and species of a plant. In their experiment, the maximum concentrations of ^{137}Cs were recorded in shoots of nitrate-grown *Amaranthus paniculatus* and *Chenopódium álbum*.

In this paper, we are not claiming to give a comprehensive interpretation of the ^{137}Cs hyperaccumulation mechanism in plants, we attempt to present a possible explanation of the mechanism on the basis of analysis and generalization of the literature data.

First, let us briefly refer to some aspects of the heavy metals (HM) hyperaccumulation that are well studied up to date. It has been established that a prerequisite for the HM hyperaccumulation is the existence of effective mechanisms to maintain their homeostasis in plants, such as the presence of biochemical mechanisms for detoxification of excess HM. One of such mechanisms is HM-ions complexation with ligands. At this, according to Cappa and Pilon-Smits (2014), chelating agents in the plant's tissues can be represented with organic acids (e.g., citrate and malate) or chelators of protein nature (such as nicotinamine, glutathione, histidine, phytochelatins, metallothioneins). As shown by Lu et al. (2014), constitutively high concentrations of organic acids, acting as chelating agents, are typical of hyperaccumulators. The content of phytochelatins in them is usually lower than in plants-non-hyperaccumulators.

It is known that the ^{137}Cs hyperaccumulation is most often found among the *Amaranthaceae* and *Chenopodiaceae* (Wiesel, 2010; Willey and Tang, 2005; Zhu and Smolders, 2000), as well as typical of common heather (*Calluna vulgaris*) (Bystrzejewska-Piotrowska et al., 2005). It should be emphasized that the normal accumulation of ^{137}Cs in the roots and the abovementioned fact of selectivity to K-transport systems of xylem parenchyma cells do not mean that ^{137}Cs is not translocated into the aboveground phytomass of plants-non-hyperaccumulators. According to Zhu and Smolders (2000), ^{137}Cs, received by the shoots, can be effectively transported through the phloem, at this, the phloem transport can be even more intense than the K one. ^{137}Cs active participation in the recirculation (and, as a result, its return into the roots) may be due to K selective absorption by leaf cells.

Hence, species-hyperaccumulators of ^{137}Cs appear to lack the transport blocking for this element at stages of loading into the xylem and uptake by leaves. Thus, ^{137}Cs received by leaves, instead of participating in the phloem transport and returning back to the roots, must be converted into a nontoxic inactive state. A possible mechanism for this detoxification may be ^{137}Cs insulation in vacuoles, similar to sodium (Schroeder et al., 2013). The results of Akamatsu et al. (2014), who used the fluorescence microscopy for Cs imaging in the *Arabidopsis thaliana* cells, are also indicative of Cs vacuolar compartmentalization. Thus, the first feature of the species-hyperaccumulators of ^{137}Cs should be Cs effective detoxification on the shoot, presumably due to the isolation in the vacuole.

The second feature of hyperaccumulators, apparent at first glance, should be active root uptake of ^{137}Cs, suggesting the presence of specific transport systems. According to Wiesel (2010), all plants have transport proteins, selectively absorbing vital element – K, but differ by the set of proteins that catalyze non-specific absorption of K and ^{137}Cs. Increased ^{137}Cs accumulation, thus, may be associated with increased expression of non-specific transport proteins. At the same time, as indicated by Coskun et al. (2016), a nonspecific type of K-transport system, LATS (low-affinity transport system), having a low affinity for ion, functions in plant roots under conditions of high ion concentration in the environment.

Plants growing in soil with excess of cations (including K$^+$), as a rule, are characterized by the nitrate-nitrogen nutrition. Scientists noticed the feature of joint NO$_3^-$ and K$^+$ absorption in the 1960s – early 1970s, when the model of internal circulation of ions in plant's vessels was proposed for the first time (Coskun et al., 2016). According to this model, plants that reduce NO$_3^-$ in shoots use K$^+$ as a counter-ion for NO$_3^-$ transport in

the xylem. In shoots, the fate of these ions differs: NO_3^- is reduced, and K^+ can enter the roots again through phloem transport in combination with organic acids. After the decarboxylation of organic acids, K^+ may participate again as a counter-ion in NO_3^- transport to the shoots (Marschner, 2012). Another important fact, vital for our further considerations, is that some limitations of the model, proposed in the 20th century, have been recently discovered. Thus, according to Coskun et al. (2016), significant downward (phloem) flow of K^+ in the complex with the organic acids is not always observed. When the absorption of cations and anions (K^+ and NO_3^-) by roots is balanced (that is in K-abundant conditions), instead of the phloem transport of K^+ in order to reuse it as a counter-ion of NO_3^- there is an accumulation of the complexes of K^+ with organic acids in vacuoles of the shoot's cells. Thus, for the nutrient-rich conditions, consistent absorption of K^+ and NO_3^- by plant roots, reducing NO_3^- in shoots, is typical, wherein K^+ is accumulated in the vacuoles of shoot's cells in complex with organic acids.

Biosynthesis of organic acids that are able to form complexes with K^+ and its analogues is another, not less important factor of hyperaccumulation. As has been demonstrated previously, it is the species with constitutively high concentrations of organic acids (for example, plants with crassulacean acid metabolism) that are hyperaccumulators of a number of HM. Apparently, a similar role – role of chelating agents – is played by the organic acids towards K and [137]Cs. It has been established that the accumulation of organic acids can be the result of NO_3^- reduction: according to Liu et al. (2015) and Lopez-Bucio et al. (2000), NO_3^- reduction results in a shift of pH due to the formation of toxic hydroxide ions (1 mole of OH^- per mole of reduced nitrate) (Liu et al., 2015.):

$$NO_3^- + 8H^+ + 8e^- = NH^3 + 2H_2O + OH^-. \qquad (2)$$

OH^- ions cannot be effectively excluded from cells. The mechanism of neutralization is the synthesis of counter-ions (organic acids) that is carried out in presence of PEP carboxylase. According to Popova (2009), an increase in the accumulation of organic acids in the presence of NO_3^- is consistent with the concept of functioning of biochemical pH-stat as a mechanism for neutralization of NO_3^- assimilation products in plants.

When developing the above concept of model of the internal circulation of ions in plants' vessels, explaining the NO_3^- and K^+ joint xylem transport, we have just briefly mentioned that this model was applicable to the plants, reducing NO_3^- in shoots. This is obvious, because if NO_3^- reduction takes place in the roots, the products of this process – amino acids that do not require K^+ as the counter-ion, in contrast to the NO_3^-, enter the xylem flow. It is well known (Alekhina et al., 2005) that a key aspect of NO_3^- reduction is participation of the enzyme nitrate reductase (NR) in this process. It is the localization of NO_3^- reduction catalyzed by NR which the metabolism of organic acids and, as will be shown further, the fate of ^{137}Cs absorbed by a plant depend on.

According to Alekhina et al. (2005), NR enzyme is localized in the cytosol, and in most species – in both the roots and the leaves. The percentage of NO_3^-, reduced in the aboveground or underground phytomass' fractions varies depending on environmental conditions (temperature, illumination, level of available NO_3^- in the soil) and genetic factors. The latter manifests itself in the species and cultivars' specifics of NO_3^- absorption, its distribution in organs, and reduction and accumulation. Thus, almost no nitrate reductase activity is detected in the roots of such plants as beet (*Beta*), cotton (*Gossypium*), goosefoot (*Chenopodium*), and cocklebur (*Xanthium*). They convert nitrate nitrogen into ammonia mainly in the leaves. The reverse reduction – the almost complete reduction of NO_3^- in the roots and transfer of nitrogen to the leaves in organic form – is typical of lupine (*Lupinus*), bilberry (*Vaccinium myrtíllus*), cranberry (*Vaccinium oxycoccus*). We would like also to note that the classification of a number of woody plants as of the latter group and, therefore, matching them on the basis of this feature against most of grass species (as is done, for example, by Alekhina et al. (2005)), is not fully justified. According to Smirnoff et al. (1984), translocation of NO_3^- into the xylem and its reduction in the leaves is a common phenomenon for woody plants. Moreover, in the case of sufficient reserves of NO_3^- in the soil, its reduction in photosynthetic organs is energetically more favorable than in the roots, because it does not require additional energy expenditures for transport of carbons that are synthesized in the leaves to the roots.

Having considered various physiological aspects of nitrogen and potassium nutrition of plants, we will try to apply them for explanation of the mechanism of [137]C hyperaccumulation.

On rich soils with a high content of nutrient cations, local flora does not require to follow the evolution path of the high specialization of the root transport systems in order to "catch" a scarce element, because the elements (including vital K) in these conditions are always in abundance. Therefore, these plants are characterized by non-specific type of K-transport system, LATS, which is able to effectively absorb not only K, but also its chemical analogues, including ^{137}Cs. High salt content is mostly typical of the arid landscapes' soils, which automorphic modes are characterized by the nonleaching water regime. According to Perelman and Kasimov (1999), local flora of arid landscapes is usually specified as so-called aridanite species characterized by active absorption of anionic elements (including NO_3^-) that have an increased bioavailability in an alkaline medium. Besides NO_3^-, plants reducing nitrates in the shoots by means of LATS rapidly absorb the nitrate counter-ion – K^+, and – if present in the soil – ^{137}Cs as well. At this, recirculation of K, particularly active in the K-deficient conditions, is reduced in aridanite species: when forming complexes with organic acids (that are formed in the reduction of nitrate nitrogen), K (and hence, "its follower" ^{137}Cs) is accumulated in the shoots, thus forming metabolically inert vacuolar pool. Such aspects of the physiology of plants as root absorption of NO_3^- and K^+, NO_3^- reduction in the aboveground phytomass, formation of excessive amounts of organic acids in shoots, and hyperaccumulation of ^{137}Cs are, in fact, links of a single chain – nitrate nutrition of aridanite species of plants.

From this standpoint, the fact that the vast majority of currently known ^{137}Cs hyperaccumulators are *Amaranthúceae* and *Chenopodiaceae* – representatives of the *Caryophyllales* – can be explained. A large part of the species in this order (and particularly in the abovementioned families) are aridanite plants adapted to growth in high salinity soil and arid climate of tropical and subtropical regions (Fyodorov, 1980).

Among other taxonomic groups, it is arid species that accumulate ^{137}Cs in shoots in excess. Thus, according to Zaidelman (2013), pioneering types of burned areas that have arisen on the site of the innings and are represented on the surface by peat combustion products (pyrogenic formations with extremely alkaline conditions) are common wormwood (*Artemisia vulgaris*) and bushgrass (*Calamagrostis epigeios*). The ability of these species to grow in extremely high pH conditions allowed us to assume that these species are likely to possess the ability to hyperaccumulation of ^{137}Cs, since they appear to have the abovementioned mechanism for neutralizing the excess of cations in the shoots. Having no own research data for these species, we found that our hypothesis is fully confirmed by the results of research fulfilled by Rakhimova in the Orenburg Region (Rakhimova, 2014; Yefremov et al, 2005). According to these results, in order to perform a phytomelioration of the soils contaminated with ^{137}Cs, it is proposed to use *Artemísia vulgáris* and *Calamagróstis epigéjos* as plant sorbents (able to effectively transport radionuclides from the root system to the aboveground phytomass). Others meliorants, referred to by Rakhimova, – tansy (*Tanacétum*) and yarrow (*Achilléa*) – are aridanite members of the *Asteraceae* family, just like wormwood; and therefore the excessive accumulation of ^{137}Cs in the aboveground organs is reasonable to expect. In this regard, the fact of the increased accumulation of ^{137}Cs in leaves and thin branches of the oak, established by us, is naturally-determined. Oak is an aridanite species that prefers soil with a neutral or slightly alkaline reaction, and even endures a moderate alkalinity (Pavlov et al., 1990). We have stated previously (Krivtsov et al., 2011) that oak actively absorbs anionic elements, especially NO_3^-, even in humid ecosystems of the mixed forests of South Meshchera. One of the links in this absorption is increased ^{137}Cs accumulation in shoots. This is consistent with the previously noted fact of recovering substantial part of nitrate nitrogen in the leaves of woody plants and, consequently, of the excessive synthesis in them of the agents neutralizing NO_3^- assimilation products – organic acids. Thus, the mechanisms of the ^{137}Cs accumulation by the oak's aboveground phytomass can be considered typical of aridanite species.

Besides the aridanite oak, reduced DF values were obtained by us also for humidokite species (according to Perelman and Kasimov (1999), species originating from humid areas and actively absorbing cations): aspen (leaves and thin branches from the different sampling regions) and birch (leaves of a tree growing on the highmoor bog). This, at first glance, contradicts the abovementioned mechanism of ^{137}Cs hyperaccumulation by aridanite species. It should not be forgotten, however, that the key point in our explanation is not the aridanite nature of plants, but the ability of plants to nitrate nitrogen enhanced nutrition and its recovery in the shoots. Aridanite nature of a plant is just one of the prerequisites for NO_3^- increased absorption. Another prerequisite defining NO_3^- absorption rate is connected with the specifics of the plant's life strategy. The main fundamental difference between plants with different types of strategies, according to Grime, is driven by the resources utilization efficiency, resistance to environmental stress, and relative growth rate. At the same time, according to Ivanov (2001), the species of ruderal growth strategy (fast-growing,

commonly weed plants) are characterized by enhanced uptake of nitrate nitrogen, accompanied by NR increased synthesis in leaves (Havill et al., 1974). This is an adaptation for NO_3^- rapid assimilation, which meets the requirements for ruderal plants' rapid growth.

Pioneer species of trees – birch and aspen – can be considered the analogue of the ruderal strategy species. According to Clough et al. (1989), it is pioneer tree species, typical of the initial stages of the secondary succession, that demonstrate an increased ability to reduce NO_3^- in leaves compared with the climax species. Thus, the abovementioned model of ^{137}Cs hyperaccumulation is applicable to typical humidokite species – birch and aspen; ^{137}Cs accumulation by them is determined by the specifics of their life strategy. Therefore, the increased ^{137}Cs concentrations, obtained by us, in the leaves of these trees are quite natural. We would like to note that our reasoning regarding the humidokite pioneer species are consistent with the study results of Willey et al. (2005), according to which, the taxa with transition stress-tolerant ruderal strategy are characterized by maximum accumulation of ^{137}Cs.

Reduced DF values, as follows from Table 1, are also characteristic of cowberry (*Vaccinium vitis-idaea*) shoots (plant of the *Ericaceae*). In this regard, it is noteworthy that the other representative of this family – common heather – is ^{137}Cs hyperaccumulator (Bystrzejewska-Piotrowska et al., 2005). At first sight, the heather's ability to store ^{137}Cs in the shoots in excess is rather unexpected. This type does not belong to either aridanite species (its present area, according to Sannikov et al. (2013) is most part of Europe, except for the arid regions of the Mediterranean and south-east of the East European Plain), or to ruderal species that actively absorb NO_3^-. Applying the method of plants' soil fertilizing with increased concentrations of NO_3^-, Havill et al. (1974) found that for the majority of *Ericaceae* there was no active NR in leaves, either before or after fertilizing. NR, being a substrate-inducible enzyme, has a constitutively low activity in some species, especially in most *Ericaceae*. Their low growth rate and preference for acidic, nutrient-poor soils are accompanied by a limited inducibility of NR in leaves, in spite of NO_3^- soil fertilizing. The exception to this rule is the *Calluna vulgaris* (and, according to Smirnoff et al. (1984), strawberry tree (*Arbutus unedo*). In these species, in contrast to the rest of the *Ericaceae*, NR activity increased significantly when feeding with NO_3^-. Consequently, *Calluna vulgaris* and *Arbutus unedo*, unlike other representatives of *Ericaceae*, are able to absorb nitrate-nitrogen and reduce it in the leaves thereby forming organic acids, which in turn can form complexes with K or ^{137}Cs. Thus, heather's identifying as one of the ^{137}Cs hyperaccumulators is natural and can be explained from the above said standpoint.

In our opinion, the cause of the heather's ability to absorb NO_3^- should be sought for in the features of the species' paleoareal. The heather's place of origin, according to Sannikov et al. (2013), could be the coast and the islands of subtropical and temperate zones of the East Atlantic. This is confirmed by the presence of heather in the Canary, Azores, British and Shetland Islands, Iceland, and the north-west of Morocco, as well as by the dominance and high vitality of its communities in the Atlantic coastal regions of Europe – from Iberia to the Kola Peninsula. Apparently, it is the evolution of *Ericaceae* in a wide variety of soil and environmental conditions that contributed to the preservation of heather's ability to absorb NO_3^- as the dominant source of inorganic nitrogen in a neutral and alkaline environment.

Presumably, our discussion concerning ^{137}Cs hyperaccumulation by *Ericaceae* can be used to a certain degree to explain the ability of a relatively close species – *Vaccínium vítis-idaéa* – to accumulate increased amounts of this radionuclide in the shoots. It should, however, be noted that, in contrast to the *Ericaceae*, hyperaccumulation trend is impermanent in the case of *Vaccínium vítis-idaéa*, manifesting itself during only one sampling season (early June). In other seasons the ^{137}Cs specific activity in the phytomass of the *Vaccínium vítis-idaéa* underground organs was higher than that in the phytomass of the aboveground organs. We emphasize that our findings are consistent with the idea of the seasonal NR activity dynamics in the plant's leaves. According to Clough et al. (1989), the maximum activity of this enzyme in photosynthetic organs of most species occurs at the beginning and the first half of the growing period and thus coincides with the period of maximum intensity of growth. In this regard, the assumption that NR activity in the *Vaccínium vítis-idaéa* shoots and ^{137}Cs hyperaccumulation trend are seasonally conditioned is feasible.

CONCLUSION

It can be concluded that the biological specifics of the plant are one of the factors determining the intensity of radionuclides uptake by plants and their accumulation in the phytomass of under- and

aboveground organs. The role of this factor in ^{137}Cs accumulation in biotic ecosystem is less than, for example, the impact of the soil type and moisture regime. However, at the stage of quasi-equilibrium state of radionuclide contamination, when there are no significant changes in the ^{137}Cs bioavailability in the soil, plants species' specifics can be an important factor determining the rate of ^{137}Cs absorption from the soil and its involvement in the biological cycle.

In this paper, we have shown that the fundamental difference in the accumulation of ^{137}Cs and K – elements of similar chemical, but fundamentally different biophile properties – lies in their contrasting distribution between phytomass of above- and underground organs. Biophile K actively goes into the shoots, while the translocation of toxic ^{137}Cs is limited by the root barrier. The selectivity degree of absorption and translocation of these elements is determined by the species' specifics of K-transport mechanisms of the plants' cells.

Another significant difference in the character of ^{137}Cs and K accumulation has been revealed for the aboveground phytomass of trees: the contrast ratio for the element distribution for ^{137}Cs is almost 3 times more than for K. However, the ^{137}Cs and K general distribution in fractions of the aboveground phytomass was on the whole similar and could be presented as a series "photosynthetic organs > thin branches > bark > wood".

Of particular interest are species accumulating increased amounts of ^{137}Cs not in the roots, but in the aboveground phytomass. These are either anatomically poorly differentiated organisms (mosses) or ancient vascular plants with a special selectivity of K-transport mechanisms (ferns). In addition, high level of ^{137}Cs is characteristic of photosynthetic organs and one-two-year shoots of oak, aspen, and birch. Based on the study of the physiological aspects of nitrogen and potassium nutrition of plants, we have suggested a possible explanation of the mechanism of ^{137}Cs hyperaccumulation in the aboveground phytomass of some species. Apparently, the root uptake of NO_3^- and K^+, NO_3^- reduction in the aboveground phytomass, the formation of excessive amounts of organic acids in shoots, and ^{137}Cs hyperaccumulation are, in fact, the links of a single process – enhanced nitrate nutrition of plants. Such nutrition is typical of aridanite species (e.g., oak) that actively absorb anionic elements (including NO_3^-) and of humidokite pioneer species (aspen and birch) that are characterized by high NR activity in leaves.

In conclusion, we would like to note that the mechanism of ^{137}Cs hyperaccumulation by plants, proposed by us, allows combining such important features of hyperaccumulators as their ability to the excess production of organic acids in the shoots, on the one hand, and the active uptake and transport of K at low selectivity of K-transport systems, on the other hand. However, we do not exclude the fact that for some ^{137}Cs hyperaccumulators these two most important aspects of physiology are unrelated. Such plants can be ones with constitutively high level of organic acids in shoots (e.g., a plant with crassulacean acid metabolism) and low selectivity of K-transport systems that may hyperaccumulate ^{137}Cs regardless of the intensity of their nitrate nutrition.

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