

Selective uptake, distribution, and redistribution of ^{109}Cd , ^{57}Co , ^{65}Zn , ^{63}Ni , and ^{134}Cs via xylem and phloem in the heavy metal hyperaccumulator *Solanum nigrum* L

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Abstract The focus of this article was to explore the translocation of ^{109}Cd , ^{57}Co , ^{65}Zn , ^{63}Ni , and ^{134}Cs via xylem and phloem in the newly found hyperaccumulator *Solanum nigrum* L. Two experiments with the uptake via the roots and transport of ^{109}Cd , ^{57}Co , and ^{65}Zn labeled by roots, and the redistribution of ^{109}Cd , ^{65}Zn , ^{57}Co , ^{63}Ni , and ^{134}Cs using flap label in *S. nigrum* in a hydroponic culture with a standard nutrient solution were conducted. The results showed that ^{109}Cd added for 24 h to the nutrient medium of young plants was rapidly taken up, transferred to the shoot, and accumulated in the cotyledons and the oldest leaves but was not efficiently redistributed within the shoot afterward leading to a rather low content in the fruits. In contrast, ^{57}Co was more slowly taken up and released to the shoot, but afterward, this element was redistributed from older leaves to younger leaves and maturing fruits. ^{65}Zn was rapidly taken up and transferred to the shoot (mainly to the youngest leaves and not to the cotyledons). Afterward, this radionuclide was redistributed within the shoot to the youngest organs and finally accumulated in the maturing fruits. After flap labeling, all five heavy metals tested (^{109}Cd , ^{57}Co , ^{65}Zn , ^{63}Ni , ^{134}Cs) were exported

from the labeled leaf and redistributed within the plant. The accumulation in the fruits was most pronounced for ^{63}Ni and ^{65}Zn , while a relatively high percentage of ^{57}Co was finally found in the roots. ^{134}Cs was roughly in the middle of them. The transport of ^{109}Cd differed from that previously reported for wheat or lupin and might be important for the potential of *S. nigrum* to hyperaccumulate cadmium.

Keywords Heavy metals · Radioisotopes · Translocation · Hyperaccumulator · *Solanum nigrum* L

Introduction

Cleaning heavy metal-contaminated soil is a challenge in various regions throughout the world (Zhou and Song 2004). Phytoremediation mainly using hyperaccumulator plants to remove heavy metals from contaminated soils is considered as a promising method (Sun et al. 2005). Hyperaccumulators are plants characterized by the possibility to accumulate heavy metals to high levels. Usually, the main characteristics of a hyperaccumulator can be summarized as follows: (1) accumulation property, i.e., the minimum concentration in the shoots of a hyperaccumulator for As, Pb, Cu, Ni, and Co should reach values above $1,000\text{ mg kg}^{-1}$ dry mass, for Zn and Mn above $10,000\text{ mg kg}^{-1}$, for Au above 1 mg kg^{-1} , and for Cd above 100 mg kg^{-1} according to Baker and Brooks (1989); (2) translocation property, elemental concentrations in the shoots of a plant should be higher than those in roots, i.e., $\text{TF} > 1$ (translocation factor, concentration ratio of shoots to roots) (Chaney et al. 1997); (3) enrichment property (enrichment factor—EF, concentration ratio of plant to media), EF value in shoots of plants should

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be higher than 1 (Wei et al. 2005); and (4) tolerance property, a hyperaccumulator should tolerate high levels of heavy metals. In plants tested under experimental conditions, their shoot biomass should not decrease significantly when growing in contaminated media (Wei et al. 2005).

Some mechanisms involved in the hyperaccumulation of heavy metals have been reported in the past. Lu et al. (2010) explored the role of Ca pathway in Cd uptake and translocation by the hyperaccumulator *Sedum alfredii* (Lu et al. 2010). The effects of phosphorus on the transportation of arsenic were investigated in *Pteris vittata* uptake and lead to the conclusion that As(V) and P behave similarly in *P. vittata* rhizoids (Sun et al. 2007a, b). Sun et al. (2007a, b) suggested that antioxidative defense and proline/phytochelatin accumulation may be relevant in *Solanum nigrum* L. hyperaccumulating Cd. Furthermore, effects of heavy metals on the metabolism of glutathione, phytochelatin, and non-protein thiols as well as on nitrogen metabolism were identified by several groups (Sun et al. 2007a, b; Zeng et al. 2009; Wang et al. 2008). The uptake and translocation of heavy metals in hyperaccumulators were less often addressed. However, the transport and mobility of heavy metals in non-hyperaccumulators such as castor bean, wheat, rice, and white lupin have been studied in several laboratories. In castor bean, Mn, Zn, Co, and Fe were confirmed to be transported via the phloem (Schmidke and Stephan 1995). In long-distance transport, nicotianamine might play an important role for the regulation of metal transfer (Takahashi et al. 2003). Usually, Zn and Cd are transported in the phloem (presumably by similar pathways) (Grant et al. 1998; Erenoglu et al. 2002), but the transport of these two elements via the phloem was found to be quite different in wheat (Riesen and Feller 2005). It was found that in rice, Zn was transported more rapidly from older to younger leaves under Zn deficiency than under adequate Zn supply (Hajiboland et al. 2001). Page et al. (2006) determined the differences of ^{109}Cd , ^{57}Co , ^{65}Zn , and ^{63}Ni uptake, transport, and redistribution in white lupin. The transport of various heavy metals via xylem and phloem may vary between elements in non-hyperaccumulators (Marschner 1995). The long-distance translocation must be considered as an important aspect for the overall behavior of such plants.

S. nigrum represents a recently identified Cd hyperaccumulator (Wei et al. 2005). The aim of this study was to determine for this species the selectivity for various heavy metals at the level of the uptake via the roots, the transfer to the shoot, and the further redistribution within the shoot. Radioisotopes of heavy metals (^{109}Cd , ^{57}Co , ^{65}Zn , ^{63}Ni) allowed a sensitive detection of these elements and a comparison with the cesium isotope ^{134}Cs (well mobile in plants like potassium). The acquisition of heavy metals via the roots, the distribution, and further redistribution are highly relevant in the context of hyperaccumulation and phytoremediation. Especially the root-to-shoot transfer and

the accumulation in various shoot parts must be considered in this context.

Materials and methods

Source of seeds

Seeds of *S. nigrum* collected at Shenyang Ecological Experimental Station, Chinese Academy of Sciences (41° 31' N and 123° 41' E) were germinated on paper with 0.1 % (w/v) KNO_3 and grown afterward hydroponically on standard nutrient medium (see below) to fruit maturity. Seeds were collected, incubated for 2 h in 0.15 N HCl and then washed repeatedly with deionized water prior to air drying on filter paper. Seeds from one single plant were used for the experiments reported here.

Uptake via the roots and transport of ^{109}Cd , ^{57}Co and ^{65}Zn in *S. nigrum*

Seeds of *S. nigrum* were soaked in 0.1 % (w/v) KNO_3 for 1 day at 4 °C and then germinated for 9 days on filter paper moistened with 0.1 % (w/v) KNO_3 in a 14-h light/10-h darkness cycle and then grown on standard nutrient medium for 3 days under the same light and temperature regime. Roots of equally developed seedlings were then placed for 24 h in small tubes containing 3 ml standard nutrient solution with the radioisotopes ^{109}Cd (30.2 Bq per plant), ^{57}Co (1.5 Bq per plant), and ^{65}Zn (19.8 Bq per plant). Standard nutrient solution contained 6 mM KH_2PO_4 , 3 mM MgSO_4 , 1.36 mM $\text{Ca}(\text{NO}_3)_2$, 0.88 mM KNO_3 , 30 μM Fe (added as Fe-EDDHA), 1 μM MnCl_2 , 5 μM H_3BO_3 , 0.16 μM ZnSO_4 , 0.2 μM Na_2MoO_4 , 0.048 μM $\text{Ni}(\text{NO}_3)_2$, 0.1 μM CuSO_4 (Page et al. 2006). After labeling, roots were dipped two times sequentially in 200 ml H_2O to remove radioactive solutes from the root surface and placed for 2 h in nutrient solution with 0.1 % Congo red to allow the identification of the root part initially labeled with radioisotopes of heavy metals after further development of the root system. Then, the roots were washed three times to remove excessive dye and incubated for 1 h on nutrient solution. Thereafter, the seedlings were transferred to standard nutrient solution (initially three plants per pot containing 240 ml standard nutrient solution). Plants were grown in a culture room in the Institute of Plant Sciences, University of Bern with a temperature of 20 °C during the night and 25 °C during the day. The photoperiod was 14 h light (200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ from 4 Lumilux, Osram FQ 39 W/840 HO and 4 Lumilux, Osram FQ 39 W/830 HO) and 10 h night. The nutrient solution was exchanged weekly. Plants were harvested at 0, 3, 8, 15, 22, 29, 36, 43, 50, and 57 days after labeling (four replicates from different pots per time point). The collected plants were dissected into roots,

cotyledons, leaves 1/2, leaves 3/4, leaves 5/6, leaves 7/8, younger leaves, stem, and flowers/fruits. Leaves were numbered from the oldest leaf (leaf 1) to the youngest leaves. Plants were harvested at the time points indicated and all plant parts were collected. The various organs were separated, dried at 60 °C and their radionuclide contents were analyzed simultaneously at the end of the experiment.

Redistribution of ^{109}Cd , ^{65}Zn , ^{57}Co , ^{63}Ni , and ^{134}Cs in *S. nigrum*

Seeds of *S. nigrum* were germinated as mentioned above and then grown on standard nutrient solution. When all plants were flowering (58 days after germination), radiolabels were introduced via a flap into the uppermost fully expanded leaf (Riesen and Feller 2005). Standard nutrient solution (1.5 ml) containing a combination of ^{109}Cd and ^{65}Zn for one series or of ^{109}Cd , ^{57}Co , ^{63}Ni , and ^{134}Cs for the other series was introduced from an Eppendorf tube into the cut xylem of the flap (mainly into the midrib). Radionuclides were purchased from Amersham Biosciences UK Limited (^{109}Cd , ^{57}Co , ^{63}Ni , and ^{134}Cs) and from PerkinElmer, Inc. (^{65}Zn). The use of nutrient solution for flap feeding was suitable, since the ions present in this solution reduced unspecific binding of radionuclides to cell walls and caused no damages to the labeled leaves. The activities applied per plant were 7.8 Bq for ^{109}Cd , 1.4 Bq for ^{65}Zn , 0.7 Bq for ^{57}Co , 162.1 Bq for ^{63}Ni , and 1.4 Bq for ^{134}Cs . Plants absorbed most of the feeding solution within 48 h. After 5 days (four replicates) and 55 days (six replicates), plants were dissected into roots, stem, fruits, labeled leaf (including the flap), and other leaves (not directly labeled via a flap). All plant parts were collected at both harvest dates, and the various organs were dried at 60 °C prior to analyzing the radioisotopes as reported previously (Riesen and Feller 2005).

Sample analyzing and data processing

The radioactivity of ^{109}Cd , ^{57}Co , ^{65}Zn , and ^{134}Cs was detected in a gamma counter (1480 Wizard 3', Wallac Oy, Turku, Finland, Institute of Plant Sciences, University of Bern) with a counting time of 40 min per sample. For ^{63}Ni measurement, plant parts were ashed afterward at 550 °C during several days. After cooling, the ash was dissolved in 0.2 ml 10 N HCl and then 2 ml H_2O was added to each sample. After mixing, 200 μl was transferred to Ready Caps (Beckman Instruments, Fullerton, CA, USA) and dried at 60 °C for 4 h. The radioactivity of ^{63}Ni was measured in a liquid scintillation counter with a counting time of 10 min and contributions from the other isotopes were deduced. Means and standard errors were calculated from the replicates and are shown in the graphs.

Results

Uptake and transport of ^{109}Cd , ^{57}Co and ^{65}Zn added to the nutrient medium

The levels of ^{109}Cd , ^{57}Co , and ^{65}Zn in various plant parts are shown in Fig. 1. The results are presented in percent of the initially added quantity to document the uptake into the plants and to allow a comparison between the three elements. Since the three radioisotopes were applied simultaneously to the same plants and quantified afterward by γ -spectrometry, direct comparisons are possible. ^{109}Cd and ^{65}Zn were essentially completely taken up into the plants during the labeling period of 24 h, while the total amount in the plants was considerably lower for ^{57}Co . Plants for the analyses of initial labeling (day 0) were unfortunately collected with a delay after all other plants were first transferred to the new nutrient medium and then carefully fixed in the pots for further growth. This point may explain the rather low content of radionuclides in these samples (release of ions from the apoplast into the medium and no possibility for reabsorption afterward) and the large standard errors (Fig. 1 and Table 1). Therefore, these values must be interpreted with caution. ^{109}Cd and ^{65}Zn were rapidly taken up and transported to the shoot, while a considerable portion of ^{57}Co was not taken up by the plants (Table 1). Furthermore, the root-to-shoot transfer occurred for ^{57}Co more slowly than for the other radionuclides. At the end of the experiment, a considerable portion of ^{65}Zn was present in the mature fruits, but only a very small quantity of ^{109}Cd reached the reproductive plant parts. Although only a small quantity of ^{57}Co was transported to the shoot, this radionuclide was further redistributed within the shoot and accumulated in the fruits. After day 20, the total content of ^{109}Cd and ^{65}Zn per plant declined considerably and to a minor extent the level of ^{57}Co decreased also. These decreases can be explained by a loss of senesced leaves containing still radionuclides.

A more detailed analysis of various shoot parts allowed a deeper insight into the redistribution within the shoot but was only possible as long as no senesced leaves were lost (Fig. 2). It became evident that ^{109}Cd was released rapidly from the roots and reached the cotyledons and the oldest leaves where it remained for several weeks. Only a minor percentage of this radioisotope was transported to younger leaves, stem, and maturing fruits. These findings imply that ^{109}Cd was rapidly transported via the xylem to the shoot but was afterward only very slowly redistributed within the shoot via the phloem. A different transport pattern was observed for ^{57}Co which was slowly released from the roots to the shoot (primarily to leaves 1/2 and not to the cotyledons) but was then efficiently redistributed to younger leaves and fruits indicating a good phloem mobility. ^{65}Zn was released from the roots with a similar time course as ^{109}Cd , but in the shoot, it was initially mainly detected in leaves 1/2 and not in the already fully

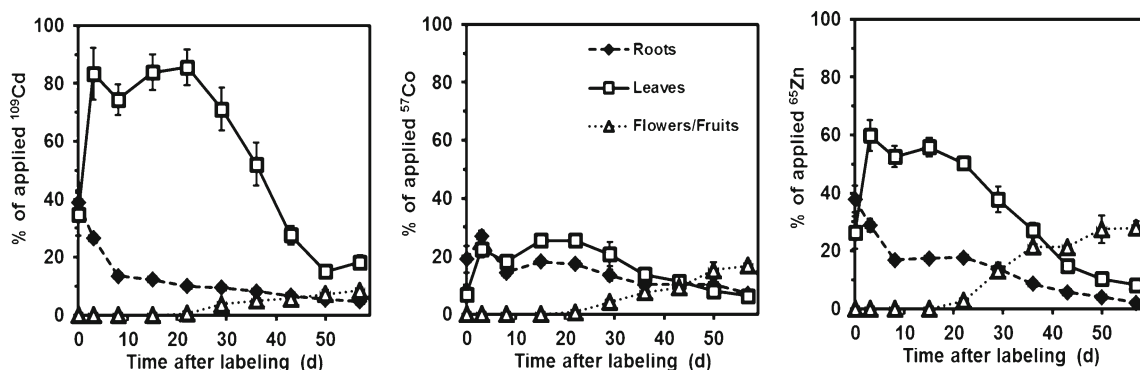


Fig. 1 Contents of radionuclides in roots, leaves, and flowers/fruits. The radionuclides ¹⁰⁹Cd, ⁵⁷Co, and ⁶⁵Zn were introduced into young plants before day 0 via the roots. The radionuclide translocation was analyzed

throughout plant development and fruit maturation. Means and standard errors (n=4) are shown

expanded cotyledons. Later, ⁶⁵Zn was repeatedly redistributed within the shoot via the phloem and accumulated finally to a rather high level in the mature fruits. After day 36, this more detailed analysis was no longer possible, since senesced leaves were lost from the plants and clear identifications were no longer possible. It appears likely that with the senesced leaves, radioisotopes still present in them were lost (especially ¹⁰⁹Cd).

The transfer factor (label in shoot/label in roots) increased initially for all three radioisotopes (¹⁰⁹Cd, ⁵⁷Co, and ⁶⁵Zn) and reached for ⁵⁷Co and ⁶⁵Zn highest values at the final harvest (Table 1). However, a decline of this value was observed for ¹⁰⁹Cd at the last harvest dates caused by the loss of senesced leaves, since this radionuclide was strongly retained in the oldest leaves and poorly redistributed within the shoot.

Redistribution of ¹⁰⁹Cd and ⁶⁵Zn or ¹⁰⁹Cd, ⁵⁷Co, ⁶³Ni and ¹³⁴Cs via flap label

The export from a mature leaf via the phloem was directly addressed by introducing the radioisotopes into a fully expanded leaf through a flap cut in the middle of the leaf (mainly midrib) as described previously for wheat (Riesen and Feller 2005). ¹³⁴Cs was included as a highly phloem-mobile solute which can be detected with the same technique. Two sets of plants were used for this experiment to avoid problems with the simultaneous detection of low amounts of ⁶⁵Zn and ¹³⁴Cs: one set with ¹⁰⁹Cd and ⁶⁵Zn (Fig. 3) and another set with ¹⁰⁹Cd, ⁵⁷Co, ⁶³Ni, and ¹³⁴Cs (Fig. 4). A higher percentage of ⁶⁵Zn than of ¹⁰⁹Cd was exported from the labeled leaf (Fig. 3).

Table 1 Total contents and root-to-shoot transfer of the radionuclides ¹⁰⁹Cd, ⁵⁷Co, and ⁶⁵Zn in *Solanum nigrum* plants. Means and standard errors (n=4) are shown

Time after labeling (days)	Total label in plants (% of label added to nutrient medium)			Transfer factor (label in shoot/label in roots)		
	¹⁰⁹ Cd	⁵⁷ Co	⁶⁵ Zn	¹⁰⁹ Cd	⁵⁷ Co	⁶⁵ Zn
0	73.83±10.35	25.83±6.86	64.26±10.17	0.89±0.15	0.34±0.07	0.66±0.08
3	110.11±8.30	49.34±4.62	88.77±5.94	3.18±0.46	0.83±0.06	2.11±0.27
8	88.07±5.67	32.60±2.58	69.53±4.29	5.51±0.35	1.30±0.16	3.09±0.13
15	100.03±6.29	46.22±2.31	77.77±3.11	7.10±0.55	1.55±0.06	3.48±0.33
22	100.49±6.83	47.32±1.48	75.52±3.73	9.00±0.73	1.74±0.12	3.24±0.06
29	91.63±10.25	43.18±7.71	71.13±9.46	8.51±0.63	2.16±0.23	4.09±0.41
36	71.37±8.33	34.45±3.73	61.49±3.90	7.65±0.85	2.48±0.40	6.13±0.28
43	45.06±2.82	32.76±1.38	44.35±1.70	5.80±0.78	2.30±0.27	6.91±0.61
50	33.22±5.22	36.30±4.77	43.28±5.72	5.11±0.38	2.53±0.09	9.51±1.32
57	36.11±3.35	31.85±2.76	39.31±3.40	6.46±0.40	3.56±0.38	17.34±0.65

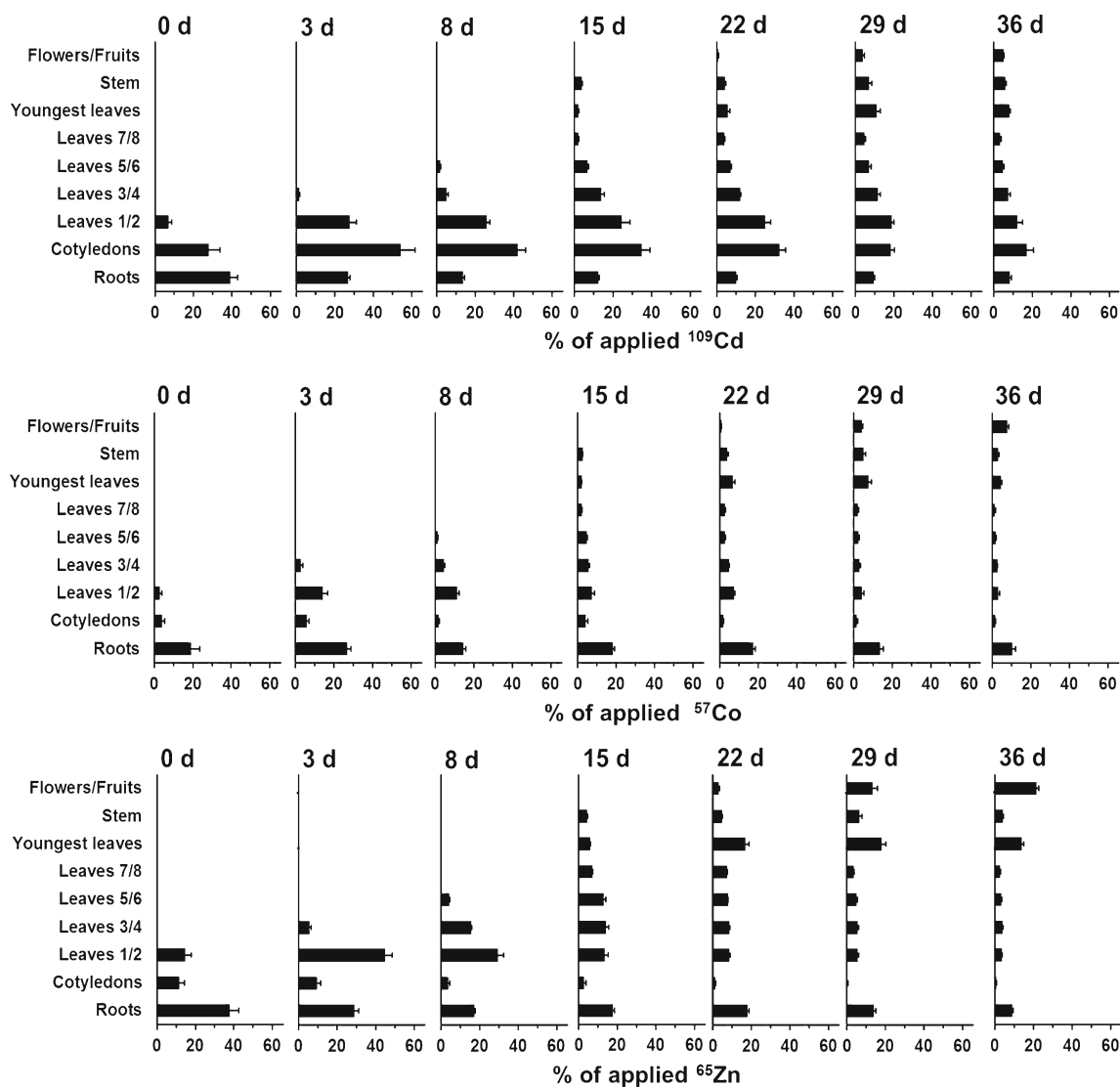


Fig. 2 Transport of ^{109}Cd , ^{57}Co , and ^{65}Zn to various leaves and remobilization from these leaves during vegetative and early reproductive growth. The radionuclides were introduced into young plants before day 0 via the roots. Means and standard errors ($n=4$) are shown

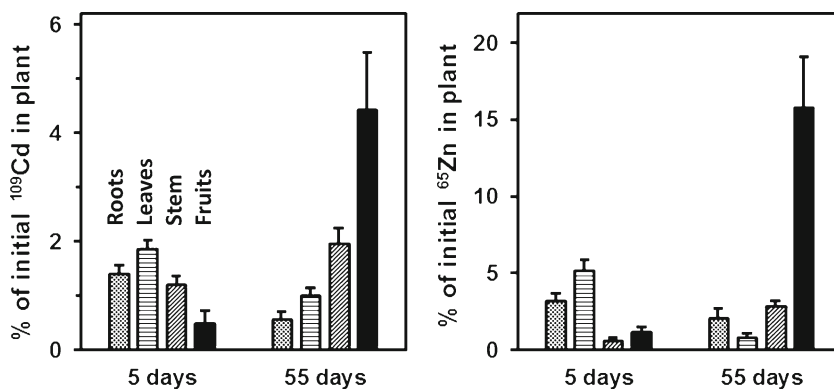
^{109}Cd was transported to various vegetative plant parts and also to the fruits. At the end of the experiment, a considerable portion of ^{109}Cd was still present in the leaves and in the stem, while a strong accumulation in the fruits and only low levels in the vegetative plant parts were observed for ^{65}Zn after 55 days. The ^{109}Cd pattern was very similar in both sets of plants indicating that this redistribution was highly reproducible (Figs. 3 and 4). ^{57}Co was exported from the labeled leaf and transported to roots, other leaves, stem, and fruits. It should be kept in mind that for this radioisotope, a large quantity was still present in the roots at the final harvest. This indicates that ^{57}Co is also retained in the roots when entering them from the shoot via the phloem. The mechanism for the retention is not

yet known. ^{63}Ni represents a highly mobile micronutrient and behaved similar to ^{65}Zn with respect to the redistribution within the shoot and final accumulation in the fruits. The final accumulation in the fruits was for ^{65}Zn and ^{63}Ni even more pronounced than for the highly phloem-mobile ^{134}Cs (behaving similar to the macronutrient potassium).

Discussion

In general, the relative mobility of the investigated heavy metals was in the Cd hyperaccumulator *S. nigrum* similar to that previously reported for wheat and lupin (Riesen and Feller

Fig. 3 Redistribution of ^{109}Cd and ^{65}Zn via the phloem. Radionuclides were introduced via a flap cut into the uppermost fully expanded leaf after the beginning of flowering. Plants were analyzed 5 and 55 days after labeling. “Leaves” include all leaves except the initially labeled leaf with the flap. Means and standard errors are shown ($n=4$ for day 5 and $n=6$ for day 55)



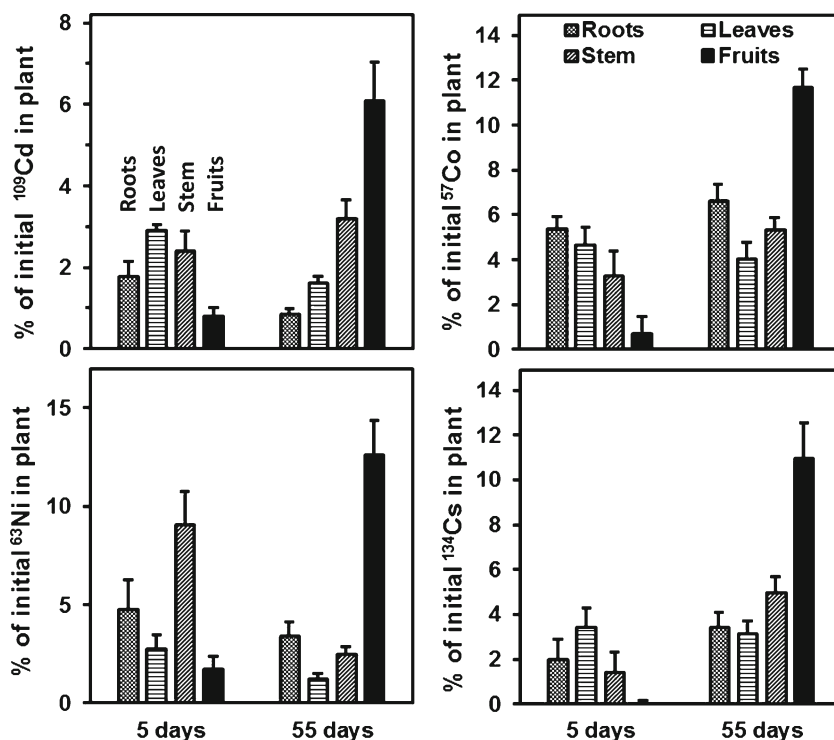
2005; Page et al. 2006). However, the strong initial retention and the slow release of ^{109}Cd to the shoot as it is known from wheat and lupin were not observed in *S. nigrum*. In contrast, ^{109}Cd was rapidly transported to the shoot. This heavy metal accumulated in the cotyledons and in leaves 1/2 of *S. nigrum* and remained there for several weeks. These findings indicate that this heavy metal was loaded efficiently into the xylem in the roots, reached afterward the photosynthetically active leaves via the transpiration stream and was not only slowly redistributed via the phloem within the shoot.

Once more, the high mobility of zinc and nickel in the phloem was confirmed. These micronutrients are apparently well redistributed via the phloem in cereals, legumes, and also

in the hyperaccumulator *S. nigrum* (Riesen and Feller 2005; Page et al. 2006). These two elements were repeatedly exported from older shoot parts and transported to developing organs and reached at the end quite high levels in the fruits. The various heavy metals are characterized by specific transport patterns on the whole level.

Another interesting point concerns the accumulation of ^{57}Co in the roots. When this radioisotope is applied via the nutrient medium, it appears possible that it does not reach the central cylinder in these roots and can as a consequence not be released into the xylem. However, ^{57}Co introduced into a leaf was transported to the roots and accumulated there. In this case, ^{57}Co is already in the central cylinder. Therefore, the

Fig. 4 Redistribution of ^{109}Cd , ^{57}Co , ^{63}Ni , and ^{134}Cs via the phloem. Radionuclides were introduced via a flap cut into the uppermost fully expanded leaf after the beginning of flowering. Plants were analyzed 5 and 55 days after labeling. “Leaves” include all leaves except the initially labeled leaf with the flap. Means and standard errors are shown ($n=4$ for day 5 and $n=6$ for day 55)



transport across the endodermis was not the crucial point. This element was retained in the roots after addition to the nutrient medium as well as after foliar application. The chemical form, the distribution on the tissue level, and the subcellular compartmentation are not yet known. It remains to be elucidated in the future how and to which extent the transport via xylem and phloem is influenced by the level of heavy metals in the root medium.

The rapid transfer to the shoot and the accumulation in leaves and stem are important properties of the hyperaccumulator *S. nigrum*. The long-distance transport characteristics for ^{109}Cd in this species are promising. On contaminated soils in the field, harvesting twice *S. nigrum* at the flowering stage might be more effective than one single harvest at full maturity (Wei et al. 2006).

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