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Soil to plant transfer of cadmium[☆]

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Abstract – In soil, cadmium (Cd) is mainly adsorbed onto organic matter and iron hydroxides. Due to the difference in transmembrane electrochemical potential, the hydrated ions (Cd^{2+}) present in the soil solution at the nanomolar level penetrate root cells. They hijack nutrient transporters such as those for iron, manganese, and zinc. Cadmium is mostly sequestered in the vacuoles of root cells, but some diffuses towards the vascular bundles, where it is released into the raw sap. It thereby reaches the aerial parts with the sap flow driven by transpiration. Transport proteins allow Cd to be released into the cells of stems and leaves, where is it stored and detoxified in the vacuoles and in the cell walls. A significant part of the Cd absorbed can be translocated *via* the phloem, depending on the plant species. It is through phloem flow that Cd reaches the seeds, either directly from the roots or through remobilisation from the stems and leaves. The Cd content in crops depends primarily on the soil Cd content and availability, and secondarily on the crop genotype. In France, while much has been done to reduce Cd availability in soils, genetic selection is a potential solution to further reduce the metal in harvests.

Keywords: cell walls / genotype / phytoavailability / transport proteins / vacuoles

Résumé – Le transfert de cadmium du sol à la plante. Dans les sols, le cadmium (Cd) est principalement adsorbé sur la matière organique et les hydroxydes de fer. En raison de la différence de potentiel électrochimique transmembranaire, les ions hydratés (Cd^{2+}), présents en solution dans le sol au niveau nanomolaire, pénètrent dans les cellules racinaires. Ils empruntent les transporteurs de nutriments, tels que ceux du fer, du manganèse et du zinc. Le cadmium est majoritairement séquestré dans les vacuoles des cellules des racines, mais une partie diffuse vers les vaisseaux du xylème, où il est libéré dans la sève brute. Il atteint ainsi les parties aériennes de la plante, porté par le flux de sève induit par la transpiration. Des protéines de transport permettent au Cd d'être déversé dans les cellules des tiges et des feuilles, où il est stocké et détoxifié dans les vacuoles et les parois cellulaires. Une part significative du Cd absorbé peut être transloquée *via* le phloème, selon les espèces végétales. C'est par ce flux phloémien que le Cd atteint les graines, soit directement depuis les racines, soit par remobilisation à partir des tiges et des feuilles. La teneur en Cd des cultures dépend avant tout de la teneur et de la biodisponibilité du Cd dans le sol, et dans une moindre mesure du génotype de la culture. En France, si de nombreux efforts ont permis de réduire la biodisponibilité du Cd dans les sols, la sélection génétique constitue une solution complémentaire pour limiter davantage la présence de ce métal dans les récoltes.

Mots-clés : parois cellulaires / génotype / phyto-disponibilité / protéines de transport / vacuoles

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[☆] Contribution to the Topical Issue: "Contaminants des huiles et corps gras / Contaminants in oils and fats".

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Highlights

Knowledge of the transfer mechanisms makes it possible to assess the risks of crop contamination by Cd under specific agro-pedological conditions and to optimise cultivation practices to reduce these risks. Existing research indicates that it would be possible to select varieties with low Cd accumulation for important crops.

1 Introduction

Cadmium is a toxic metal that accumulates in humans, with a biological half-life exceeding 30 years. It primarily targets bones and kidneys, contributing to conditions such as osteoporosis, kidney damage, heart disease, and even cancer. Aside from tobacco, food is the main source of population exposure to Cd. Shellfish and crustaceans are sources of exposure to Cd, and cereals, vegetables, roots and tubers are also responsible for the overexposure of certain segment of the populations of France and Europe (EFSA, 2012). In France, a little less than half of the French adult population has cadmiuria above the critical concentration threshold (Santé publique France, 2021). Cadmium in plants, including tobacco, comes mainly from the soil where it is taken up by the roots, translocated to the aerial parts and distributed in the different plant organs. Oilseed crops such as sunflower, rapeseed, soybean, and flax tend to accumulate more Cd than other crops, possibly due to their root system characteristics and metal transport mechanisms. While Cd content in wheat (*Triticum aestivum*) grain is often below 0.1 $\mathrm{mg\,kg^{-1}}$ (the maximum value in cereal according to the European regulation), that in sunflower (*Helianthus annuus*) kernels is frequently above 0.6 $\mathrm{mg\,kg^{-1}}$ (Li *et al.*, 1995 ; Zehra *et al.*, 2020). In soybean (*Glycine max*), it is often 0.1 $\mathrm{mg\,kg^{-1}}$, up to 0.4 $\mathrm{mg\,kg^{-1}}$ (Arao *et al.*, 2003), while in flaxseed (*Linum usitatissimum*) it is often above 0.3 $\mathrm{mg\,kg^{-1}}$ (Grant and Bailey, 1997). With average contents below 0.1 mg, mg Cd $\mathrm{kg^{-1}}$ in grain, rapeseed (*Brassica napus*), accumulates more Cd in stems and leaves than in other crops (Zhang *et al.*, 2024). Cocoa (*Theobroma cacao*) products can also contain high levels of Cd (Abt and Robin, 2020 ; Maddela *et al.*, 2020), so the European Commission (European Commisison, 2006) has fixed the maximum content at 0.6 mg Cd $\mathrm{kg^{-1}}$ in cocoa powder. As a point of comparison, Gramlich *et al.* (2018) measured an average content of 1.1 mg Cd $\mathrm{kg^{-1}}$ in cocoa beans grown on 55 cocoa farms in Honduras.

To reduce human exposure to Cd, it is necessary to lower metal levels in plant-based foods. To achieve this, the mechanisms that determine these levels must be understood. Historically, research into cadmium uptake by plants initially focused on the chemistry of the metal in soils and its availability for root absorption. The study of its absorption by roots and its distribution in the plant was initially carried out using ecophysiological approaches. This was followed by research into the biochemical mechanisms of cadmium toxicity, and more recently, molecular biology has enabled the identification of genes that influence plant tolerance to the metal and its distribution across organs and tissues.

Here we present an abbreviated synthesis of the mechanisms that govern the soil Cd supply to roots, its entrance into and its distribution around the plant. A more detailed presentation can be found elsewhere (Sterckeman and Thomine, 2020).

2 Cadmium in soil

Cadmium concentration in the upper continental crust is around 0.1 $\mathrm{mg\,kg^{-1}}$. It is generally higher in the surface horizon of cultivated soils, which receives Cd with atmospheric deposition, fertilisers or amendments. Current sources of Cd are phosphate fertilisers, representing about 60% of the inputs, organic amendments for about 25% and atmospheric deposition representing around 15% of the inputs in France (Belon *et al.*, 2012), where the mean Cd content in cultivated topsoil is 0.32 $\mathrm{mg\,kg^{-1}}$ (Saby *et al.*, 2019). This varies according to the geochemical background, *i.e.,* the Cd content of the soil parent material. For this reason, the mean Cd content in Aquitaine is 0.19 $\mathrm{mg\,kg^{-1}}$ probably because of the sandy soils from the Landes and 0.50 $\mathrm{mg\,kg^{-1}}$ in Poitou-Charentes because of a naturally enriched substrate. In Nord-Pas de Calais, the mean content is 0.43 $\mathrm{mg\,kg^{-1}}$, above the national mean, because of historical atmospheric deposition from industry, in particular from Pb and Zn metallurgy (Bourennane *et al.*, 2010 ; Sterckeman *et al.*, 2018).

In soil, cadmium exists primarily in the +2 oxidation state. Its concentration in soil solution is significantly lower than in the solid phase, typically below 10 nM. The dissolved metal forms various complexes with inorganic and organic ligands. The free hydrated ion Cd^{2+} is in equilibrium with inorganic complexes, such as $CdNO_3^+$, $CdHPO_4$, $CdCl^+$ or $CdSO_4$. It can also form dissolved complexes with organic ligands such as humic substances or organic acids (Ren *et al.*, 2015 ; Schneider *et al.*, 2019). The Cd content in the soil solution is controlled by the adsorption on mineral surfaces and the binding to particulate humic substances. Indeed, the soil is generally undersaturated in cadmium carbonate and phosphate —the minerals in which the metal is supposed to first precipitate (Tye *et al.*, 2003). Cd^{2+} sorbs on the edges of clay minerals and on iron hydroxides through surface complexation reactions, forming inner-(hydration) sphere complexes. It also adsorbs on permanently negatively charged clay minerals sites, forming outer-sphere complexes. A significant percentage of soil Cd binds with particulate fulvic or humic acid (Lofts and Tipping, 1998 ; Dijkstra *et al.*, 2009). All these sorption reactions imply an exchange of protons against Cd^{2+} and are reversible. Sorption of Cd in the solid phase is therefore strongly favoured by an increase in the soil pH. This can also be affected by the presence of Ca^{2+}, which can occupy binding sites.

On average, approximately half of the sorbed Cd^{2+} is in equilibrium with the metal in the soil solution (Sterckeman *et al.*, 2009), the rest being irreversibly bound to the solid phase, at least on the time scale of the measurement method (isotopic dilution). The distribution coefficient K_d ($\mathrm{L\,kg^{-1}}$) — defined as the ratio of element reversibly sorbed on the soil solid phase to the element in solution —is commonly used to model the sorption of the metal. For Cd, K_d is of the order of several hundreds, which indicates a strong sorption of the

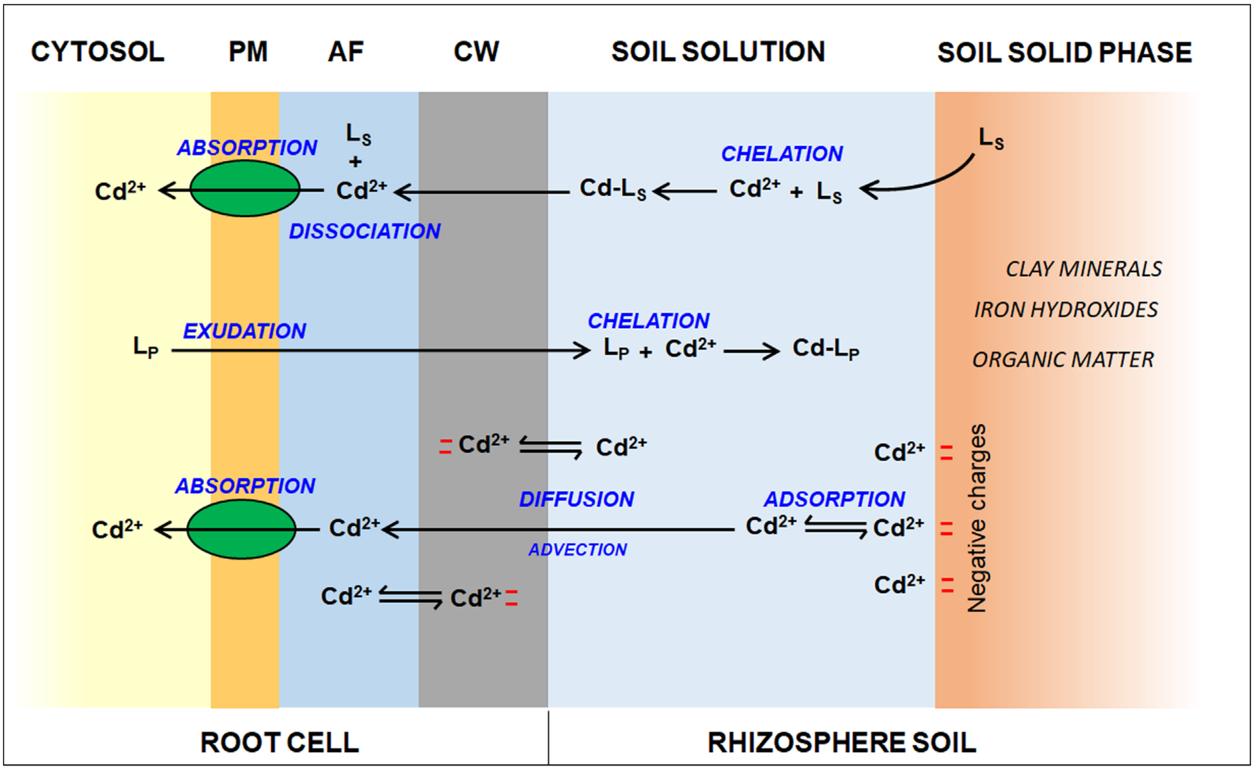

Figure 1. Schematic representation of the main reactions and processes controlling cadmium uptake at the root-soil interface. PM: plasma membrane, with two transport proteins (in green); AF: apoplastic fluid; CW: cell wall; L_S: organic ligand originating from the soil; L_P: organic ligand originating from the root exudates.

metal and it is often predicted by functions of the type (Degryse *et al.*, 2009):

$$\log(K_d) = a + b\,pH + c\log(C_{org}) \qquad (1)$$

This relationship reflects the importance of soil proton (pH) and organic carbon (C_{org}) contents on Cd sorption.

It is likely that compounds exuded by roots alter soil cadmium speciation, and thereby influence its bioavailability for root uptake. Excretion of H^+ or OH^- affects the sorption of Cd^{2+} and thus its concentration in the rhizosphere solution (Hinsinger *et al.*, 2003). Organic acids and phytosiderophores secreted by grass roots can complex Cd in solutions (Naidu and Harter, 1998 ; Shenker *et al.*, 2001).

3 Root uptake of cadmium

The transport mechanisms of Cd from soil to root are similar to that of other cations. The main cadmium form absorbed by root cells is Cd^{2+}. Root cells maintain a negative gradient of electrochemical potential across their plasma membrane, which drives the uptake of cations, including Cd^{2+}. The Cd^{2+} concentration at the root surface decreases as root cells absorbs the ion. This generates a concentration gradient along the radial distance to the root, which in turn drives diffusion of Cd^{2+} toward the root. Cadmium species also move toward the root at the same speed as water is taken up by the plant for transpiration. However, in the case of Cd, this transport by advection is generally negligible when compared to diffusion.

Additionally, as the Cd^{2+} concentration decreases in soil solution, the ion is desorbed from the solid phase to replenish the soil solution as the root depletes it (Figure 1).

The entry of Cd^{2+} into the root occurs through the outermost cell wall. The network of root cell walls constitutes the apoplast, through which the ion diffuses towards the root stele, where root vascularisation takes place. Some of the ions are absorbed into the apoplast, which contains electronegative sites capable of complexing the metal. When these meet the first apoplastic barrier, *i.e.*, deposits of impermeable polymers such as lignin (Casparian strip) or suberin in the apoplast, the Cd enters the cytoplasm, passing through transport proteins inserted in the cell membrane.

Depending on the plant species or location along the root, the first apoplastic barrier is the exodermis, located just after the root epidermis, or the endodermis which delimits the stele (Figure 2). It has been shown that the influx of Cd^{2+} is higher at the root tip than in older root parts (*e.g.*, Pineros *et al.* (1998); Chen *et al.* (2018)), due to incomplete development of apoplastic barriers or more intense activity of the membrane transporters. However, this would have no significant influence on the overall root uptake of Cd (Laporte *et al.*, 2013).

We wrote that plant roots mainly absorb Cd^{2+}, because it seems that they could absorb other species, such as $CdCl^+$, $CdCl_2$, or Cd-EDTA complexes (Smolders and McLaughlin, 1996; Schaider *et al.*, 2006). Direct absorption of complexes has not been proven, however, and would appear to be low, should it exist. Thus, it has been shown that the addition of EDTA to a nutrient solution containing Cd^{2+} strongly reduces

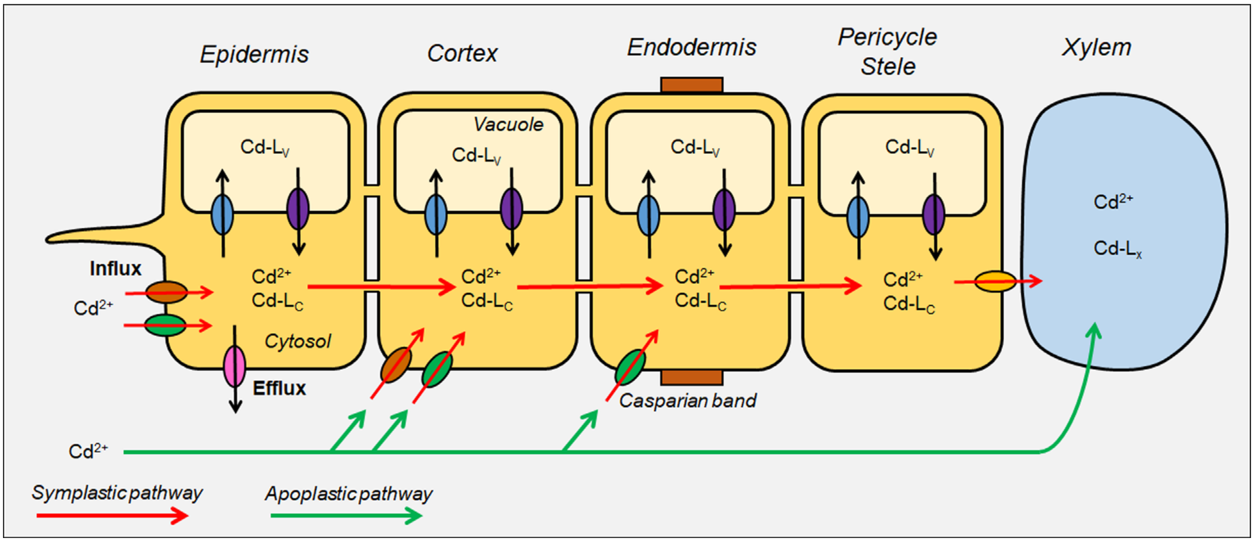

Figure 2. Schematic representation of root tissues with transport proteins involved in Cd transport. The cell walls are not shown. The apoplastic pathway travels through cell walls and apoplastic fluid and reaching the xylem in the root parts, where apoplastic barriers (Casparian band, suberin lamellae) are absent. Cadmium is represented as free hydrated ions (Cd^{2+}) or as complexes with organic ligands (Cd–L). L$_C$: Ligands of Cd in cytosol; L$_V$: ligands in vacuole; L$_X$: ligands in xylem.

the uptake of Cd by maize (Custos *et al.*, 2014). However, Cd complexes dissociate near the root surface, due to thermodynamic equilibrium when the Cd^{2+} concentration decreases as a consequence of root absorption (Figure 1). Therefore, these complexes are not inert regarding Cd root uptake and can be considered as a buffer, supplying the soil solution with Cd^{2+} as roots deplete it. However, the contribution of the complexes to the root uptake flux is minor, because the complex dissociation is not fast enough compared to the diffusion and desorption from the soil solid phase (Lin *et al.*, 2016 ; Sterckeman, 2023).

Since Cd is not essential for plants, it is not clear how a membrane transporter specific to its absorption would have appeared during plant evolution. It is therefore considered that Cd^{2+} hijacks micronutrient transporters with similar ionic properties. In particular, it has been shown with various plant species that the iron-regulated transporter IRT1, which transports Fe^{2+}, allows the transmembrane passage of Cd^{2+} and other divalent cations such as Co^{2+}, Mn^{2+} and Zn^{2+}. In *Arabidopsis thaliana*, this is mainly expressed in root epidermis and to a lesser extent in root cortex (Vert *et al.*, 2002). IRT2 which transports Fe^{2+} in rice (*Oryza sativa*) is also susceptible to transporting Cd^{2+} (Nakanishi *et al.*, 2006). Transport proteins of the NRAMP family, which are involved in Fe^{2+} and Mn^{2+} transport are also used by Cd^{2+} to enter the root cells. This is the case, in particular, for NRAMP1 and NRAMP5, which have been observed in species such as *A. thaliana* and rice (Thomine *et al.*, 2000 ; Ishimaru *et al.*, 2012).

Once in the root cell cytosol, Cd^{2+} can be chelated, stored in the vacuole or uploaded into the xylem sap. Phytochelatins (PC) are non-proteinogenic peptides which chelate Cd^{2+}, thereby contributing to its detoxification. Cadmium can be sequestered in the vacuole either as free Cd^{2+} or as PC-Cd complexes. The transport system located in the tonoplast and mediating the vacuolisation can be from the CAX family, which gathers H+/cations antiporters, like CAX2 and CAX4. It can also be from the P1B-ATPase subfamily HMA, such as HMA3. Transporters of the ABC family, like MRP3, MRP7, ABCC1, or AtABCC2 would enable the influx of PC-Cd complexes into the vacuole.

Cadmium can be leached from roots into the soil, as has been demonstrated by applying radioactive cadmium to the leaves of various plant species (Fismes *et al.*, 2005). A protein of the ABC family, PDR8, appears to be responsible for Cd root efflux in *A. thaliana* (Kim *et al.*, 2007).

4 Translocation and distribution of cadmium in aerial organs

In most plants, Cd is more concentrated in roots than in shoots, whereas the opposite is true for certain Cd-hyperaccumulators species such as, *Noccaea caerulescens*, *Solanum nigrum,* and *Sedum alfredii*. Close correlations between Cd concentration in xylem sap and in the shoots and grain of rice have demonstrated the key role of xylem transport in Cd accumulation (Uraguchi *et al.*, 2009). If chelation and vacuolisation explain the Cd sequestration in roots, they do not exclude the transport of the metal towards the xylem vessels and its loading into the xylem sap. Indeed, the metal can leak out of vacuoles —this efflux being caused by transport proteins located in the tonoplast, such as NRAMP3 and NRAMP4 (Oomen *et al.*, 2009). Diffusing in the cytosol from cell to cell through plasmodesmata, Cd reaches the stele and the tissues surrounding the xylem vessels. The efflux of Cd^{2+} into xylem is mediated by ATPases located in the cell membrane of the parenchyma cells around the tracheids. HMA4 has been shown to cause the Cd efflux into the xylem sap in *A. thaliana,* as well as in *N. caerulescens* (Papoyan and Kochian, 2004 ; Verret *et al.*, 2004). HMA2 appears to play a similar role in rice (Nocito *et al.*, 2011 ; Satoh-Nagasawa *et al.*, 2012). In the xylem sap, Cd is present either as free hydrated ions, or as complexes with organic and inorganic ligands (*e.g.* Wei *et al.* (2007) ; Cornu *et al.* (2016)). The proportions of the chemical

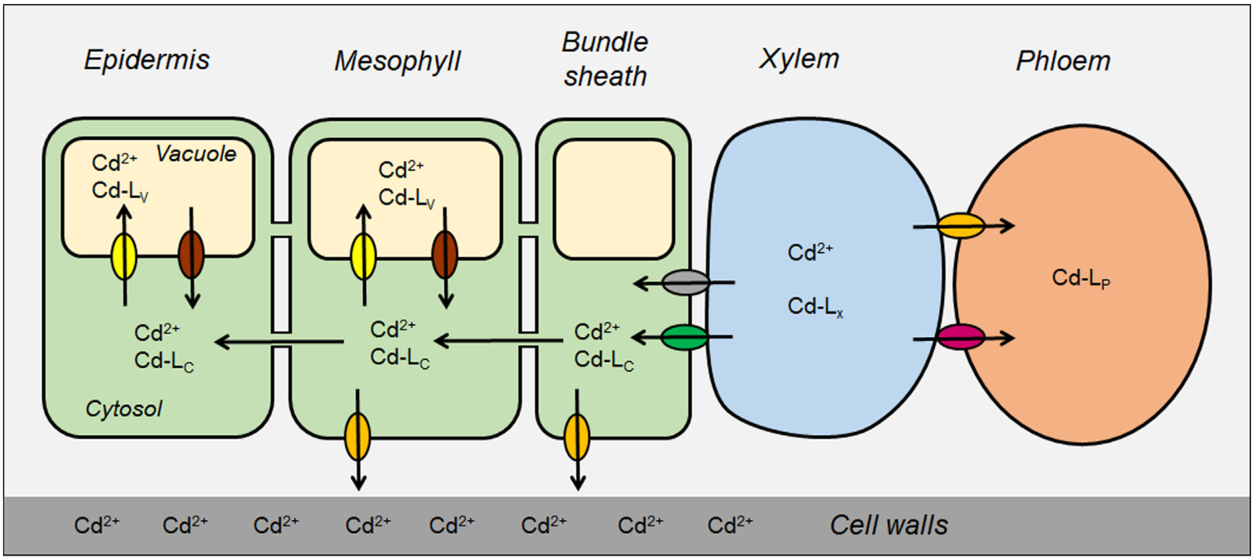

Figure 3. Schematic representation of leaf tissues with transport proteins involved in Cd transport. The cell walls are not shown. Cadmium is represented as free hydrated ions (Cd^{2+}) or as complexes with organic ligands (Cd–L). L_C: ligands of Cd in cytosol; L_V: ligands in vacuole; L_X: ligands in xylem; L_P: ligands in phloem.

species and the type of complexes vary according to the plant and the exposure conditions. Once in the xylem sap, Cd is carried to the aerial parts with the sap flow which is driven by plant transpiration and enabled by intermolecular forces.

Little is known about the unloading of Cd from the xylem sap and the distribution of the metal in the stem and leaf tissues (Figure 3). It is supposed to follow nutrient pathways, starting from the branched network of veins, which are particularly developed in the leaf blade. Cadmium ions may be transported from the xylem parenchyma through leaf cells using the symplastic pathway. More information is available where hyperaccumulating species are concerned, probably because Cd content in their aerial parts is sufficiently high to be measurable. HMA3 and HMA4, which are expressed in bundle sheath or in mesophyll depending on the species, seem to play a role in *A. halleri* and *N. caerulescens* (Mishra *et al.*, 2017). No difference was observed in the Cd absorption characteristics of mesophyll protoplasts from different species or populations of Cd hyperaccumulators (Cosio *et al.*, 2004). Vacuolar sequestration seems to drive the distribution of Cd in leaves (Cosio *et al.*, 2005 ; Leitenmaier and Küpper, 2011). In *N. caerulescens* and *S. alfredii*, Cd seems to be stored in vacuoles as complexes with malate (Ueno *et al.*, 2005 ; Tian *et al.*, 2011 ; Tian *et al.*, 2017). A significant part of the metal in the leaves was observed in cell walls, which also appear as a site for storing and detoxifying it (Cosio *et al.*, 2005 ; Vollenweider *et al.*, 2006).

At low Cd exposure, Cd is more concentrated in young leaves of *N. caerulescens*, while it is preferentially accumulated in older leaves of plants at higher exposure (Cosio *et al.*, 2005). In different species, it has been shown that the metal preferentially accumulated in the epidermis rather than in the mesophyll, because of higher absorption and vacuolisation influxes in the epidermal cells (Chardonnens *et al.*, 1998 ; Cosio *et al.*, 2005 ; Vogel-Mikuš *et al.*, 2008 ; Leitenmaier and Küpper, 2011).

Phloem also plays an important role in the distribution of Cd in plant tissues, in particular in fruits and seeds, where xylem can be interrupted unlike phloem. In rice, it seems that phloem can contribute to the direct allocation of Cd from the roots. Using direct observation by ^{107}Cd positron emission, Fujimaki *et al.* (2010) observed that the increase in Cd concentration in rice leaves was much slower than the flow of xylem sap. After 36 h, the metal had yet to reach the leaf blades, while it was detected in the panicles after 7 hours. In addition, Cd accumulated in the nodes and redistributed to the non-exposed roots. In fact, it was shown that Cd can be loaded into the rice phloem at the level of the first node immediately after the metal has been transported from the root (Kobayashi *et al.*, 2013). Phloem also appears to be involved in Cd transport from root to leaves in *Solanum melongena* and *Tagetes erecta* (Qin *et al.*, 2013 ; 2015).

As the iron transporter IRT1 is expressed in the rice phloem, stem and leaves (Ishimaru *et al.*, 2006), it cannot be excluded that it also contributes to the loading of Cd into the phloem. Moreover, the low-affinity cation transporter LCT1, expressed in the rice nodes and leaf blades seems to be responsible for xylem to phloem Cd transfer in the nodes and reallocation of Cd from leaves to grains (Uraguchi *et al.*, 2011 ; Uraguchi *et al.*, 2014). Another transporter, HMA2, highly expressed in the nodes close to the phloem, could also be involved in the Cd transfer from the xylem sap to the phloem (Yamaji and Ma, 2017).

As for other elements, the reallocation of Cd from shoots to fruits and seeds is considered to occur through the phloem mass flow, driven by an osmotically generated pressure gradient. In durum wheat (*Triticum durum*), Cd remobilised from pre-anthesis organs contributes to about half of the Cd accumulated in mature grains. The trace metal is mainly remobilised from the stem and roots, and poorly remobilised from leaves, which appear to be irreversible stores (Yan *et al.*, 2018 ; 2019). In sunflower, remobilisation through the phloem was estimated to account for 14% of the total Cd in mature seeds (Liñero *et al.*, 2018).

5 Conclusions: practical consequences

By integrating mechanisms and quantifying their effect, modelling is a research method to test hypotheses. It can also be a tool for predicting Cd content in the harvested organs, for diagnosing the risk linked to the agro-pedological conditions and for recommending practices designed to minimise the plant uptake of Cd. For instance, statistical models combining multiple Gaussian and logistic regressions with the random forest algorithm can be used to predict whether durum wheat grain Cd conforms to regulatory thresholds, based on soil variables and cultivars (Nguyen *et al.*, 2021). A mechanistic model of Cd uptake by roots has also been developed (Sterckeman *et al.*, 2004). The latter formalises the transport of different Cd species in the rhizosphere soil by diffusion and advection. The integration of this flux at the surface of growing roots allows an accurate prediction of Cd uptake by plants grown under controlled conditions (Custos *et al.*, 2014; Sterckeman and Moyne, 2021). The model is based on many variables and parameters related to the soil and roots and has made it possible to determine the most important of these by sensitivity analysis (Lin *et al.*, 2016). Such a model is more a research tool than a decision support one. However, it is not excluded that it could be integrated into a crop model, which would render it possible to predict the Cd content in the harvested part. To do this, it is necessary to formalise the distribution of metal in the aerial parts. At the moment, there is no model that allows this, as the laws of Cd allocation have yet to be clearly demonstrated.

To restrain Cd content in harvests, the first action is to reduce the input of Cd into soils, by continuing to limit emissions of the metal into the atmosphere and by reducing its content in the inputs used in agriculture. While we are encouraged to recycle our organic waste in agriculture in order to close biogeochemical cycles (in particular for P, C, and N), we must at the same time reduce the entry of Cd into these products. This involves reducing the use of Cd as much as possible and by treating the different wastes separately, so that the metal does not end up in those used as soil amendments. Phosphate fertilisers are currently the main source of Cd in soils in France and Europe (Six and Smolders, 2014 ; Sterckeman *et al.*, 2018). It is therefore appropriate to reduce the metal content in these fertilisers and to limit their use to what is strictly necessary.

For a long time, the use of the Cd hyperaccumulation capacity of certain species has been envisaged in order to remove Cd from the soil by phytoextraction. Simulations of phytoextraction scenarios in the French context showed that a Cd hyperaccumulating crop with a 10 t dry matter (DM) ha^{-1} yield every 25 years would reduce the soil Cd content from 0.31 $\mathrm{mg\,kg}^{-1}$ to around 0.11 $\mathrm{mg\,kg}^{-1}$ after a century (Sterckeman *et al.*, 2019b). However, this scenario is unrealistic, because such a high dry matter yield is unlikely and the cost of the process is high. Alternatively, phytoextraction as a cover crop every four to five years would decrease the soil Cd content more quickly and at a lower cost. This requires a 2.5 t DM ha^{-1} yield, which appears realistic. In France, it would need an annual sowing of around 4 million ha and the production of around 10 million t of dry biomass, which would have to be valorised, despite its toxic metal content. The breeding of such a hyperaccumulator should favour traits allowing a 3–4 month-cultivation period in the autumn. Unfortunately, the available hyperaccumulating plants have yet to be domesticated, which leads to difficulties in cultivating them and to insufficient dry matter production (Sterckeman and Puschenreiter, 2021). Although it seems there is no trade-off between Cd accumulation and dry matter production and a good heritability of metal accumulation properties (Sterckeman *et al.*, 2017; Sterckeman *et al.*, 2019a), we remain far from developing an efficient cultivar for cd phytoextraction.

We must therefore limit the availability of Cd in soils for absorption by roots, *i.e.* reduce its concentration in soil solution. Equation (1) tells us that in order to increase the sorption of Cd on the solid phase, it is necessary to increase the pH of the soil and its organic matter content. This can be done by liming soils that are too acidic, by limiting the use of acidifying fertilisers such as ammonium nitrate, by spreading organic amendments or restoring crop residues as much as possible and by planting green manures. However, in a country like France, these practices have largely already been implemented, and further reduction in the Cd content in crops through reinforcement would likely be minimal.

Various studies have shown that the concentration and distribution of Cd in a plant depend on the plant species and, within a species, on cultivars or genotypes (Florijn and Van Beusichem, 1993; Li *et al.*, 1995; Arao and Ae, 2003; Arao *et al.*, 2003; Greger and Lofstedt, 2004; Laporte *et al.*, 2015). The importance of genetic factors in Cd accumulation is not surprising given the determining role of transport proteins in the uptake and distribution of the metal, as shown above. This genetic variability indicates that Cd accumulation may be a selection criterion for the production of varieties with low Cd concentrations in the harvested parts. This criterion has been used in breeding programmes for durum wheat, sunflower, soybean and rice, in Canada, the USA and Japan, but these programmes have rarely led to cultivars being released onto the market (Grant *et al.*, 2008). Plant breeding is a long and complex process whose main steps are: 1) evaluating the genetic variation in the Cd content of the existing accessions, 2) describing the inheritance of the low-Cd genetic character, 3) developing a breeding strategy to combine low-Cd traits with other necessary traits and 4) developing methods to combine the low-Cd characteristic with other desired traits (Grant *et al.*, 2008). In addition, more steps are necessary for placing cultivars on the market (registration, multiplication, and show on). Moreover, identifying low-Cd phenotypes is more expensive and time-consuming than phenotyping for other traits, because of the cost of analysis (Grant *et al.*, 2008). This is why, to our knowledge, if step 1) has been carried out for various crops, only the selection of durum wheat, initiated in the 1990s, has led to the marketing of cultivars with low Cd accumulation (Clarke *et al.*, 2005). A breeding programme was also conducted in North Dakota to reduce the Cd content of sunflower kernels, which initially ranged from 0.31 to 1.34 $\mathrm{mg\,kg}^{-1}$ (Li *et al.*, 1995). This led to the release of lines with Cd concentrations below the average value, which could be used to produce hybrids with 50% less Cd in the kernels (Miller *et al.*, 2006). Although Cd accumulation is often higher in soybean, cocoa, flax, and rapeseed than in other species, no genetic selection has as yet led to the marketing of low-accumulation cultivars.

In France, Cd accumulation has not been a criterion for plant breeding until now, although Cd content in grain is now considered by growers when selecting a durum wheat cultivar (Nguyen *et al.*, 2021). This approach is beginning to be implemented, but much remains to be done to provide farmers with varieties that have low Cd accumulation.

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