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ORIGINAL PAPER

ACCUMULATION, DISTRIBUTION AND REDISTRIBUTION OF ^{109}Cd AND ^{65}Zn IN WHEAT (*TRITICUM AESTIVUM* L.) AND BEAN (*PHASEOLUS VULGARIS* L.) PLANTS ON NUTRIENT MEDIA WITH ELEVATED ZINC OR CADMIUM*

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ABSTRACT

The aim of the work was to identify the effects of elevated zinc or of cadmium on the dynamics of previously introduced ^{65}Zn and ^{109}Cd, considering especially the effects of high zinc supply on ^{109}Cd and of cadmium on ^{65}Zn transport and redistribution in the whole plant. The translocation of radiolabelled zinc (^{65}Zn) and cadmium (^{109}Cd) was compared in wheat (*Triticum aestivum* L.) and in bean (*Phaseolus vulgaris* L.) plants, considering the root-to-shoot transport and further redistribution within the shoots. Visible symptoms of heavy metal toxicity were observed in both plant species. Dry matter was reduced by increased Cd, but not by increased Zn. At day 12 (but not before), the dry matter of bean roots and of trifoliate 1 was significantly lower in plants subjected to increased Cd in the nutrient medium than in control plants, while other bean organs were not significantly affected. In contrast, dry matter in wheat was significantly lowered by increased Cd supply only in the youngest (4th) leaf at day 3 (but not afterwards and not in roots or other leaves). ^{65}Zn was translocated more rapidly than ^{109}Cd from roots to the aerial parts in both species, but this transport was more efficient in wheat than in bean. Strong accumulation in the roots was observed for ^{109}Cd. An increased Zn concentration in the nutrient medium, but not Cd, negatively influenced the root-to-shoot transfer of ^{65}Zn in bean plants. The redistribution of ^{65}Zn from primary leaves to the youngest trifoliate leaves was also negatively affected by an increased Zn supply. In wheat plants, an increased Zn concentration in the nutrient medium also negatively influenced the root-to-shoot transfer of ^{65}Zn, as well as the redistribution of this radionuclide from the oldest to the youngest leaves. Transport

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and distribution of zinc and cadmium differed clearly between bean and wheat, but effects of increased zinc on cadmium transport and *vice versa* were less pronounced than expected.

Keywords: xylem, phloem, cereals, legumes, heavy metals, hydroponic culture, radioisotopes

INTRODUCTION

Intensive mining processes as well as industrial and agricultural progress the main reasons for high levels of heavy metals (HM) in agricultural soils (Lim et al. 2013). Application of phosphate fertilizers, untreated wastewater, contaminated sewage sludge and manure are the main sources of cadmium pollution (Cd). Subsequent utilization of these contaminated soils for crop production is a risk to human and animal health. Plant Cd accumulation potential depends on various factors, such as Cd availability and mobility in the soil and its subsequent uptake by the roots and translocation via the xylem to the shoots (Sarwar et al. 2010). The presence of Cd may result in various morphological and physiological changes, including growth inhibition, leaf rolling, chlorosis and necrosis (Benabid, Ghorab 2013), reduced stomatal conductance and lowered transpiration rate (Saifullah et al. 2014). Inhibition of photosynthesis (Malčovská et al. 2014, Tuma, Svojanovska 2015), imbalance of mineral nutrients (Gouia et al. 2000), induction of oxidative stress (Malčovská et al. 2014), and modifications of gene expression (Herbette et al. 2006) are other characteristic processes typical for excess of Cd. Cd^{2+} ions can also compete with other cations (e.g., Na^+, Ca^{2+} and Zn^{2+}) for transmembrane carriers (Tudoreanu, Phillips 2004).

Zinc (Zn) is an essential trace element, which has many biological functions in plants and is a component of many proteins in plants. In excess, however, it can become toxic (Tuma et al. 2008, Tuma, Svojanovska 2015), with typical symptoms like chlorosis of young leaves or inhibition of photosynthesis (Vaillant et al. 2005). The close relationship between Cd and Zn, which results from similar geochemical and environmental properties, could result in their interactions during the uptake, transport, accumulation, and their functions in plants (Mohammad, Moheman 2010). Generally, these interactions are considered antagonistic. It is known that Zn can minimize accumulation of Cd by plants (Benáková et al. 2017). Nutrient dynamics, yield and quality of harvested products are the main plant properties affected by these interactions (Sanaeiostovar et al. 2011). Based on the above considerations, it can be hypothesized that an increased zinc supply affects cadmium uptake and cadmium dynamics in plants, and *vice versa* an increased cadmium supply influences zinc dynamics in crop plants.

Common bean (*Phaseolus vulgaris* L., Fabaceae) is one of the most important food legumes of developing countries and in the Middle East (Howladar 2014). Wheat (*Triticum aestivum* L., Poaceae) belongs to the most important economic crops worldwide, and is cultivated on a global scale.

Cereal products are estimated to account for approximately 40% of alimentary Cd in Europe (Greger, Landberg 2008) with possible Cd translocation to grains (Harris, Taylor 2013). It has been reported previously that the Cd and Zn release to the shoots and the subsequent redistribution within the shoots differ considerably between cereal (Page, Feller 2005) and legume (Page et al. 2006) species. Subcellular compartmentation (Kupper et al. 2000, Yang et al. 2006), presence of heavy metal chelators (Stolt et al. 2003, Richau et al. 2009, Hazama et al. 2015), loading into the xylem in roots (Miyadate et al. 2011) and phloem mobility (Page, Feller 2005, Page et al. 2006, Hazama et al. 2015) are key points for the relative mobilities of Cd and Zn in various plant species.

Classical breeding programs as well as the production of transgenic plants can lead to producing crop varieties (Arao, Ishikawa 2006, Li, Zhou 2012) with high (e.g. for biofortification or soil remediation) or low (e.g. for food and feed production on polluted soils) Cd and Zn content (Kramer, Chardonnens 2001, Welch, Graham 2002). The physiological processes leading to increased or decreased Cd and/or Zn levels are highly relevant in this context on the species level as well as on the variety level.

The questions of Cd and Zn uptake and partitioning were addressed during the past decades in several investigations on wheat (Page, Feller 2005, Harris, Taylor 2013) and legumes (Page et al. 2006). Furthermore, the influence of ammonium (Cheng et al. 2018) and of nitrate (Wang et al. in press) on Cd/Zn interactions in wheat have been comprehensively reviewed more recently. The focus of these publications was the translocation and the distribution (including subcellular distribution) of Cd and Zn, and the findings led to the conclusion that the chemical form of a nitrogen source influences the interactions between these two heavy metals. However, little is known about the influence of changes in the nutrient medium (e.g. a drastic increase in the Cd or Zn concentration in a medium) on the dynamics of Cd and Zn previously present in the plants.

One cereal and one legume were used in the experiments reported here, as these are among the major crop plants grown throughout the world. The aim of this study was to compare the redistribution of Cd and Zn in the whole plant of wheat (cereal) and dwarf bean (legume). Radionuclides are often used as tools for detailed investigations of the distribution and further redistribution of toxic elements in different biological systems (Page, Feller 2005, Page et al. 2006, Benabid, Ghorab 2013). Therefore, radioisotopes of these two heavy metals, ^{109}Cd and ^{65}Zn, were chosen for sensitive detection of their content in roots, the root-to-shoot translocation and further redistribution within the shoots after a drastic increase of the Cd or Zn concentrations in a nutrient medium. Since Cd and Zn previously present in the plants were radiolabelled and the additionally supplied heavy metals were unlabelled, it became possible to selectively investigate the effects of the high external concentrations on the dynamics of Cd and Zn previously present in the plants.

MATERIALS AND METHODS

Seeds of wheat (*Triticum aestivum* L. cv. Rubli) and bean (*Phaseolus vulgaris* L. cv. Saxa) were germinated on wet tissue paper (14 days and 2 days, respectively) in a plastic dish at 19 - 23°C and 14 h/10 h day/night cycle. Beans were transferred after 2 days to wet coarse quartz sand, while wheat plants remained on wet tissue paper. Afterwards, bean plants (12 days old) and wheat plants (14 days old) were transferred to a standard nutrient solution containing 5.8 mmol dm^{-3} KH_2PO_4, 3 mmol dm^{-3} $MgSO_4$, 1.3 mmol dm^{-3} $Ca(NO_3)_2$, 0.88 mmol dm^{-3} KNO_3, 64 μmol dm^{-3} Fe-EDDHA, 0.98 μmol dm^{-3} $MnCl_2$, 4.93 μmol dm^{-3} H_3BO_3, 0.17 μmol dm^{-3} $ZnSO_4$, 0.2 μmol dm^{-3} Na_2MoO_4, 0.05 μmol dm^{-3} $Ni(NO_3)_2$, 0.11 μmol dm^{-3} $CuSO_4$ (Page et al. 2012). After 5 days of cultivation on this nutrient medium, plants were placed for 48 h in pots with 125 ml of the standard nutrient solution with a mixture of the two radioisotopes ^{109}Cd (30.2 Bq per plant) and ^{65}Zn (19.8 Bq per plant). Three plants were in each pot, bean and wheat separately. After labelling, roots were dipped two times sequentially in 200 ml H_2O to remove radioactive solutes from the root surface. Next, six plants (3 wheat and 3 beans plants per pot) were placed in a pot with 900 ml of the standard nutrient solution.

Plants were grown in a culture chamber under the following conditions: photoperiod of 14/10 h day/night (150 μmol photons m^{-2} s^{1}) with temp. of 23°C/19°C day/night, and relative humidities of 30-33%/36-39% day/night. Three different variants were chosen, each in four replications: control with no added unlabelled Cd or Zn; 2Cd (2 μmol dm^{-3} Cd added); 20Zn (20 μmol dm^{-3} Zn added). Plants were harvested 3, 6 and 12 days after labelling (four replicates from different pots for each time point). Collected bean plants were dissected into the roots, primary leaves, stem, trifoliate 1 (the oldest), trifoliate 2, trifoliate 3 and trifoliate 4 (the youngest). Wheat plants were dissected into the roots, leaf 1 (the oldest), leaves 2, 3, 4, 5 and leaf 6 (the youngest) and tillers. Separated organs were dried at 60°C to determine the dry matter (DM), and subsequently the radionuclide content was analysed. The radioactivity of ^{109}Cd and ^{65}Zn was detected in a gamma counter (1480 Wizard 3′, Wallac Oy, Turku, Finland) with a counting time of 40 min per sample.

Student's *t*-test at the $P<0.05$ level was used to identify significant differences between variants (Statistica ver. 10.0, Analytical Software, Tallahassee FL, USA). Results shown in figures represent means + SE of 4 independent replicates.

RESULTS AND DISCUSSION

Visible symptoms of heavy metal toxicity were observed in both plant species, being more evident in bean than in wheat plants. In bean plants, leaf chlorosis appeared in both primary and in trifoliate leaves, and was evident already 3 days after labelling in variant 2Cd. The symptoms became more pronounced afterwards, which finally led to massive leaf yellowing. In addition, leaves of 2Cd plants were markedly smaller and senesced earlier than those of control plants. There were no visible differences between the control and 20Zn variants. In wheat plants, a slightly reduced plant size was observed in 20Zn variant compared with the other treatments. This variant was also characterized by a brighter colour of the leaves. Chlorosis suggested that toxic effects of Cd mainly affected leaves, which are more sensitive to Cd than the other parts of bean plants. We also observed darkening and browning around the leaf veins in this plant. This is consistent with the report by Page et al. (2006), who observed small quantities of ^{109}Cd in all parts of the leaves, but a large amount of this element was located in the major leaf veins. It has also been documented that the general symptoms of excess Zn are leaf chlorosis, root browning, stunting of shoot, curling and rolling of young leaves, death of leaf, reduction of the chlorophyll content (Rout, Das 2009, Tuma, Svojanovska 2015). In our experiment, the response of the two species to elevated Zn supply differed, as only subtle lightening of leaves was observed in wheat plants.

A decrease in the plant height and biomass production is considered to be the first indication of Cd toxicity, as previously reported by Ekmekçi et al. (2008). Because the symptoms of toxicity can appear during different developmental stages (Sarwar et al. 2010) and one of our aims was to elucidate redistribution processes within the shoot, various time periods of harvesting after the labelling with radionuclides were chosen. In our experiment, this negative effect was detectable also after a longer time lapse. The reduction of DM (Figure 1) in some leaves was detectable after 6 days, and became more evident after 12 days. It is interesting to notice that Cd addition to a nutrient medium for bean caused a stronger decrease in DM (especially in trifoliate 1) than the addition of Zn. Kolbert et al. (2012) argue that under stress conditions plants utilize most of their resources for the improvement of detoxification mechanisms rather than growth and development. On the other hand, this was not evident in our experiment for wheat plants. Here, the reduction of plant DM, especially in leaves 2, 3 and 4, was caused by the addition of Zn. It is known that Zn is an essential nutrient for plant growth, but it becomes toxic at higher concentrations in a nutrient medium. The element can be highly phytotoxic, especially when it accumulates in plants in an early phase of development (Rout, Das 2009). This phytotoxic effect is well documented for many plant species and is usually represented by growth inhibition (Vaillant et al. 2005, Tuma, Svojanovska 2015).

Differences in the effects of the two heavy metals on DM and physiological activities in bean and wheat shoots may be caused by the species-specific metal translocation from the roots to the aerial plant parts. This root-to-shoot transfer of ^{65}Zn and ^{109}Cd is evident from Figure 2. The diagrams clearly demonstrate that ^{65}Zn was more rapidly transferred from the roots to the aerial parts than ^{109}Cd in both species. This transfer is more efficient

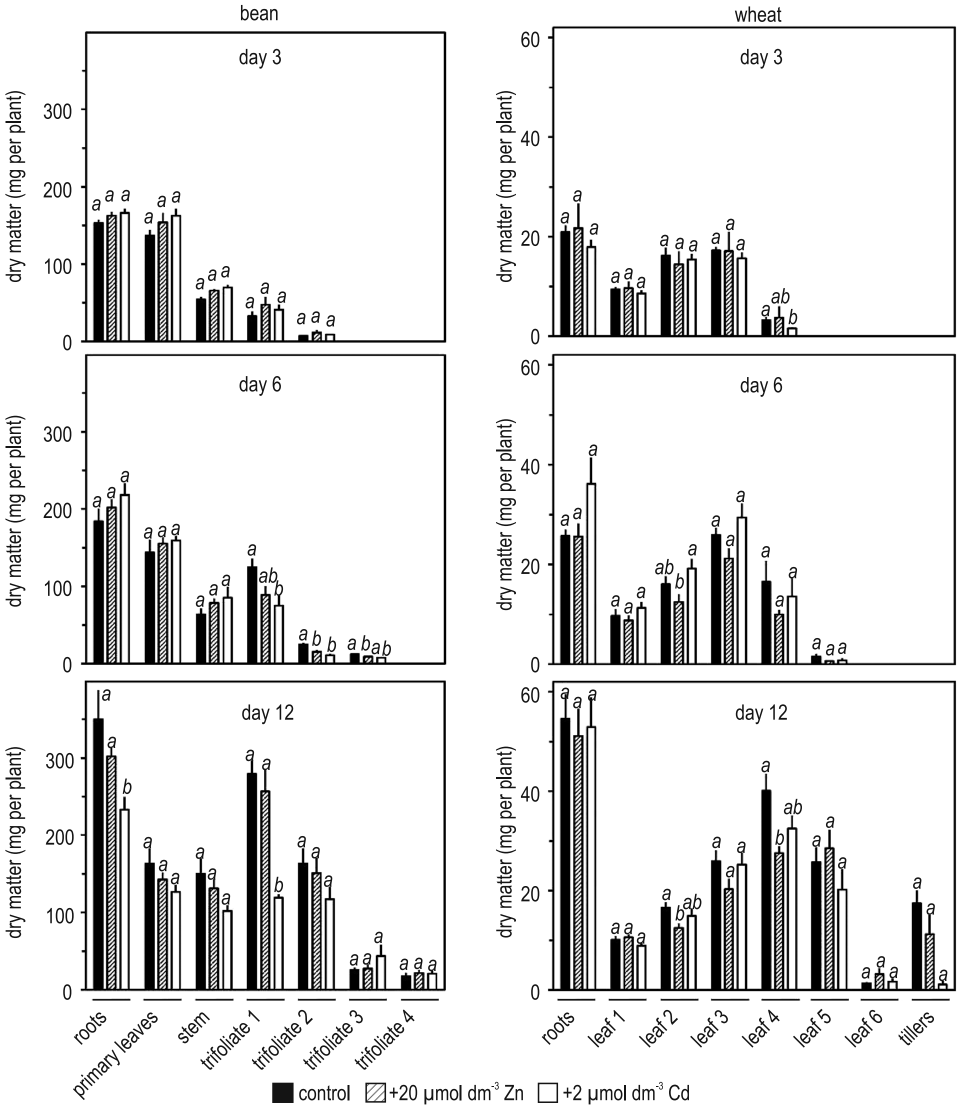

Fig. 1. Changes in the dry matter per plant part in bean (*Phaseolus vulgaris* L.) and wheat (*Triticum aestivum* L.) during exposure to elevated Cd or Zn in the nutrient medium. Trifoliate bean leaves are numbered from the oldest (trifoliate 1) to the youngest (trifoliate 4), and wheat leaves are numbered starting with the oldest leaf. Means and standard errors (on one side only for clarity) of 4 independent replicates are shown. Columns with the same letter for values of the same harvest date and the same plant part are not significantly different at the $P<0.05$ level

in wheat than in bean. Cd was strongly retained in the roots (around 90% in bean and around 60% in wheat). The content of ^{65}Zn in bean shoots was influenced by the addition of unlabelled Zn in a typical manner, while the ^{109}Cd content was far less affected.

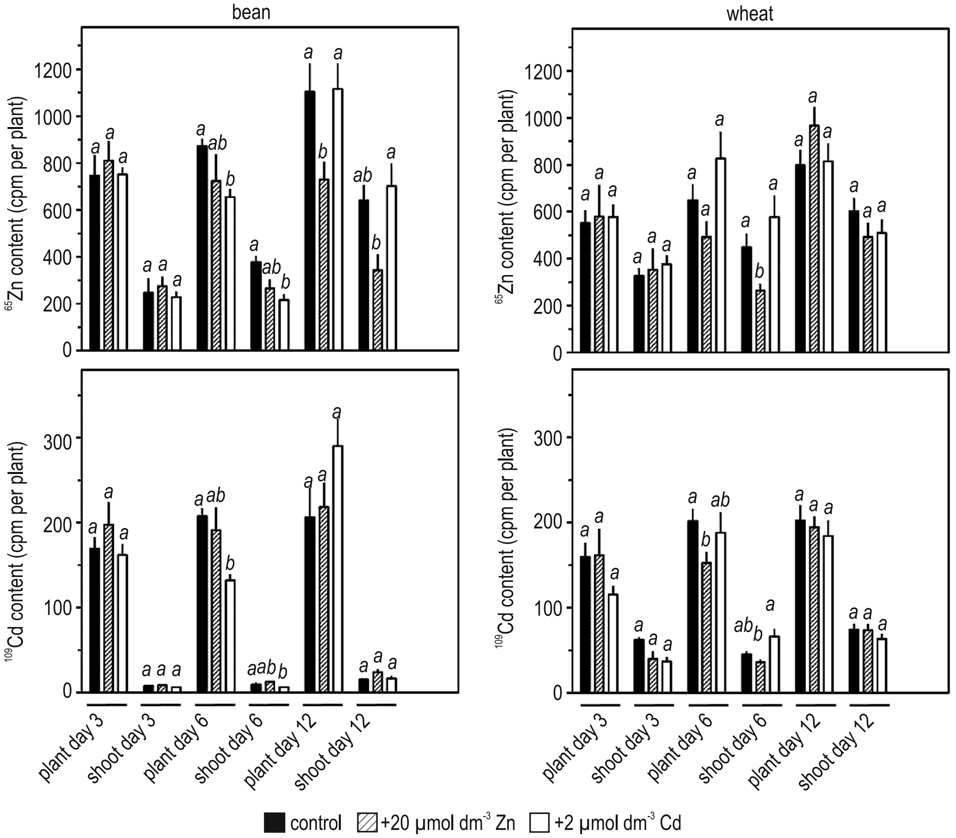

Fig. 2. Content of ^{65}Zn and ^{109}Cd in whole plants and in shoots of bean (*Phaseolus vulgaris* L.) and wheat (*Triticum aestivum* L.) during exposure to elevated Cd or Zn in the nutrient medium. Means and standard errors (on one side only for clarity) of 4 independent replicates are shown for the contents in counts per minute (cpm). Columns with the same letter in the same triplet are not significantly different at the $P<0.05$ level

After tracing the translocation of elements from the roots to shoots, it is important to evaluate their further redistribution within the shoot. Relative contents of ^{65}Zn and ^{109}Cd in various plant parts at various time points are shown in Figure 3 (bean) and Figure 4 (wheat). Figure 3 shows that an increased Zn concentration (but not an increased Cd concentration) in the medium negatively influenced the root-to-shoot transfer of Zn in bean plants (see days 6 and 12). Furthermore, the redistribution from the primary leaves to the youngest trifoliate leaves was also affected. Around 40-70% of ^{65}Zn was retained in the roots. Differences between ^{65}Zn and ^{109}Cd retention in the root system are obvious. Around 90% of ^{109}Cd remained in bean roots, regardless of the variant or harvest time.

Figure 4 shows that an increased Zn concentration in the nutrient medium negatively influenced its root-to-shoot transfer (see days 6 and 12) in wheat

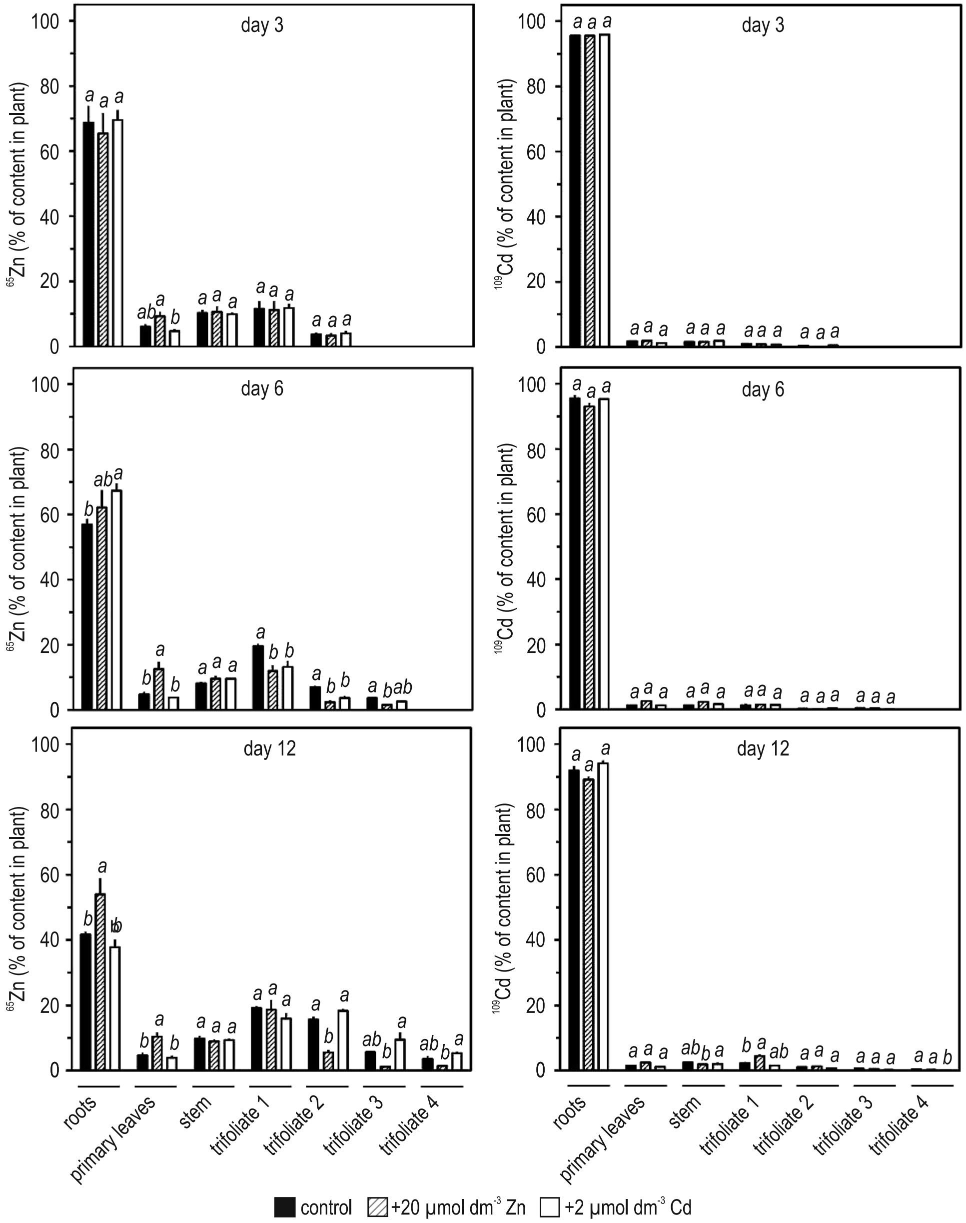

Fig. 3. Relative content of ^{65}Zn and ^{109}Cd (% of total content in plant) in various plant parts of bean (*Phaseolus vulgaris* L.) during exposure to elevated Cd or Zn in the nutrient medium. Trifoliate leaves are numbered from the oldest (trifoliate 1) to the youngest (trifoliate 4). Means and standard errors (on one side only for clarity) of 4 independent replicates are shown. Columns with the same letter in the same triplet are not significantly different at the $P<0.05$ level

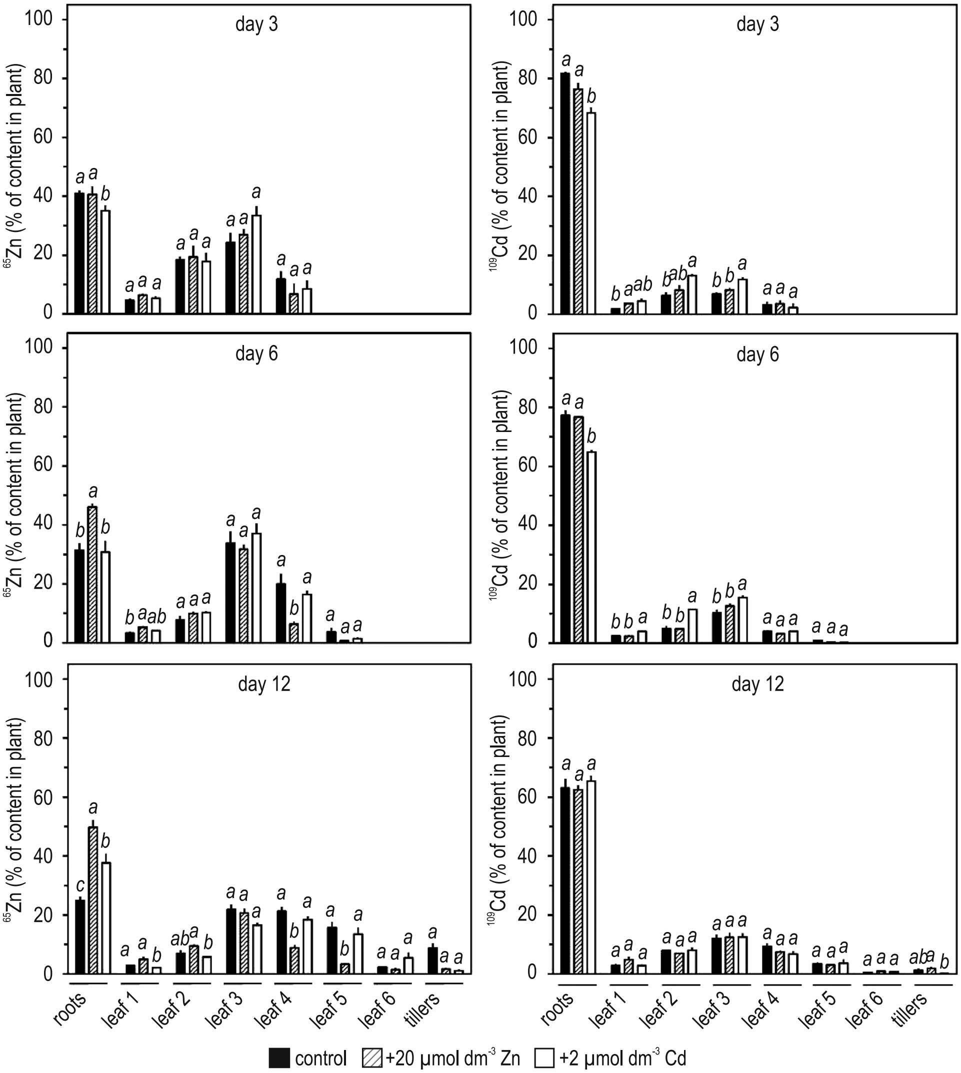

Fig. 4. Relative content of ^{65}Zn and ^{109}Cd (% of total content in plant) in various plant parts of wheat (*Triticum aestivum* L.) during exposure to elevated Cd or Zn in the nutrient medium. Leaves are numbered starting with the oldest leaf (leaf 1). Means and standard errors (on one side only for clarity) of 4 independent replicates are shown. Columns with the same letter in the same triplet are not significantly different at the *P*<0.05 level

plants. The redistribution from leaves 1 and 2 to the youngest leaves was also affected. Around 30-50% of ^{65}Zn was in the roots. A large amount of ^{65}Zn moved towards the leaves during their expansion. ^{109}Cd was more mobile in wheat than in bean plants. Around 60-80% of ^{109}Cd remained in the roots. An increased Cd concentration in the medium positively influenced the root-to-shoot transfer for Cd (see days 3 and 6) in wheat plants. ^{109}Cd was translocated much faster from the roots to the developing leaves in wheat than in bean. Apparently ^{109}Cd was far less efficiently loaded into the phloem and transported from older to younger wheat leaves compared to ^{65}Zn.

The more rapid translocation of ^{65}Zn, compared with ^{109}Cd, from the roots to the aerial parts in both species can be caused by various transfer mechanisms, which are more efficient in wheat than in bean. According to SARWAR et al. (2010), Cd toxicity not only decreases plant biomass, but also enhances the translocation of Cd to aerial parts. Similarly, EKMEKÇI et al. (2008) suggested that a lack of sufficient energy for Cd sequestration in the roots may also be responsible for translocation of Cd from roots to the aerial parts. It may be suggested that wheat and bean have different translocation processes, such as Cd transport out of parenchymal cells into the xylem system, or Cd loading into and out of the phloem. Another explanation is that Cd may be recognized as a toxic compound by the roots of both wheat and bean, thus leading to the activation of mechanisms such as sequestration into the vacuole or accumulation in the cell walls (TUDOREANU, PHILLIPS 2004, PAGE, FELLER 2005, PAGE et al. 2006, SANAEIOSTOVAR et al. 2011). The reason for such strong retention of ^{109}Cd in the roots may be the involvement of defensive mechanisms at the root surface and in the root apoplast, whose activities lead to insolubilization. Compartmentation in root tissues may contribute to avoid the release of HM to the xylem (PAGE, FELLER 2015). In general, roots accumulate the highest percentage of Cd compared to other plant tissues (ARAO, ISHIKAWA 2006, PAGE et al. 2006, SANAEIOSTOVAR et al. 2011, TUMA et al. 2014), but retention in the roots also depends on the plant species and the efficiency of root detoxification mechanisms (BENABID, GHORAB 2013). Cd dynamics in crop plants are relevant for the entry into the food chain and depend on various physiological processes including the production of complexes with organic acids, phytochelatins or nicotianamine as ligands (TUDOREANU, PHILLIPS 2004, SANAEIOSTOVAR et al. 2011, PAGE, FELLER 2015).

Negative influences of increased Zn concentrations in the medium on the root-to-shoot transfer of previously applied ^{65}Zn in bean plants, and negative influences of an increased Cd concentration in the medium on the root-to--shoot transfer of previously introduced ^{109}Cd in wheat plants may be linked to detoxification mechanisms in the roots. BENÁKOVÁ et al. (2017) reported that Zn can minimize Cd accumulation in plants. The root uptake, distribution and accumulation of Zn and Cd in plant tissues also differ depending on the crop genotype and not only on the species (ARAO, ISHIKAWA 2006, LI, ZHOU 2012).

However, with leaf aging, the content of ^{65}Zn decreased in wheat leaves. This finding is consistent with observations by PAGE et al. (2006). As reported previously by PAGE, FELLER (2015), HM transported via the transpiration stream to the shoot accumulate primarily in photosynthetically active (transpiring) leaves, if there is no further redistribution. Export from these leaves via the phloem allows redistribution from senescing leaves to sinks, but another possibility is also transfer to the phloem before the xylem sap reaches the mesophyll cells by a direct xylem-to-phloem transfer in bundles (Herren, Feller 1997, Page, Feller 2015). Such selective transfer may cause different distribution patterns for various HM during and after the transport from the roots to the shoot. For a more comprehensive analysis, the reproductive phase including seed loading with heavy metals must be borne in mind, and will be eventually relevant for the quality of harvested products (Khan et al. 2014).

CONCLUSIONS

Although Cd and Zn dynamics differ between wheat and dwarf bean, the release from the roots via the xylem to the shoot is a key process for the accumulation of the heavy metals in various aerial parts. Since genotypes of the same species may also differ with respect to Cd and Zn distribution and redistribution, the findings reported in this paper may be relevant for genotype selection or plant breeding for crop production on polluted soils.

REFERENCES

Arao T., Ishikawa S. 2006. *Genotypic differences in cadmium concentration and distribution of soybean and rice.* Jpn. Agric. Res. Q., 40: 21-30. DOI: 10.6090/jarq.40.21

Benabid H., Ghorab M.F. 2013. *Study of the translocation and distribution of cadmium into bean plants (Phaseolus vulgaris) using labelled Cd-109.* World J. Nano Sci. Eng., 3: 108-111. DOI: 10.4236/wjnse.2013.33015

Benáková M., Ahmadi H., Dučaiová Z., Tylová E., Clemens S., Tůma J. 2017. *Effects of Cd and Zn on physiological and anatomical properties of hydroponically grown Brassica napus plants.* Environ. Sci. Pollut. Res., 24: 20705–20716. DOI: 10.1007/s11356-017-9697-7

Cheng Y., Wang C., Chai S., Shuai W., Sha L., Zhang H., Kang H., Fan X., Zeng J., Zhou Y., Wang Y. 2018. *Ammonium N influences the uptakes, translocations, subcellular distributions and chemical forms of Cd and Zn to mediate the Cd/Zn interactions in dwarf polish wheat (Triticum polonicum* L.*) seedlings.* Chemosphere, 193: 1164-1171. DOI: 10.1016/j.chemosphere.2017.11.058

Ekmekçi Y., Tanyolaç D., Ayhan B. 2008. *Effects of cadmium on antioxidant enzyme and photosynthetic activities in leaves of two maize cultivars.* J. Plant Physiol., 165: 600-611. DOI: 10.1016/j.jplph.2007.01.017

Gouia H., Ghorbal M. H., Meyer C. 2000. *Effects of cadmium on activity of nitrate reductase and on other enzymes of the nitrate assimilation pathway in bean.* Plant Physiol. Biochem., 38: 629-638. DOI: 10.1016/S0981-9428(00)00775-0

Greger M., Landberg T. 2008. *Role of rhizosphere mechanisms in Cd uptake by various wheat cultivars.* Plant Soil, 312: 195-205. DOI: 10.1007/s11104-008-9725-y

Harris N.S., Taylor G.J. 2013. *Cadmium uptake and partitioning in durum wheat during grain filling.* BMC Plant Biol., 13: 103. DOI: 10.1186/1471-2229-13-103

Hazama K., Nagata S., Fujimori T., Yanagisawa S., Yoeneyama T. 2015. *Concentrations of metals and potential metal-binding compounds and speciation of Cd, Zn and Cu in phloem and xylem saps from castor bean plants (Ricinus communis) treated with four levels of cadmium.* Physiol. Plant., 154: 243-255. DOI: 10.1111/ppl.12309

HARRIS N.S., TAYLOR G.J. 2013. *Cadmium uptake and partitioning in durum wheat during grain filling.* BMC Plant Biol., 13: 103. DOI: 10.1186/1471-2229-13-103

HERBETTE S., TACONNAT L., HUGOUVIEUX V., PIETTE L., MAGNIETTE M.L., CUINE S., AUROY P., RICHAUD P., FORESTIER C., BOURGUIGNON J., RENOU J.P., VAVASSEUR A., LEONHARDT N. 2006. *Genome-wide transcriptome profiling of the early cadmium response of Arabidopsis roots and shoots.* Biochimie, 88: 1751-1765. DOI: 10.1016/j.biochi.2006.04.018

HERREN T., FELLER U. 1997. *Transport of cadmium via xylem and phloem in maturing wheat shoots: Comparison with the translocation of zinc, strontium and rubidium.* Ann. Bot., 80: 623-628. DOI: 10.1006/anbo.1997.0492

HOWLADAR S.M. 2014. *A novel Moringa oleifera leaf extract can mitigate the stress effects of salinity and cadmium in bean (Phaseolus vulgaris* L.*) plants.* Ecotoxicol. Environ. Saf., 100: 69-75. DOI: 10.1016/j.ecoenv.2013.11.022

KHAN M.A., CASTRO-GUERRERO N., MEDOZA-COZATL D.G. 2014. *Moving toward a precise nutrition: Preferential loading of seeds with essential nutrients over non-essential toxic elements.* Front. Plant Sci., 5: 51. DOI: 10.3389/fpls.2014.00051

KOLBERT Z., PETŐ A., LEHOTAI N., FEIGL G., ERDEI L. 2012. *Long-term copper (Cu^{2+}) exposure impacts on auxin, nitric oxide (NO) metabolism and morphology of Arabidopsis thaliana* L. Plant Growth Regul., 68: 151-159. DOI: 10.1007/s10725-012-9701-7

KRAMER U.**,** CHARDONNENS A.N. 2001. *The use of transgenic plants in the bioremediation of soils contaminated with trace elements.* Appl. Microbiol. Biotechnol., 55**:** 661-672. DOI: 10.1007/ /s002530100631

KUPPER H., LOMBI E., ZHAO F.J., MCGRATH S.P. 2000. *Cellular compartmentation of cadmium and zinc in relation to other elements in the hyperaccumulator Arabidopsis halleri.* Planta, 212: 75-84. DOI: 10.1007/s004250000366

LI D.D., ZHOU D.M. 2012. *Acclimation of wheat to low-level cadmium or zinc generates its resistance to cadmium toxicity.* Ecotoxicol. Environ, Saf., 79: 264-271. DOI: 10.1016/j.ecoenv. 2012.01.012

LIM J.E., AHMAD M., USMAN A.R.A., SOO LEE S., JEON W.-T., OH S.-E., YANG J.E., OK Y.S. 2013. *Effects of natural and calcined poultry waste on Cd, Pb and As mobility in contaminated soil.* Environ. Earth Sci., 69: 11-20. DOI: 10.1007/s12665-012-1929-z

MALČOVSKÁ S.M., DUČAIOVÁ Z., MASLAŇÁKOVÁ I., BAČKOR M. 2014. *Effect of silicon on growth, photosynthesis, oxidative status and phenolic compounds of maize (Zea mays* L.*) grown in cadmium excess.* Water Air Soil Pollut., 225: 2056. DOI: 10.1007/s11270-014-2056-0

MIYADATE H., ADACHI S., HIRAIZUMI A., TEZUKA K., NAKAZAWA N., KAWAMOTO T., KATOU K., KODAMA I., SAKURAI K., TAKAHASHI H., SATOH-NAGASAWA N., WATANABE A., FUJIMURA T., AKAGI H. 2011. *OsHMA3, a P-1B-type of ATPase affects root-to-shoot cadmium translocation in rice by mediating efflux into vacuoles.* New Phytol., 189: 190-199. DOI: 10.1111/j.1469-8137.2010.03459.x

MOHAMMAD A., MOHEMAN A. 2010. *The effects of cadmium and zinc interactions on the accumulation and tissue distribution of cadmium and zinc in tomato (Lycopersicon esculentum* Mill.*).* Arch. Agron. Soil Sci., 56: 551-561. DOI: 10.1080/03650340903141551

PAGE V., BLÖSCH R.M., FELLER U. 2012. *Regulation of shoot growth, root development and manganese allocation in wheat (Triticum aestivum) genotypes by light intensity.* Plant Growth Regul., 67: 209-215. DOI: 10.1007/s10725-012-9679-1

PAGE V., FELLER U. 2005. *Selective transport of zinc, manganese, nickel, cobalt and cadmium in the root system and transfer to the leaves in young wheat plants.* Ann, Bot., 96: 425-434. DOI: 10.1093/aob/mci189

PAGE V., FELLER U. 2015. *Heavy metals in crop plants: Transport and redistribution processes on the whole plant level.* Agronomy, 5: 447–463. DOI: 10.3390/agronomy5030447

PAGE V., WEISSKOPF L., FELLER U. 2006. *Heavy metals in white lupin: uptake, root-to-shoot transfer and redistribution within the plant.* New Phytol., 171: 329-341. DOI: 10.1111/j.1469-8137. 2006.01756.x

Richau K.H., Kozhevnikova A.D., Seregin I.V., Voojis R., Koevoets P.L.M., Snith J.A.C., Ivanov V.B., Schat H. 2009. *Chelation by histidine inhibits the vacuolar sequestration of nickel in roots of the hyperaccumulator Thlaspi caerulescens.* New Phytol., 183: 106-116. DOI: 10.1111/j. 1469-8137.2009.02826.x

Rout G.R., Das P. 2009. *Effect of metal toxicity on plant growth and metabolism.* I. *Zinc.* In: *Sustainable Agriculture.* Lichtfouse E., Navarrete M., Debaeke P., Véronique S., Alberola C. (eds.). Netherlands, Springer, pp 873-884. DOI: 10.1007/978-90-481-2666_53

Saifullah, Sarwar N., Bibi S., Ahmad M., Ok Y.S. 2014. *Effectiveness of zinc application to minimize cadmium toxicity and accumulation in wheat (Triticum aestivum* L.*).* Environ. Earth Sci., 71: 1663-1672. DOI: 10.1007/s12665-013-2570-1

Sanaeiostovar A., Khoshgoftarmanesh A.H., Shariatmadari H. 2011. *Effects of zinc activity in nutrient solution on uptake, translocation, and root export of cadmium and zinc in three wheat genotypes with different zinc efficiencies.* Soil Sci. Plant Nutr., 57: 681-690. DOI: 10.1080/00380768.2011.617290

Sarwar N., Saifullah, Malhi S.S., Zia M.H., Naeem A., Bibi S., Farid G. 2010. *Role of mineral nutrition in minimizing cadmium accumulation by plants.* J. Sci. Food Agric., 90: 925-937. DOI: 10.1002/jsfa.3916

Stolt J.P., Sneller F.E.C., Bryngellson T., Lundborg T., Schat H. 2003. *Phytochelatin and cadmium accumulation in wheat.* Environ. Exp. Bot., 49: 21-28. DOI: 10.1016/S0098--8472(02)00045-X

Tudoreanu L., Phillips C.J.C. 2004. *Modeling cadmium uptake and accumulation in plants.* Adv. Agron., 84: 121-157. DOI: 10.1016/S0065-2113(04)84003-3

Tuma J., Skalicky M., Tumova L., Malir F., Matejovska D. 2008. *The translocation of zinc in Avena sativa* L. *depending on fertilisation with zinc and mobile anions.* Cereal Res. Commun., 36: 1083-1086.

Tuma J., Skalicky M., Tumova L., Flidr J. 2014. *Influence of cadmium dose and form on the yield of oat (Avena sativa* L.*) and the metal distribution in the plant.* J. Elem., 19: 795-809. DOI: 10.5601/jelem.2014.19.3.448

Tuma J., Svojanovska H. 2015. *Avena sativa cadmium content, distribution and toxicity in dependence on concentration of zinc and nickel in nutrient medium.* Fresen. Environ. Bull., 24: 1798-1803. http://www.prt-parlar.de/download/

Vaillant N., Monnet F., Hitmi A., Sallanon H., Coudret A. 2005. *Comparative study of responses in four Datura species to a zinc stress.* Chemosphere, 59: 1005-1013. DOI: 10.1016/j. chemosphere.2004.11.030

Wang X,. Cheng W., Shuai W., Zeng J., Kang H., Fan X., Sha L., Zhang H., Wang Y., Zhou Y. 2018. *Nitrate N influences the accumulations and subcellular distributions of Cd and Zn to mediate the Cd/Zn interactions in dwarf Polish wheat (Triticum polonicum* L.*) seedlings.* Soil Sci. Plant Nutr. (in press.) DOI: 10.1080/00380768.2018.1559705

Welch R.M., Graham R.D. 2002. *Breeding crops for enhanced micronutrient content.* Plant Soil, 245: 205-214. DOI: 10.1023/A:1020668100330

Yang X., Li T.Q., Yang J.C., He Z.L., Lu L.L., Memg F.H. 2006. Z*inc compartmentation in root, transport into xylem, and absorption into leaf cells in the hyperaccumulating species of Sedum alfredii* Hance. Planta, 224: 185-195. DOI: 10.1007/s00425-005-0194-8