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Cd and Zn are differentially distributed in *Populus tremula* x *P. alba* exposed to metal excess

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Abstract: Poplar plants were exposed during 61 days to a soil added with heavy metals so as to contain 300 mg $Zn^{2+}.kg^{-1}$ soil dry weight (SDW) or 50 mg $Cd^{2+}.kg^{-1}$ $_{SDW}$. The Cd treatment induced a delayed growth of poplar, whereas Zn induced no change in physiological parameters. Both treatments resulted in a significant metal accumulation in plants. Zn^{2+} and Cd^{2+} exhibited contrasting distribution within tissues, indicating dissimilar handling by the plant. The main difference was the efficient compartmentalization of Zn^{2+} in specific organ parts: old leaves and bark, while Cd^{2+} did not exhibit such a compartmentalization.

Résumé: Des plants de peuplier ont été exposés durant 61 jours à un sol contaminé de manière à contenir 300 mg $Zn^{2+}.kg^{-1}$ $_{sol\ sec}$ ou 50 mg $Cd^{2+}.kg^{-1}$ $_{sol\ sec}$. Le traitement par Cd cause un retard de croissance alors qu'aucun changement dans les paramètres physiologique n'est observé suite à l'exposition au Zn. Les deux traitements entraînent une accumulation significative de métal dans la plante. Les distributions de Zn^{2+} et Cd^{2+} dans les tissus de la plante sont divergentes, indiquant que la plante les gère de manières différentes. Le Zn^{2+} se retrouve compartimenté dans des organes spécifiques : les feuilles âgées et l'écorce. La plante ne compartimentalise pas le Cd^{2+}.

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Introduction

Environmental constraints affect many aspects of plants metabolisms, impacting on their growth and yield. Abiotic factors causing plant stresses can be linked to natural phenomena, such as drought or can be due to anthropogenic activities, *e.g*. industrial discharge of heavy metals.

In the soil the presence of heavy metals decreases microbial activity and soil fertility, leading to inhibition of plant growth by indirect and direct effects (Gu et al. 2007). Though some heavy metals display a high cellular toxicity, some of them can be readily taken up by many plants, and accumulate all along the food chains. This is the case of cadmium (Cd) (Sanita di Toppi and Gabbrielli 1999). Cd has no known physiological role, except for one Cd-carbonic anhydrase in marine diatoms (Lane and Morel 2000). Its accumulation in the environment is mainly resulting from industrial emissions, use of Cd-rich phosphate fertilisers, sewage sludge spreading and runoff water from roadways. Moreover, Cd pollution is often accompanied by zinc (Zn) pollution (Garrett 2000).

Conversely to Cd, Zn is an essential element for plants metabolisms (Sommer and Lipman 1926). After iron, zinc is the most abundant biological heavy metal, it is involved as a cofactor in numerous enzymes activities, especially some SODs (Broadley et al. 2007). Nevertheless, Zn can reach toxic levels, like Cd, causing a decrease in chlorophyll content and photosynthetic activity (Gallego et al. 1996), hence decreasing growth and biomass production (Arisi et al. 2000). Cd-hyperaccumulator species described so far are mostly reported to also accumulate Zn (Verbruggen et al. 2009). While Cd accumulation and Cd tolerance are two independent traits in these species (Zha et al. 2004), a co-segregation of Cd and Zn accumulation and a co-segregation of Cd and Zn tolerance traits have been shown in at least one of them, namely *Arabidopsis halleri* (Bert et al. 2003). Moreover Aravind *et al* (2005a) showed that Zn could prevent Cd toxicity in *Ceratophyllum demersum*. This indicatesa link between Cd and Zn homeostasis which should prompt studies to compare Cd and Zn behavior and impact in plants.

It is generally admitted that plants do not possess specific Cd^{2+}-transporters, except perhaps for Cd-hyperaccumulator species (Liu et al. 2008). However, Cd^{2+} is shown to accumulate also in none-hyperaccumulator plants like poplar (Unterbrunner et al. 2007). It means that adventitious Cd^{2+} uptake and translocation involve molecular agents that are still unknown (Plaza et al. 2007; Cosio et al. 2004).

In plants, the metal homeostasis imply an organised combination of mechanisms: its uptake from soil to roots, the buffering realised by cell wall binding, the symplastic or

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apoplastic pathways towards cells, the transfer from xylem to phloem and the trafficking of metals into the cells. The same processes, associated with chelation in roots exsudates, vacuolization and storage in specific organs like trichomes help the plant to cope with metal excess and could avoid its potential toxicity (Clemens 2001; Clemens et al. 2002; Zhao et al. 2000; Song et al. 2003). Thus tolerance can arise from two contrasting strategies: metal exclusion or metal accumulation, which imply two distinct sets of mechanisms (Baker 1987). Exclusion is a more common behavior which inhibits root-to-shoot metal translocation. This explains why most of studies performed on tree species show that heavy metals particularly accumulate in roots (Zacchini et al. 2009). On the contrary metals accumulate more in the aerial parts of hyperaccumulators than in their roots (Tanhan et al. 2007). Thus, root-to-shoot metal translocation is a crucial step of metal accumulation (Papoyan et al. 2007) that constitutes one limiting factor for the use of trees in a phytoremediation perspective. Hyperaccumulation ability seems to depend on metal pumps and transporters (Hanikenne et al. 2008) that ensure the final destination of metal ions in a plants organs, tissues and cells. Hence, it appears important to understand xylem loading processes and the distribution of heavy metals in the whole-plant.

So far published studies on woody plants and metal stress were mostly performed on willow and poplar which present an overall ability to accumulate heavy metals like Cd and Zn, but also Cu, Mn, *etc.* (Laureysens et al. 2004; Dos Santos Utmazian et al. 2007; Kieffer et al. 2008). However scarcely any studies have attempted to describe the profile of metal distribution among the tree organs and the wood tissues.

In this regard, we harvested poplar plants after 61 days of exposure to a soil containing50 mg $Cd.kg^{-1}$ $_{SDW}$, and 9.5 µM Cd in the soil solution or to a soil containing 300 mg $Zn^{2+}.kg^{-1}$ $_{SDW}$, and 140.4 µM in the soil solution. As plants exhibited no change in gas exchanges despite a delayed growth for Cd stressed plants, it was possible to describe the profile of metal distribution among the organs in a functional context.

Materials and methods

Plant material and metal treatments

Young rooted cuttings of *Populus tremula L. x P. alba* L. (*Populus x canescens* (Aiton) Smith) genotype INRA 717-1B4 were obtained as described in Caruso *et al*. (2002) from 1- year-old cut-back stems. The plants were cultivated in a growth chamber at 21°C ±

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2°C, 70% of relative humidity ± 5% and an irradiance of 1000 µmol.m^{-2}.s^{-1} provided during 16 h per day, they were watered each second day to field capacity.

At the beginning of the metal treatment, the 3 months old rooted cuttings were transferred from 0.5 dm^3 pots to 10 dm^3 pots containing sand and peat moss (25:75%, v/v, pH 6.9). Concomitantly, plants were pruned in order to make sure that the new leafy stems were entirely formed while plants were exposed to metal. The initial soil which corresponded to the control samples contained 72.3 mg Zn^{2+}.kg^{-1} soil dry weight (SDW) and no trace of Cd^{2+}. Soils of Zn-treated plants was enriched at the beginning of the experiment with zinc in order to reach 300 mg Zn^{2+}.kg^{-1} $_{SDW}$ whereas Cd-treated soils was enriched with cadmium in order to reach 50 mg Cd^{2+}.kg^{-1} $_{SDW}$. During the 2 months of experiment, plants were watered only with tap water.

At the end of the treatment, plants samples were divided into roots, cutting, new stem entirely formed during the experiment, and leaves entirely formed during the experiment.

Leaves and stems were further separated into three groups depending on their position on the foliar axis. The first group reassembled the mature or senescent organs which corresponded to the region of the leaves which were already present in the bud which have produced the newly formed tissues (low part). The second group corresponded to the young mature organs (middle part); these leaves had achieved their growth at the time of the sampling. The third group corresponded to the young growing tissues (high part). The cutting was also dissected into three parts: xylem, cambial zone and bark.

Growth and water content

During the treatment, the stem height as well as the total leaf area was estimated as described by Brignolas *et al*. (2000) on 5 replicates. The assessment of the secondary growth was carried out through the monitoring of the time course of the plant cutting diameter with an automatic point dendrometer described in Morabito et al. (2006). The leaf Relative Water Content (RWC) was calculated as follow, RWC (%) = (fresh weight – dry weight) x 100 / (saturated weight – dry weight). The root and stem Water Content was calculated as WC = (fresh weight – dry weight) x 100 / fresh weight.

Metal content determination in soil and plant

Metal concentration in the soil, in the soil solution and in the plant organs were measured using a Jobin-Yvon® HR-ICP-AES as described in (Marchand et al. 2006), from 3 biological replicates.

Statistics

SPSS MANOVA was used to compare metal concentrations and metal partitioning in organs between treatments. Relative partitioning data expressed in percentage (x%)

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were transformed by arcsin($x^{1/2}$) before statistical analyses were completed. Physiological measurements (primary, secondary growth, gas exchanges) were given as the mean of 3 to 5 biological replicates. Statistical comparison of the means resulted from Student t-test.

Results

Physiological impact of metal treatment

After 61 days of experiment, the Cd treatment resulted in the inhibition of the total leaf area (-28%) and the stem height (-26%) of plants, whereas no significant changes occurred under Zn exposure (Table 1).

The dry weight of roots and cutting were not significantly changed under Cd treatment, whereas tissues entirely developed during the experiment, exhibited lower dry weight: -41% for stem, and -42% for leaves (Table 1). Zn treatment had no effect on the dry weight of organs. The net CO_2 assimilation and the stomatal conductance were not affected by Cd nor by Zn constraint. No change in organ water content occurred consequently to Zn or Cd treatments.

The stem diameter increase, measured throughout the experiment was summarized in the Table 1 by a final measurement. This parameter exhibited no changes under metal treatments.

Metal quantification in soil and plant organs

Zinc plant content: on day 1, $[Zn^{2+}]_{soil\ solution}$ was 8.3 µM in control conditions and reached 140.4 µM in Zn-treated conditions (Fig. 1). $[Zn^{2+}]_{soil\ solution}$ was not significantly altered by theaddition of 50 mg $Cd^{2+}.kg^{-1}_{SDW}$ treatment.

On day 61 (Table 2), under Zn treatment, while the $[Zn^{2+}]$ content significantly augmented, compared to control, in leaves, stem, roots and cutting by a ratio of 4.9, 3.9, 3.4 and 1.3 respectively, the Zn^{2+} distribution was significantly higher in leaves (+13.1%) and lower in cutting (-12.3%). The relative Zn^{2+} distribution in stem and roots did not change.

$[Zn^{2+}]$ was measured in stems and leaf in 3 separated positions along the foliar axis (Fig. 2). Under control conditions, $[Zn^{2+}]$ presented a homogenic distribution, with a slightly greater content in the oldest leaves; the 3 levels of stem tissue had the same $[Zn^{2+}]$. Zn-treated plants exhibited a greater $[Zn^{2+}]$ when the tissues are older: old leaves contained 500.4 mg $Zn^{2+}.kg^{-1}_{DW}$, *i.e.* 1.8 fold more than the youngest leaves, whereas the oldest part of stem contained 281mg $Zn^{2+}.kg^{-1}_{DW}$, *i.e.* twice as much as the youngest part.

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Among the cutting tissues, and for all three treatments, $[Zn^{2+}]_{xylem}$ (Fig. 3) was between 3.2 and 7 fold lower compared to $[Zn^{2+}]_{bark}$, and between 5.1 and 5.8 times lower compared to $[Zn^{2+}]_{cambial\ zone}$. Compared to control plants, the Zn^{2+} exposure-induced highest increase of $[Zn^{2+}]$ in the bark where it raised from104.9 to 199.6 mg $Zn.kg^{-1}_{DW}$ (Fig. 3). Xylem and cambial zone $[Zn^{2+}]$ were not significantly affected by Zn or Cd treatments.

Under Cd exposure, and compared to control, the $[Zn^{2+}]_{leaf}$ increased from 86.6 to 143.7 $mgZn.kg^{-1}_{DW}$, but the relative distribution of Zn^{2+} in leaves showed no variation (Table 2). The Cd treatment also resulted in an increase of $[Zn^{2+}]_{stem}$ from 61.3 to 139.2 mg $Zn.kg^{-1}_{DW}$, and modified the incorporated Zn^{2+} distribution in this organ from 17.5% to 24.5%. No change occurred in content and distribution of Zn^{2+} in cutting and root. The quantification of Zn in the leaves and stems collected along the foliar axis at 3 parts of distinct ages showed that the Cd treatment induced an increase of $[Zn^{2+}]$ only in young mature stem, compared to control (Fig. 2).

Cadmium plant content: no Cd^{2+} was detected in control or in Zn-treated plants (Table 2). Under Cd exposure, Cd^{2+} was mainly localized in leaves (Table 2) which contained 79.7 $mgCd^{2+}.kg^{-1}_{DW}$ and represent 52.6% of the Cd^{2+} present in the plant. Woody aerial parts, *i.e.* 'stem' and 'cutting' contained 39.1% of the Cd taken up by the plant, with a greater $[Cd^{2+}]$ in the stem tissues (63.8 mg $Cd^{2+}.kg^{-1}_{DW}$). For leaves and stem organs, their position on the foliar axis had no significant effect on the $[Cd^{2+}]$ (Fig. 4).

Among the cutting tissues, Cd content of the xylem was significantly lower than those in the cambial zone or in the bark which reached 115.4 and 122.5 mg $Cd^{2+}.kg^{-1}_{DW}$ respectively (Figure 5).

Discussion

Young poplar plants grown in a growth chamber were exposed to a soil content of 300 mg $Zn.kg^{-1}_{SDW}$ which exceeds the natural average content of 64 mg $Zn.kg^{-1}_{SDW}$ in the majority of soils (Emsley 2003). In parallel, other poplar plants were exposed to 50 mg $Cd.kg^{-1}_{SDW}$, which corresponds to a heavily polluted soil (Peters and Shem 1992). Metal toxicity in soil has complex dependencies towards total soil composition and, often more closely, free-ions partition in soil solution (Oorts et al. 2006; Sauvé et al. 2000) in relation with, *e.g.* pH, soil organic matter and dissolved organic carbon. Typically, less than 10% of the Zn^{2+} is under soluble or exchangeable form in soil, hence available for the plant

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(Broadley et al. 2007) whereas for Cadmium the part of soluble or exchangeable Cd varies between 2 and 20% of total soil load (Ma and Rao 1997; Sauvé et al. 2000).

Poplar exhibits a zinc management strategy.

Under Zn treatment, $[Zn^{2+}]_{soil\ solution}$ reached 140.4 µM; this was 17-fold higher than the control value. Nevertheless, the Zn treatment did not induce any change in primary or secondary growth, in organs dry weight or water content, in stomatal conductance nor net CO_2 assimilation (Table 1). Thereby the fate of Zn^{2+} within poplar organs under Zn exposure should be considered as the result of an efficient metal homeostasis. Moreover, as compartmentalization is part of the mechanisms involved in metal homeostasis, the metal localization reflects the plant strategy to cope with metal excess. $[Zn^{2+}]_{roots}$ was equal to 65.8 mg $Zn.kg^{-1}$ $_{DW}$ in control and to 224.3 mg $Zn.kg^{-1}$ $_{DW}$ in Zn258treated plants. In both cases, it represents 5% of the Zn incorporated in the plant (Table 2) ; thus control and Zn-treated plants showed an equivalent root-to-shoot translocation of Zn^{2+}. In above-ground parts, although $[Zn^{2+}]$ increased in all organs, the distribution patterns were contrasted. The Zn treatment induced a significantly increased localization of Zn^{2+} in the leaves, where its highest value was reached. This is in accordance with existing literature where Zn^{2+} is shown to predominantly distribute in the leaves, and particularly into trichomes, according to Zhao et al. (2000). As *P. canescens* 717-1B4 presents an important density of trichomes on the abaxial face of its leaves, the involvement of these trichomes in Zn^{2+} handling could be investigated. While $[Zn^{2+}]$ exhibited a significant increase in all organs, the relative distribution in the cutting was reduced from 20.5% to 8.2% due to a weaker loading of Zn^{2+} in this organ. This can result from different causes: it is likely that Zn^{2+} is not heavily loaded into mature xylem; the cutting tissues that developed during the 61 days of metal exposure represent less than those already formed prior to the experiment (this is especially true for metal incorporated in xylem that was 'diluted' in the total xylem mass). It is noteworthy that $[Zn^{2+}]_{cambial\ zone}$ was not significantly altered by Zn treatment, whereas $[Zn^{2+}]_{bark}$ was 1.9 fold higher. This suggests an efficient targeting of excessive Zn^{2+} in specifictissues. Under Zn exposure, in leaf and stem, $[Zn^{2+}]$ reached 427.5 and 240.4 mg $Zn.kg^{-1}$ $_{DW}$, respectively. When considering leaf position along the stem and corresponding stem sections, a significant $[Zn^{2+}]$ gradient could be observed (Fig. 2). Zn^{2+} was preferentially stored in older tissues; oldest leaves contained 1.8 fold more Zn^{2+} than the youngest. Such a $[Zn^{2+}]$ gradient was not observed in control plants. This raises the hypothesis of an inducible strategy for Zn compartmentalization.

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The cadmium management strategy, if existing, differs from the zinc one.

The Cd treatment exposure to 50 mg $Cd^{2+}.kg^{-1}$ DW that resulted in 9.5µM $[Cd^{2+}]_{soil\ solution}$ was comparable in intensity to many studies presented in the literature in hydroponic conditions (Aravind and Prasad 2005b; Mishra et al. 2006; Thomine et al. 2000; Cosio et al. 2006; Kieffer et al. 2008). This treatment caused a 26 to 28% reduction of the plants primary growth rates. The organs dry weight were also reduced. However, in the same time, the secondary growth was sustained, the stomatal conductance and the net CO_2 assimilation of young mature leaves were not affected (Table 1). There were no visible toxicity symptoms on the plants to which correlate the retarded primary growth. Since Cd^{2+} actually accumulated in the tissues while the plant showed a narrowed but healthy development, it should be considered that the potential Cd toxicity was partly avoided.

The highest $[Cd^{2+}]$ occurred in leaves and stem. The determination of $[Cd^{2+}]_{leaf}$ and $[Cd^{2+}]_{stem}$ according to the position of the organs showed a continuum of the $[Cd^{2+}]$ along the foliar axis. Hence, Cd was not preferentially compartmentalized in older leaves as it was observed in *Salix viminalis* (Cosio et al. 2006) or in *Salix fragilis* (Luyssaert et al. 2001). Among the tissues of the cutting, Cd^{2+} presented a lower content in xylem than in cambial zone and bark. A previous study on poplar showed similar results with a greater $[Cd^{2+}]$ in bark than in wood (Gu et al. 2007). To our knowledge the determination of $[Cd^{2+}]_{cambial\ zone}$ has never been reported so far. A measurement of metal ions content in the xylem layers formed during the metal constraint would be informative.

Cd and Zn distribution in above ground organs of Cd- and Zn-exposed plants, respectively, exhibited discrepancies (Table 2). Excessive Zn^{2+} was significantly more present in the leaves than Cd^{2+} (70.2% vs 52.6%), while Cd^{2+} was more localized in the cutting than Zn^{2+} (20.3% vs 8.2%). This pattern deviance must be balanced with the 40% reduced mass of leaf organ under Cd constraint, which is part of the plant response to Cd. The measurement of metal

content in leaf and stem according to the age and position of the organs showed that the handling of Cd^{2+} at the organ level does not fit in the model of the Zn^{2+} compartmentalization.

Effect of Cd treatment on plant Zn content.

Results also underlined interactions or hindrances between Cd^{2+} and Zn^{2+} homeostasis. Under the Cd constraint, although $[Zn^{2+}]_{soil\ solution}$ was not modified compared to control (Fig. 1), significant changes occurred in Zn^{2+} distribution and content among organs (Table 2). $[Zn^{2+}]_{leaf}$ increased by 66% and $[Zn^{2+}]_{stem}$ increased by 127%. Hence the tissues developed and formed during the exposure to Cd showed an important increase

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in their [Zn^{2+}]. Interestingly, literature reported both decrease (Zornoza et al. 2002) or increase (Yang et al. 2004) in $[Zn^{2+}]_{plant}$ consequently to a Cd exposure.

Cd^{2+} can disturb Zn^{2+} homeostasis in a direct or an indirect way. Indeed interferences can intervene directly on Zn^{2+} transport, by a deregulation of Zn^{2+} transporters. This would be consistent with the hypothesis of Cd^{2+} being conveyed by unspecific –or insufficiently specific– Zn^{2+} transporters (Gitan et al. 2003; Bert et al. 2003). Based on all current knowledge on plant metal transporters, the existence of specific Cd^{2+} transporters in plants seems unlikely (Clemens 2006). The observed changes can also result from a rise in the demand for Zn^{2+} in active tissues where an increase [Zn^{2+}] would help preventing the binding of Cd^{2+} to biomolecules. This would be in accordance with the thesis of Cd^{2+} toxicity resulting from the competition with Zn^{2+} and other divalent cations for the binding to biomolecules, in plants as in animals (Waalkes and Poirier 1984; Jemai et al. 2007).

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Conclusion

The Zn compartmentalization response to Zn treatment appears to be an inducible mechanism that allows a tuned regulation of Zn homeostasis, a kind of response that is lacking for Cd. The results also show that the control of Zn homeostasis is based on the compartmentation of the metal ion in aged tissues.

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References

Aravind, P. and Prasad, M. N. V. 2005a. Cadmium-induced toxicity reversal by zinc in *Ceratophyllum demersum* L. (a free floating aquatic macrophyte) together with exogenous supplements of amino- and organic acids. Chemosphere **61**: 1720-1733.

Aravind, P. and Prasad, M. N. V. 2005b. Modulation of cadmium-induced oxidative stress in *Ceratophyllum demersum* by zinc involves ascorbate–glutathione cycle and glutathione metabolism. Plant Phys Biochem **43**: 107-116.

Arisi, A.-C. M., Mocquot, B., Lagriffoul, A., Mench, M., Foyer, C. H., and Jouanin, L. 2000. Responses to cadmium in leaves of transformed poplars overexpressing γ-glutamylcysteine synthetase. Physiol Plant **109**: 143-149.

Baker, A. J. M. 1987. Metal tolerance. New Phytol. **106**: 93-111.

Bert, V., Meerts, P., Saumitou-Laprade, P., Salis, P., Gruber, W., and Verbruggen, N. 2003. Genetic basis of Cd tolerance and hyperaccumulation in *Arabidopsis halleri*. Plant Soil **249**: 9-18.

Besson-Bard, A., Gravot, A., Richaud, P., Auroy, P., Duc, C., Gaymard, F., Taconnat, L., Renou, J. P., Pugin, A., and Wendehenne, D. 2009. Nitric oxide contributes to cadmium toxicity in Arabidopsis by promoting cadmium accumulation in roots and by up-regulating genes related to iron uptake. Plant Physiol **149**: 1302-1315.

Comment citer ce document :
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Brignolas, F., Thierry, C., Guerrier, G., and Boudouresque, E. 2000. Compared water deficit response of two Populus x euramericana clones, Luisa Avanzo and Dorskamp. Annals of Forest Science **57**: 261-266.

Broadley, M. R., White, P. J., Hammond, J. P., Zelko, I., and Lux, A. 2007. Zinc in plants. New Phytol. **173**: 677-702.

Caruso, A., Morabito, D., Delmotte, F., Kahlem, G., and Carpin, S. 2002. Dehydrin induction during drought and osmotic stress in *Populus*. Plant Phys Biochem **40**: 1033-1042.

Clemens, S. 2006. Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. Biochimie **88**: 1707-1719.

Clemens, S. 2001. Molecular mechanisms of plant metal tolerance and homeostasis. Planta **212**: 475-486.

Clemens, S., Palmgren, M. G., and Krämer, U. 2002. A long way ahead: understanding and engineering plant metal accumulation. Trends Plant Sci **7**: 309-315.

Cosio, C., Martinoia, E., and Keller, C. 2004. Hyperaccumulation of cadmium and zinc in *Thlaspi caerulescens* and *Arabidopsis halleri* at the leaf cellular Level. Plant Physiol **134**: 716-725.

Cosio, C., Vollenweider, P., and Keller, C. 2006. Localization and effects of cadmium in leaves of a cadmium-tolerant willow (*Salix viminalis L.*): I. Macrolocalization and phytotoxic effects of cadmium. Environ exp Bot **58**: 64-74.

Dos Santos Utmazian, M. N., Wieshammer, G., Vega, R., and Wenzel, W. W. 2007. Hydroponic screening for metal resistance and accumulation of cadmium and zinc in twenty clones of willows and poplars. Environ Pollut **148**: 155-165.

Comment citer ce document :
Durand, T., Baillif, P., Albéric, P., Carpin, S., Label, P., Hausmann, J.-F., Morabito, D. (2011). Cadmium and Zinc are differentially distributed in Populus tremula x P. alba exposed to metal excess. Plant Biosystems, 145 (2), 397-405. DOI : 10.1080/11263504.2011.567787

Emsley, J. 2003. Nature's building blocks: An A-Z guide to the elements. Oxford University Press, Oxford, England, UK. Gallego, S. M., Benavides, M. P., and Tomaro, M. L. 1996. Effect of heavy metal ion excess on sunflower leaves: evidence for involvement of oxidative stress. Plant Sci **121**: 151-159.

Garrett, R. G. 2000. Natural sources of metals to the environment. Hum ecol risk assess **6**: 945-963.

Gitan, R. S., Shababi, M., Kramer, M., and Eide, D. J. 2003. A cytosolic domain of the yeast Zrt1 Zinc transporter is required for its post-translational inactivation in response to zinc and cadmium. J Biol Chem **278**: 39558-39564.

Gu, J., Qi, L., Wusheing, J., and Liu, D. 2007. Cadmium accumulation and its effects on growth and gas exchange in four *Populus* cultivars. Acta Biologica Cravoviensia **49**: 7-14.

Hanikenne, M., Talke, I. N., Haydon, M. J., Lanz, C., Nolte, A., Motte, P., Kroymann, J., Weigel, D., and Kramer, U. 2008. Evolution of metal hyperaccumulation required cisregulatory changes and triplication of HMA4. Nature **453**: 391-395.

Jemai, H., Messaoudi, I., Chaouch, A., and Kerkeni, A. 2007. Protective effect of zinc supplementation on blood antioxidant defense system in rats exposed to cadmium. Journal of Trace Elements in Medicine and Biology **21**: 269-273.

Kieffer, P., Dommes, J., Hoffmann, L., Hausman, J.-F., and Renaut, J. 2008. Quantitative changes in protein expression of cadmium-exposed poplar plants. Proteomics **8**: 2514-2530.

Lane, T. W. and Morel, F. M. M. 2000. A biological function for cadmium in marine diatoms. PNAS **97**: 4627-4631.

Manuscrit d'auteur / Author manuscript
Manuscrit d'auteur / Author manuscript
Manuscrit d'auteur / Author manuscript
Version postprint

Comment citer ce document :
Durand, T., Baillif, P., Albéric, P., Carpin, S., Label, P., Hausmann, J.-F., Morabito, D. (2011). Cadmium and Zinc are differentially distributed in Populus tremula x P. alba exposed to metal excess. Plant Biosystems, 145 (2), 397-405. DOI : 10.1080/11263504.2011.567787

Laureysens, I., Blust, R., De Temmerman, L., Lemmens, C., and Ceulemans, R. 2004. Clonal variation in heavy metal accumulation and biomass production in a poplar coppice culture: I. Seasonal variation in leaf, wood and bark concentrations. Environ Pollut **131**: 485-494.

Liu, M. Q., Yanai, J., Jiang, R. F., Zhang, F., McGrath, S. P., and Zhao, F. J. 2008. Does cadmium play a physiological role in the hyperaccumulator *Thlaspi caerulescens*? Chemosphere **71**: 1276-1283.

Luyssaert, S., Van Meirvenne, M., and Lust, N. 2001. Cadmium variability in leaves of a *Salix fragilis*: simulation and implications for leaf sampling. Can J For Res **31**: 313-321.

Ma, L. Q. and Rao, G. N. 1997. Chemical fractionation of cadmium, copper, nickel, and zinc in contaminated soils. J environ Qual **26**: 259-264.

Marchand, C., Lallier-Vergès, E., Baltzer, F., Albéric, P., Cossa, D., and Baillif, P. 2006. Heavy metals distribution in mangrove sediments along the mobile coastline of French Guiana. Marine Chemistry **98**: 1-17.

Mishra, S., Srivastava, S., Tripathi, R. D., Govindarajan, R., Kuriakose, S. V., and Prasad, M. N. V. 2006. Phytochelatin synthesis and response of antioxidants during cadmium stress in *Bacopa monnieri* L. Plant Phys Biochem **44**: 25-37.

Morabito, D., Caruso, A., Carpin, S., Carli, C., Laurans, F., Depierreux, C., Kahlem, G., and Label, P. 2006. Cambial activity of *Populus tremula* × *Populus alba* clone 717-1B4 in hydroponic culture. Can J For Res **36**: 719-724.

Manuscrit d'auteur / Author manuscript
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Comment citer ce document :
Durand, T., Baillif, P., Albéric, P., Carpin, S., Label, P., Hausmann, J.-F., Morabito, D. (2011). Cadmium and Zinc are differentially distributed in Populus tremula x P. alba exposed to metal excess. Plant Biosystems, 145 (2), 397-405. DOI : 10.1080/11263504.2011.567787

Oorts, K., Ghesquiere, U., Swinnen, K., and Smolders, E. 2006. Soil properties affecting thetoxicity of $CuCl_2$ and $NiCl_2$ for soil microbial processes in freshly spiked soils. Environ Toxicol Chem **25**: 836-844.

Papoyan, A., Pineros, M., and Kochian, L. V. 2007. Plant Cd^{2+} and Zn^{2+} status effects on rootand shoot heavy metal accumulation in *Thlaspi caerulescens*. New Phytol. **175**: 51-58.

Peters, R. W. and Shem, L. 1992. Adsorption/desorption characteristics of lead on various types of soil. Environmental Progress **11**: 234-240.

Plaza, S., Tearall, K. L., Zhao, F. J., Buchner, P., McGrath, S. P., and Hawkesford, M. J. 2007. Expression and functional analysis of metal transporter genes in two contrasting ecotypes of the hyperaccumulator *Thlaspi caerulescens*. J exp Bot **58**: 1717-1728.

Sanita di Toppi, L. and Gabbrielli, R. 1999. Response to cadmium in higher plants. Environ exp Bot **41**: 105-130.

Sauvé, S., Norvell, W. A., McBride, M., and Hendershot, W. 2000. Speciation and complexation of cadmium in extracted soil solutions. Environ Sci Technol **34**: 291.

Sommer, A. L. and Lipman, C. B. 1926. Evidence on the indispensable nature of zinc and boron for higher green plants. Plant Physiol **1**: 231-249.

Song, W.-Y., Sohn, E. J., Martinoia, E., Lee, Y. J., Yang, Y.-Y., Jasinski, M., Forestier, C., Hwang, I., and Lee, Y. 2003. Engineering tolerance and accumulation of lead and cadmium in transgenic plants. Nature Biotechnology **21**: 914-919.

Tanhan, P., Kruatrachue, M., Pokethitiyook, P., and Chaiyarat, R. 2007. Uptake andaccumulation of cadmium, lead and zinc by Siam weed [*Chromolaena odorata* (L.) King & Robinson]. Chemosphere **68**: 323-329.

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Comment citer ce document :
Durand, T., Baillif, P., Albéric, P., Carpin, S., Label, P., Hausmann, J.-F., Morabito, D. (2011). Cadmium and Zinc are differentially distributed in Populus tremula x P. alba exposed to metal excess. Plant Biosystems, 145 (2), 397-405. DOI : 10.1080/11263504.2011.567787

Thomine, S., Wang, R., Ward, J. M., Crawford, N. M., and Schroeder, J. I. 2000. Cadmium and iron transport by members of a plant metal transporter family in *Arabidopsis* with homology to Nramp genes. PNAS **97**: 4991-4996.

Unterbrunner, R., Puschenreiter, M., Sommer, P., Wieshammer, G., Tlustos, P., Zupan, M., and Wenzel, W. W. 2007. Heavy metal accumulation in trees growing on contaminated sites in Central Europe. Environ Pollut **148**: 107-114.

Verbruggen, N., Hermans, C., and Schat, H. 2009. Molecular mechanisms of metal hyperaccumulation in plants. New Phytol. **4**: 759-776.

Waalkes, M. P. and Poirier, L. A. 1984. In vitro cadmium-DNA interactions: Cooperativity of cadmium binding and competitive antagonism by calcium, magnesium, and zinc. Toxicology and Applied Pharmacology **75**: 539-546.

Yang, X. E., Long, X. X., Ye, H. B., He, Z. L., Calvert, D. V., and Stoffella, P. J. 2004. Cadmium tolerance and hyperaccumulation in a new Zn-hyperaccumulating plant species (*Sedum alfredii* Hance). Plant Soil **259**: 181-189.

Zacchini, M., Pietrini, F., Scarascia Mugnozza, G., Iori, V., Pietrosanti, L., and Massacci, A. 2009. Metal tolerance, accumulation and translocation in poplar and willow clones treated with cadmium in hydroponics. Water, Air, Soil Pollut **197**: 23-34.

Zha, H. G., Jiang, R. F., Zhao, F. J., Vooijs, R., Schat, H., Barker, J. H. A., and McGrath, S. P. 2004. Co-segregation analysis of cadmium and zinc accumulation in *Thlaspi caerulescens* interecotypic crosses. New Phytol. **163**: 299-312.

Zhao, F.-J., Lombi, E., Breedon, T., and McGrath, S. P. 2000. Zinc hyperaccumulation and cellular distribution on *Arabidopsis halleri*. Plant Cell Environ **23**: 507-514.

Zornoza, P., Vazquez, S., Esteban, E., Fernandez-Pascual, M., and Carpena, R. 2002. Cadmium-stress in nodulated white lupin: strategies to avoid toxicity. Plant Phys Biochem **40**: 1003-1009.

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Comment citer ce document :
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Figure captions

Fig. 1. Concentration of Zn^{2+} (A) and Cd^{2+} (B) in the solution of soils containing 300 mg $Zn.kg^{-1}$ SDW (Zinc) or 50 mg $Cd.kg^{-1}$ SDW (Cadmium). Letters indicate differences between values (n=3, $p<0.001$). Bars refer to standard error.

Fig. 2. Zn^{2+} content ($mg.kg^{-1}$ DW) in leaves (A) and stem (B) of *Populus tremula x P. alba* genotype 717-1B4 after 61 days of exposure to a soil containing 300 mg $Zn.kg^{-1}$ SDW (Zinc) or 50 mg $Cd.kg^{-1}$ SDW (Cadmium). Leaves and stems were separated into three parts depending on their position on the foliar axis. High part ( ), middle part ( ) and Low part ( ). Letters indicate differences between means (n=3, $p<0.05$). Bars refer to standard error.

Fig. 3. Zn^{2+} content ($mg.kg^{-1}$ DW) in xylem ( ), cambial zone ( ) and bark ( ) of the cutting of *Populus tremula x P. alba* genotype 717-1B4 after 61 days of exposure to a soil containing 300 mg $Zn.kg^{-1}$ SDW (Zinc) or 50 mg $Cd.kg^{-1}$ SDW (Cadmium). Letters indicate differences between means (n=3, $p<0.05$). Bars refer to standard error.

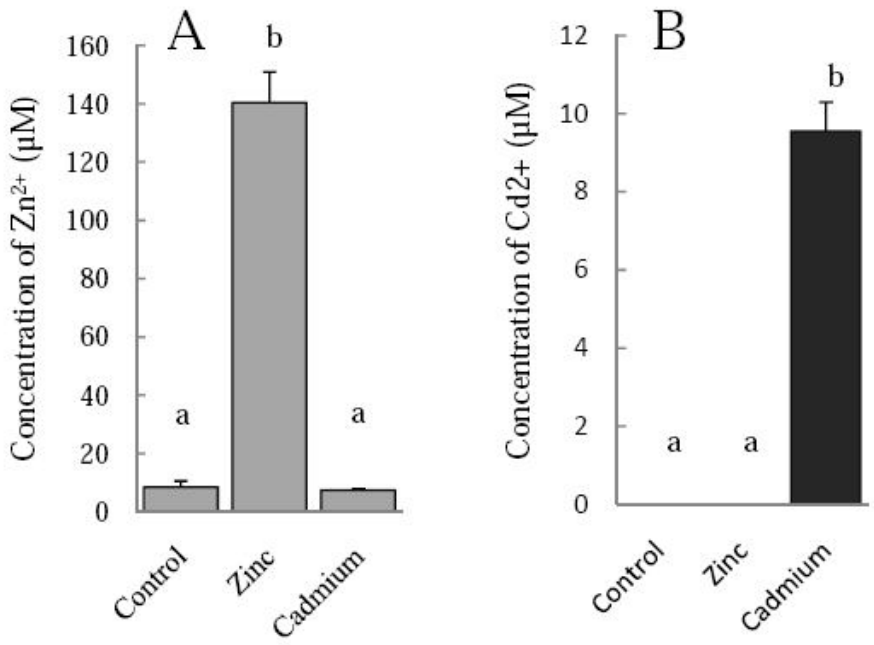
Fig. 4. Cd^{2+} content ($mg.kg^{-1}$ DW) in leaves (A) and stem (B) of *Populus tremula x P. alba* genotype 717-1B4 after 61 days of exposure to a soil containing 50 mg $Cd.kg^{-1}$ SDW. Leaves and stems were separated into three parts depending on their position on the foliar axis. In control and Zn-treated plants, no cadmium was detected. Letters indicate differences between means (n=3, $p<0.05$). Bars refer to standard error.

Fig. 5. Cd^{2+} content ($mg.kg^{-1}$ DW) in xylem, cambial zone and bark of the cutting of *Populus tremula x P. alba* genotype 717-1B4 after 61 days of exposure to a soil containing 50 mg $Cd.kg^{-1}$ SDW. In control and Zn-treated plants, no cadmium was detected. Letters indicate differences between means (n=3, $p<0.05$). Bars refer to standard error.

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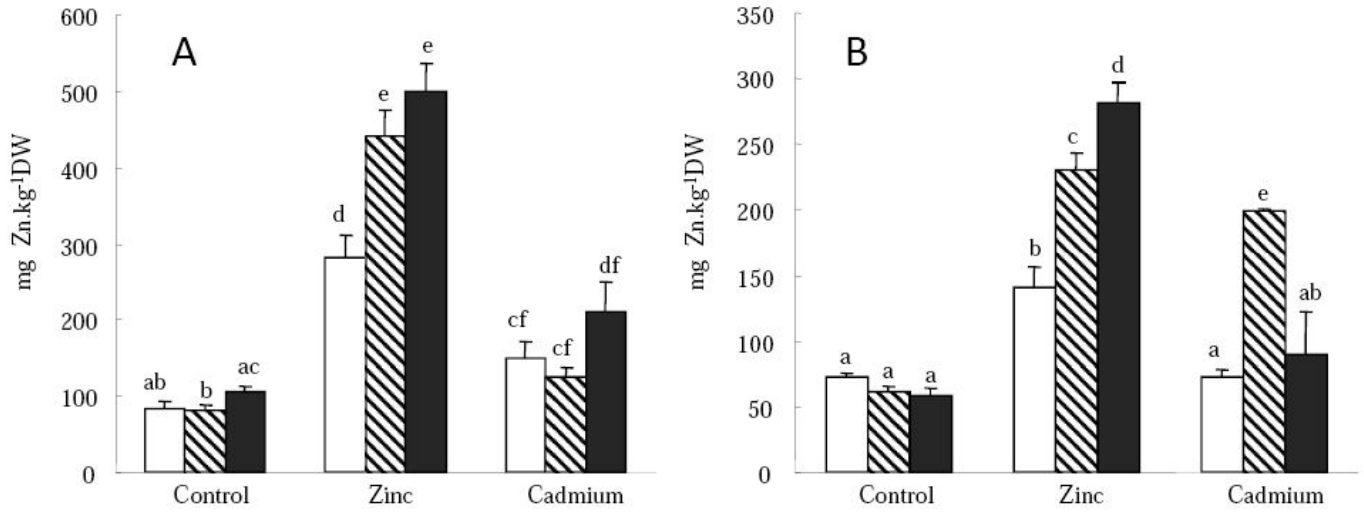
Fig.1



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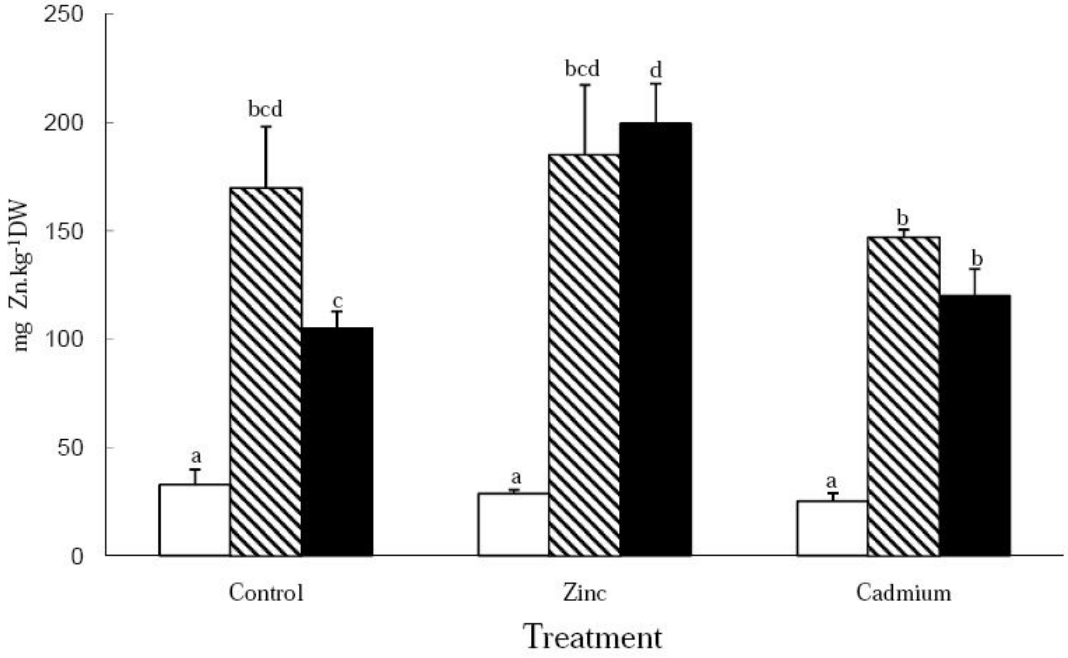
Fig.2



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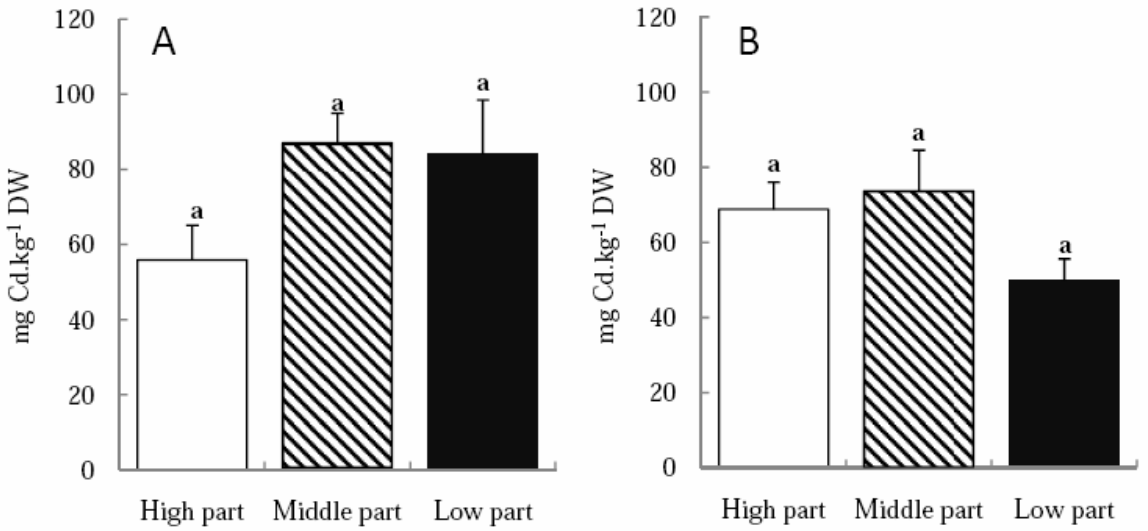
Fig.3



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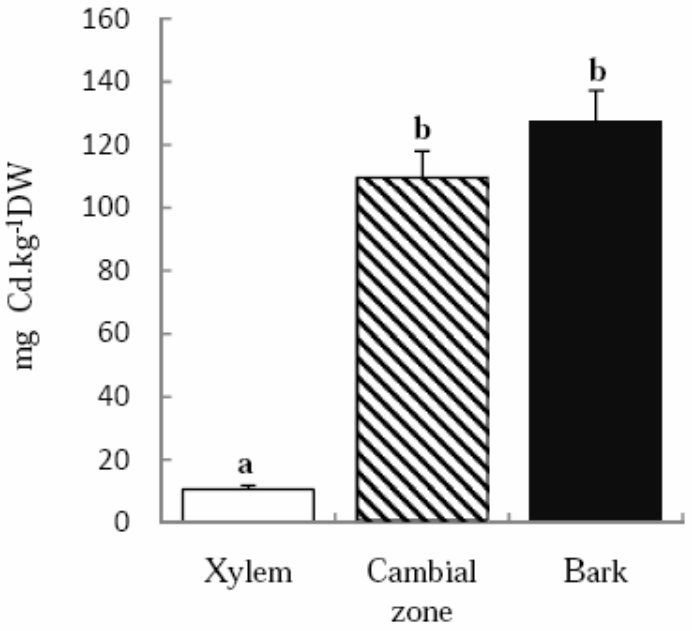
Fig.4



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Fig.5



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Table 1. Physiological traits of *Populus tremula x P. Alba* genotype 717-1B4 after 61 days of exposure to a soil containing 300 mg $Zn.kg^{-1}$ SDW (Zinc) or 50 mg $Cd.kg^{-1}$ SDW (Cadmium). Means were compared to control (n=3 or 5,* $p<0.05$).

	Treatment		
	Control	**Zinc**	**Cadmium**
Total leaf area (cm^2)	6060 ± 235	5249 ± 578	4325 ± 79 *
Stem height (cm)	98.2 ± 6.9	79.8 ± 4.2	72.5 ± 1.5 *
Stem diameter increase during 61 days (µm)	1126 ± 221	1100 ± 483	822 ± 555
Root dry weight (g)	4.07 ± 1.67	3.48 ± 0.63	2.76 ± 0.39
Cutting dry weight (g)	18.86 ± 1.35	19.97 ± 2.51	14.79 ± 2.69
Stem dry weight (g)	13.33 ± 1.40	10.64 ± 0.94	7.81 ± 0.27 *
Leaves dry weight (g)	29.81 ± 2.11	25.53 ± 2.66	17.45 ± 0.59 *
Root Water Content (%)	86.9 ± 1.3	88.8 ± 1.0	89.7 ± 1.0
Cutting Water Content (%)	59.8 ± 1.2	58.8 ± 0.8	61.7 ± 2.3
Stem Water Content (%)	70.2 ± 4.2	75.5 ± 2.2	74.5 ± 0.3
Leaf Relative Water Content (%)	74.2 ± 2.1	73.6 ± 0.6	75.3 ± 0.3
Net CO_2 assimilation (µmol CO_2. $m^2.s^{-1}$)	12.2 ± 1.91	11.43 ± 2.26	11.5 ± 1.95
Stomatal conductance (mmol H_2O. $m^2.s^{-1}$)	155.67 ± 29.04	154.0 ± 27.86	190.0 ± 21.78

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Table 2. Ion content ($mg.kg^{-1}_{DW}$) in different organs of *Populus tremula x P. alba* genotype 717-1B4 after 61 days of exposure to a soil containing 300 mg $Zn.kg^{-1}_{SDW}$ (Zinc) or 50 mg $Cd.kg^{-1}_{SDW}$ (Cadmium). Means were compared to control (n=3, **p<0.01, ***p<0.001). The relative distribution in the plant (%) is given between brackets. nd = non detectable.

Ion	Treatment	Roots	Cutting	Stem	Leaves
Zn^{2+}	Control	65.8 ± 2.12 (4.9%)	48.4 ± 4.8 (20.5%)	61.3 ± 1.9 (17.5%)	86.6 ± 3.4 (57.1%)
	Zinc	224.3 ± 22.4*** (5.1%)	64.1 ± 5.2** (8.2%**)	240.4 ± 12.4** (16.5%)	427.5 ± 23.7*** (70.2%**)
	Cadmium	60.2 ± 6.2 (3.9%)	46.3 ± 3.6 (15.2%)	139.2 ± 12.2** (24.5%***)	143.7 ± 12.2** (56.4%)
Cd^{2+}	Control	nd	nd	nd	nd
	Zinc	nd	nd	nd	nd
	Cadmium	79.0 ± 8.3*** (8.4%)	36.7 ± 3.8*** (20.3%)	63.8 ± 8.5*** (18.8%)	79.7 ± 7.7*** (52.6%)

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