PLANT CELL RESPONSES TO LEAD

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ABSTRACT

Current views on plant cell reactions to lead are reviewed. Lead uptake, translocation, early and secondary disturbing effects, as well as resistance mechanisms (avoidance and tolerance), with general characteristics of some metal binding compounds are focused on.

KEY WORDS: lead, disturbing effects, heavy metal resistance

INTRODUCTION

The dominant anthropogenic source of lead since about 1950 is combustion of leaded gasoline (Dörr et al. 1990). Lead emitted by automobiles is in aerosol form, and like the natural radioactive lead isotope ^{210}Pb (22 year half-life), is subject to atmospheric mixing and transport. After an average lifetime of about 5 days the lead exhaust aerosol particles are removed from the atmosphere by wet and dry deposition. Once in the soil, lead becomes very tightly bound to soil organic matter and is not taken up readily by plants, although sometimes its uptake may be high. For example it is an order of magnitude greater from acidic sandy soil than from other soils (Rostron 1990).

UPTAKE OF LEAD BY PLANTS

The main and the best known site of lead uptake from the environment into the plant is the root. Plant roots absorb different solutes (including lead solution) and water at the epidermis and/or the cortex of the root apex and release them into the vessels in the stele. The root cortex seems then to function as a collection system for solutes and water from the environment.

It is a matter of controversy, however, whether solute or water absorption occurs at the peripheral root layer (i.e., the epidermis and the subepidermal cortex) or deep within the cortex (Drew 1987). As for solution absorption, findings are increasingly supporting the view that the root periphery is almost the exclusive site of solute absorption (e.g. Malone et al. 1977, Kochian and Lucas 1983). For example, suberin incrustations in the radial cell walls of the hypodermis (Casparian bands), similar to those at the endodermis, develop close to the root tip of maize (Perumalla and Peterson 1986).

The apoplastic movements of some solutions such as fluorescent dyes: K^+ , P , and SO_4^{2-} seem to be restricted by suberin lamella in the hypodermis (Clarkson et al. 1987, Peterson 1987). It has been found, however, that in maize roots, the

presence of suberin incrustation in the hypodermis does not indicate a reduction of solute or water uptake (Clarkson et al. 1987). It would seem to be reasonable, therefore, to assume as follows: most solutes are absorbed at the peripheral layer of the roots (i.e., at the epidermis and the hypodermis); the cells of the mid- and deep-cortex participate not in solute uptake, but in the symplastic transport of solutes and water. They form a symplast together with the cells of the epidermis, and the hypodermis and stele (Taura et al. 1988). Cell and cell walls in the epidermis and the hypodermis are always juxtaposed in contrast to those in the mid- and deep-cortex, where aerenchyma often appears depending on the conditions of cultivation (Drew 1987). The peripheral cells are quite active in solute absorption (Kochian and Lucas 1983). The apoplast in the epidermis and the hypodermis can be considered a network of apoplast cell-wall canals, as has previously been proposed (Katou et al. 1987). According to the symplast model, an apoplast canal extends from the epidermis to the hypodermis only (Taura et al. 1988). The epidermal end is open to the root surface and the hypodermal end is plugged by the Casparian band. Solutes and water would enter the canal from the outer medium through the epidermal end and flow along the canal. The solutes and the water which enter the canal would be absorbed completely during the passage along the canal because the Casparian bands at the hypodermal end would restrict the passage of solutes. Epidermal cells also absorb solutes and water directly from the medium across the surface membranes (Taura et al. 1988). Lead enters the root by the cells of root hair zone, protodermal cells of the root tip and peripheral cells of the root cap (e.g. Książek and Woźny 1990 and literature cited therein). Probably no zone takes up more lead than others (Wierzbicka 1987). After it has been taken up, lead moves vertically and horizontally, probably within the primary cortex parenchyma cells. The endodermis functions as a barrier to radial Pb transport near the root tips. However, Pb can enter the central cylinder region due to the passage cells and/or breaks in the continuity of the endodermis as a result of the formation of lateral roots and of secondary growth (Książek and Woźny 1990).

Lead may reach the protoplast probably by two pathways:

- By passive diffusion across the plasmalemma because, for example, neither shoot removal, nor root death affect the lead

uptake rate (Jones et al. 1973, Arvic and Zimdahl 1974), - and/or by endocytosis. The presence of lead in coated and uncoated pits in the plasmalemma, and in coated and uncoated vesicles, as well as in endoplasmic reticulum and Golgi structures (Woźny 1987), allows to suppose that it could also be taken-up by endocytosis. This hypothesis is supported by the speed of appearance of lead in cells. A dozen or so minutes of incubation of roots in an aqueous solution of plumbous salt is enough to detect lead at the surface and inside the epidermal external cell wall. After one hour lead containing vesicles are present in the peripheral layer of the cytoplasm (Woźny 1987). Thus lead uptake by plant roots is not a simple non-metabolic absorption: lead ions in free intracellular root spaces were displaced only very slightly by barium ions, although both are of approximately the same size. In soil, lead could easily be replaced by barium (Jones et al. 1973). Results on lead uptake by onion roots (Wierzbicka 1987) also confirm the findings that lead can be taken-up from the surrounding solution against concentration gradients and deposited in large amounts in the root. The deposits are not easily washed out, even from fixed material, suggesting that most of the lead present in roots is bound.

REACTION OF PLANT CELLS TO AN EXCESS OF LEAD

DISTURBING EFFECTS

An excess of heavy metal ions may induce a series of biochemical and physiological alterations in plant cells.

Membrane damage (Kennedy and Gonsalves 1987), alterations of enzyme activities (Valle and Ulmer 1972, van Assche and Clijsters 1988) and the inhibition of root growth (Wilkins 1978, Breckle 1989) are considered characteristic features of heavy metal stress (Foy et al. 1978).

These early events lead to considerable secondary effects, such as hormone imbalance deficiency of essential nutrients (Burzyński 1987a, 1988, Meyer et al. 1987), inhibition of photosynthesis (Bazzaz et al. 1974, 1975, Clijsters and Van Assche 1985, Baszyński 1986 and literature cited therein, Poskuta et al. 1987, 1988), alterations of water relations (Burzyński 1987b), reduction of nuclei and cytoplasm dry mass, (Romaniuk and Gabara 1988), etc. which further enhance metal-induced growth reduction.

Plant cell membranes are generally considered to be the primary sites of metal injuries (Kennedy and Gonsalves 1987). Nano molar levels of triethyl lead (Et_3Pb^+) destroyed H^+ gradients in tonoplast vesicles of *Zea mays* coleoptiles (Hager et al. 1987). The electrolyte permeability in excised *Hordeum vulgare* leaf cell (Czarnecka 1990) and *Lupinus luteus* cell (Woźny 1987) plasma membrane increased with increasing Pb concentrations.

Cell expansion is generally severely inhibited by very low lead doses, which may be caused by the changes in cell wall characteristics (Lane et al. 1978, Sieghardt 1981, Burzyński and Jakób 1983). The inhibitory effect of lead on both root and plant growth has also been attributed to the lowering of mitotic activity (Mukherji and Maitra 1977, Przymusiński and Woźny 1985, Wierzbicka 1987, Woźny and Jerczyńska 1991). Cytokinesis was also found to be sensitive to lead (Röderer 1979b, 1986, Wierzbicka 1989). For example, triethyl lead is 250 times more effective than colchicine in inhibiting cytokinesis (Röderer 1979a).

At mitosis and cytokinesis of *Peterioochromonas malhamensis* were selectively disturbed by Et_3Pb^+ , it was reasonable to assume that Et_3Pb^+ interacts with the respective microtubule (MT) populations (Röderer 1986). Comparison with the effect of colchicine which is known to interact with MTs of numerous species in vivo and in vitro (Dustin 1978) clearly showed that colchicine selectively disturbed mitosis and cytokinesis of the algae (Röderer 1979a,b, 1981) causing effects qualitatively identical with those of Et_3Pb^+ . These effects were characteristic for the organic form of lead, while inorganic lead, even at much higher concentrations remained ineffective (Röderer 1986). On the other hand, when the adventitious roots of *Allium cepa* were treated with sublethal, as well as partly lethal Pb^{2+} derived from inorganic lead compounds (PbCl_2 and $\text{Pb}(\text{NO}_3)_2$), it was found that lead ions act as a strong poison to the mitotic spindle, inducing typical C-mitoses (Wierzbicka 1988).

HEAVY METAL RESISTANCE

Resistance reactions develop in the cells of all plants, but only in the cells of the resistance ecotypes do they develop enough to enable them to survive and reproduce (Baker 1987).

Generally, resistance mechanisms can act along either of two strategies (Levitt 1980): metal avoidance or metal tolerance.

- Avoidance mechanisms in higher plants include different processes limiting the rate of uptake of the toxic ion into the organ, tissue or cell.

- Tolerance mechanisms permit the plant to absorb the ion but act upon it in such a way as to minimize its effects.

Both strategies are found in plant resistance to lead:

Metal avoidance by:

a. exudation of metal chelating factors (e.g. polygalacturonic acid) into the rhizosphere and pH barrier at the root surface (Morel et al. 1983, 1986, 1987).

The addition of synthetic or natural chelators to culture solution usually decreases metal uptake and consequently, metal toxicity (Verkleij and Schat 1989). Metal uptake and toxicity is governed by its free ionic concentration and not influenced by the concentration of chelated metal (Sunda and Huntsman 1985). Resistant ecotypes release into their medium not only more, but also more effective chelators than not-resistant ones (Butler et al. 1980). Increased exudation of metal chelating compounds may represent a major mechanism of metal resistance in algae (Butler et al. 1980) and some flowering plants (Horst et al. 1982). However, the last point of view is sometimes not accepted (Verkleij and Schat 1989).

b. immobilization in the cell wall

Pb^{2+} and other metal ions have a special affinity to the pectic acid of the cell wall (Lane et al. 1978). The pectic fractions have a considerable cation exchange capacity and the ability to form cross-linked structures, hence one of the major roles of Ca in plant metabolism, so well suited to the binding of polyvalent cations (Fitter and Hay 1989).

High levels of Pb within cell walls were found in *Zea mays* (Malone et al. 1974), *Raphanus sativus* (Lane and Martin 1980, 1982), *Lupinus luteus* (Woźny et al. 1982), the aquatic species *Potamogeton pectinatus* (Sharpe and Denny 1976), the moss *Rhytidiadelphus squarrosus* (Gullvåg et al. 1974) and in tissue cultures of *Populus* (Książek et al. 1984). It was found that in the case of other metal ions like Cu^{2+} , Cd^{2+} , Zn^{2+} , the cell wall may contain 80-95% of the total

amounts of these metals which have been taken up by the cell (Nishizono et al. 1987, 1989).

c. selective permeability of the plasma membrane

Excessive uptake of nonessential or essential metals may be mediated by a less specific transferase system (Silver et al. 1972, Foy et al. 1978) or result from passive diffusions, either carrier-mediated or not. It is conceivable that changes in the composition or the molecular arrangement of the plasma membrane, which prevent unintended passive ion passage, might play a role in metal resistance, although there is no evidence for this idea (Verkleij and Schat 1989).

METAL TOLERANCE

Comparative work on intact cell cultures and leaf protoplasts of *Anthoxanthum odoratum* (Poulter et al. 1985) showed that the cell wall is necessary for lead tolerance. Higher plants, like other organisms, are believed to also possess intracellular systems which serve to reduce the availability of nonessential metals. When metal ions enter the symplast (cytoplasmic continuum) they may be complexed by special metal binding compounds like phytochelatins, homophytochelatins, organic acids, metallothionein-like proteins. Then those complexes are probably transported into the less active parts of the cell, e.g. into the vacuole. During the few last years studies of mechanisms involving special metal binding compounds inside the cell constituted a major proportion of the investigations connected with metal tolerance (Verkleij and Schat 1989 and literature cited therein). In spite of the fact that these mechanisms are better known for other metals like Cd, Cu, Zn, we would like to describe them here, especially because they are also connected with lead resistance.

Phytochelatins are characteristic for plants - these are small, cysteine-rich peptides which bind metal ions (Grill et al. 1985). Phytochelatins were isolated from cells of many plant species: water hyacinth (Fujita 1985, Fujita and Kawanishi 1986), *Silene cucuballus* (Verkleij et al. 1989), *Silene vulgaris* (Verkleij et al. 1990), *Zea mays* (Tukendorf and Rauser 1990), *Polygonum cuspidatum* (Kubota et al. 1988).

Phytochelatins are synthesized from glutathione (commonly present in eucaryotic cells (Law and Halliwell 1986, Mac Nicol 1987), have low molecular weights (2-6 kD) and are built from only three kinds of amino acids: L-glutamic acid, L-cysteine, and carboxyterminal glycine (Grill et al. 1985, 1987). The general structure of these peptides is $(\text{Glu}(\text{Cys})_n - \text{Gly})$, $n = 2 - 11$. They form mercaptide complexes between metal ions and thiolate groups (SH) (Grill et al. 1985, 1987, Tukendorf 1989, Steffens 1990) and then they are probably transported into the vacuole (Tukendorf - personal communication).

It has also been found that plants from the order *Fabales* exposed to Cd produced compounds similar to phytochelatins which are called homophytochelatins (h-PC) (Grill et al. 1986). They are homologous to phytochelatins but instead of glycine they contain β -alanine. Because of the repetitive Y-glutamic acid bonds as well as the presence of β -alanine in h-PC, both phytochelatin types can not be regarded as primary gene products. Phytochelatins are synthesized by ribosome independent enzyme reactions, which are self-regulated by the „free“ heavy metal ions that are subsequently chelated by peptides, thus terminating the reactions (Grill et al. 1989).

Similar complexes via thiolate coordination with heavy metal ions form metallothionein-like proteins. They were found in plant cells of *Zea mays* (Rauser et al. 1983), *Lycopersicon esculentum* (Bartolf et al. 1980, Lue-Kim and Rauser 1986,

Rauser 1986), *Polygonum cuspidatum* (Nishizono et al. 1988). Metallothionein-like proteins are different from phytochelatins because they have higher molecular weights, and contain a low proportion of aromatic acids (Nishizono et al. 1988).

Other groups of metal binding compounds inside the cytoplasm are organic acids. They form complexes with heavy metal ions through their COOH groups. The presence of metal ions, especially Zn^{2+} , which has a special affinity to COOH, Pb^{2+} (Qureshi et al. 1986), Cu^{2+} (Kishinami and Widholm 1987) induces a rise in the level of organic acids in the cell (Mathys 1975, 1977, Thurman 1981). A hypothesis has been presented which tries to explain the role of organic acids in plant cell resistance to Zn^{2+} (Mathys 1977). According to it, metal ions are bound in the cytoplasm by malic acid. Next, they are transported via an unknown route, into the vacuole. Inside, Zn^{2+} is passed on to citric acid. Free malic acid returns to the cytoplasm.

Data making it possible to determine which mechanism plays the major role in resistance of plant cells to lead is still incomplete (Woolhouse 1983).

To date most authors associate the resistance with:

- chelating metal ions by exuding substances within the rhizosphere

- accumulation of lead inside the root cells where it is bound by different compounds and transported into the vacuole.

Generally, it seems probable that all of these mechanisms take part in resistance of plants to heavy metals.

Such resistance seems to be a success but only from the „point of view“ of a single plant which can live under conditions which are lethal for other plants, and because it is able to colonize highly contaminated areas. However the „cost“ of resistance may be large and manifest itself, for example in slower growth rates and lower biomass production of many resistant plants in comparison with non-tolerant counterparts. This is the result of the expenditure of energy for generation of the resistance mechanism (Cook et al. 1972, Ernst 1976). Moreover, exceeding the lethal dose of the metal (different for every individual) always results in the death of the plant, even a resistant one.

Our final reflection is: we must remember that resistant plants especially those which accumulate large amounts of heavy metals in their organisms, may be dangerous for humans and animals as a link in the biological chain.

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REAKCJE KOMÓRKI ROŚLINNEJ NA OŁÓW

STRESZCZENIE

Przedstawiono współczesne poglądy dotyczące zarówno problemów pobierania, transportu oraz pierwotnych i wtórnych efektów działania ołowiu, jak również mechanizmów odporności na ołów (unikanie, tolerancja). Ponadto scharakteryzowano ogólnie niektóre związki wiążące metale ciężkie, takie jak: fitochelatyny, homofitochelatyny, kwasy organiczne i białka metalotioneino-podobne.

SŁOWA KLUCZOWE: ołów, efekty zakłócające, odporność na metale ciężkie.