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Regions of lead uptake in *Lemna minor* plants and localization of this metal within selected parts of the root

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Abstract

Investigations were carried out to determine the sites of lead uptake within the frond and the root of *Lemna minor*. With the sodium rhodizonate four regions favoured in lead uptake were distinguished: the frond region between the base and the node, the basal part of the root, and the regions at the proximal and distal ends of the root cap. For analysis in electron microscope only the root regions were chosen. The highest rate of lead uptake was found in the basal part of the root. Lead was present in the apoplast of this region after 5 min of exposure and was observed in the stelar cells after 30 min of incubation. Lead deposits were detected mostly in the cell walls adjacent to the plasma membrane and in the lumen of several endomembrane compartments - the endoplasmic reticulum (ER), dictyosomal vesicles, nuclear envelope and the vacuoles. Lead induced changes of cell ultrastructure; an increase in the number of membraneous structures, swelling of ER cisternae and distortion of the dictyosomal cisternae were observed after 2 to 6 h of exposure.

Additional key words: duckweed, Pb, ultrastructure.

Introduction

Lead, a non-essential toxic element, enters the environment through various industrial processes (Antonovics *et al.* 1971), burning of leaded gasoline (Cannon and Bowles 1962, Dörr *et al.* 1990) and to lesser extent from natural sources such as volcanic eruptions and fires (Nriagu 1979). Moreover, some agricultural practices, such as disposition of sewage sludge or application of town-refuse composts may increase lead accumulation in soil, its transfer to crops and thus to the food chain (Hinesly *et al.* 1972).

Studies on lead accumulation and effect on plants reveal that this metal is strongly phytotoxic and causes growth inhibition and even plant death (Foy *et al.*

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1978). The presence of lead in the environment has increased in some areas to levels which threaten the health of terrestrial and aquatic organisms. As a result of localized pollution, highly elevated levels of lead are found in plant roots and foliage. Movement of lead into higher plants through roots has been convincingly demonstrated, but not of lead particles deposited on leaf surfaces (Malone *et al.* 1974, Zimdahl and Koeppe 1977). When an analysis is made of the effects of lead on plants, questions relating to uptake patterns and deposition within the plant are often the first to be considered. In case of terrestrial plants there are no univocal answers yet, but there is even less information concerning lead uptake and its accumulation by aquatic macrophytes. It was the purpose of this research to investigate the initial stages of lead uptake and accumulation by *Lemna minor* L. in order to provide comparative material for further study.

Materials and methods

Lemna minor L. cultured aseptically for several years in the Laboratory of General Botany at the University of Poznań was used for all experiments. Stock cultures were maintained on Bollard medium (Bollard 1966) slightly modified by Lasociński (unpublished), pH 5.6, under continuous irradiance of 66 μmol(PAR) m^{-2} s^{-1}, temperature of 23 ± 1 °C and relative humidity of about 57 %.

Plants of identical morphological features, originating from a stabilized stock culture which was 5 - 6-d-old, were rinsed with bidistilled water and transferred to 100 cm^3 Erlenmeyer flasks containing 70 cm^3 of bidistilled water supplemented with 0.3 mM of lead in the form of lead nitrate. The experiment was conducted in three series, out of each ten randomly selected plants were taken for analysis.

Lead localization in whole plants by the rhodizonate method: The analyses of lead distribution in whole plants were performed with the light microscope, using the sodium rhodizonate method (Glater and Hernandez 1972) after treating the plants with $Pb(NO_3)_2$ at the concentration described above for 5, 15, 30, 120 and 360 min. Red staining indicated the presence of lead.

Lead localization in root cells by transmission electron microscopy technique: For electron microscopy studies the whole plants were fixed for several hours in a mixture (v/v) of 2 % glutaraldehyde and 2 % paraformaldehyde in 0.05 M cacodylate buffer of pH 6.8 (Karnovsky 1965). After fixation the plants were rinsed (3 × 15 min) with 0.05 M cacodylate buffer of the same pH. The root ends cut off at about half root length were then postfixed in 2 % osmium tetroxide in cacodylate buffer. The material was subsequently contrasted in 2 % water solution of uranyl acetate of pH 5.0, dehydrated in a series of acetones of increasing concentration and embedded in low viscosity resin (Spurr 1969). Ultrathin sections were obtained with *Ultrotomme III* (*LKB,* Sweden) ultramicrotome from three root regions (Fig. 1). The first region at the distal end of the root cap consisted only of root cap cells. The proximal end of the root cap comprised one root cap cells layer, the epidermis, 3 layers of parenchymatous cortex cells, the endodermis and the stele with one

tracheal element and two sieve elements. The root cap was separated from the root epidermis by an intercellular space filled with water. The third region - the basal part of the root just under the frond - consisted of the same layers, but the roots were enclosed by a root sheath instead of the root cap. The root sheath is a one-layered, membraneous tube formed by the epidermal cells.

The photographs of unstained sections were taken by a *JEM 7A* (*JEOLCo,* Japan) transmission electron microscope at 80 kV.

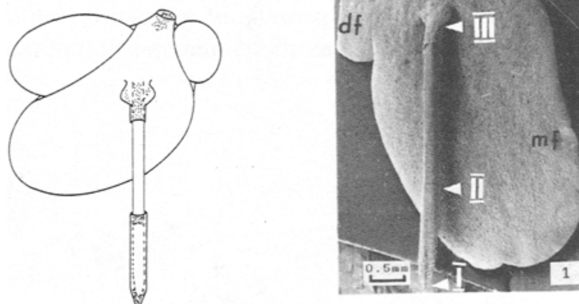


Fig. 1. Morphology of *Lemna minor*. Root regions from which the transverse sections were obtained (I region - distal end of the root cap, II region - proximal end of the root cap, III region - basal part of the root, mf - mother frond (seen from below), df - daughter frond).

Fig. 2. Localization of lead with the sodium rhodizonate method - shading marks the places in which the red staining, indicating the presence of lead, was visible. Light microscope, 15 min of incubation in aqueous lead solution. Drawing based on colour photographs.

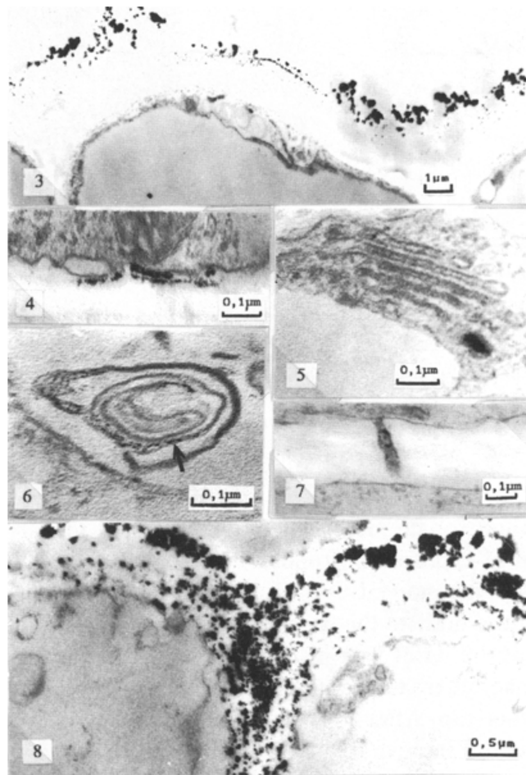
Results

With the sodium rhodizonate method lead was detected in *Lemna minor* plants as early as after 5 min of exposure in fronds as well as in roots. After this time, as well as after 15 min, the only stained part of the frond was the tract of elongated cells that run from the frond node to the base, and connected the frond with its progenitor (Fig. 2). In the root the basal part just under the frond showed the most intensive staining (Fig. 2). The other stained parts of the root were these at the proximal and distal ends of the root cap. After 15 min of exposure also some cells at the margins of the frond became red stained. After 30 min the staining was visible on the bottom side of the frond in the cell walls of the epidermis. The localization of the staining did not change with prolonging the time of exposure to 2 and 6 h, but its intensity slightly increased. In the root the intensity of red staining increased after 15, 30 min and 2 h of exposure, while the differences between the basal part and the other two regions disappeared. After 6 h of exposure to lead the slight, irregular, insular-like stains along the entire root length became also visible.

The light microscopical analysis served to identify the regions of *Lemna minor* plants most favoured in lead uptake. For the ultrastructural study of lead distribution within the cells of the most favoured regions the transmission electron microscopy

technique was used. Excluded from further analysis was the tract of elongated cells that run from the frond node to the base and connect the frond with its progenitor. In mature fronds this connection is severed and thus the continuity of the cells is broken. Therefore the positive result of reaction with sodium rhodizonate may be partly due to traumatic effect. Presented below are the detailed analyses of the cross sections at the distal and proximal ends of the root cap and of the region at the basal part of the root.

Because the root regions at the distal and proximal ends of the root cap contain relatively little lead after short periods of exposure, we resigned from the ultrastructural studies of these regions after 5 min up to 2 h of incubation.



Figs. 3 - 7. I region - distal end of the root cap. Transverse sections, transmission elrctron microscope. 2 h of incubation in aqueous lead solution. Fig. 3. Pb on the surface of the root cap. Fig. 4. Inner tangential wall of the cell from the most external layer. Pb in in the cell wall and in the space between the wall and the plasma membrane. Fig. 5. Pb in the dictyosome-derivated vesicle. Fig. 6. Pb (*arrow*) in the membraneous structure localized in vacuole. Fig. 7. Pb in the plasmodesma between the cells of the external and the subexternal cell layer of the root cap.

Fig. 8. I region - distal part of the root cap, 6 h of incubation in aqueous lead solution. Pb in the outer tangential and radial walls of the surface cells.

Distal end of the root cap: After 2 h numerous lead deposits were observed on the root cap surface (Fig. 3). In the cells of the most external layer lead deposits were present only in small numbers and located in the cell walls on the side of the plasma membrane (Fig. 4).

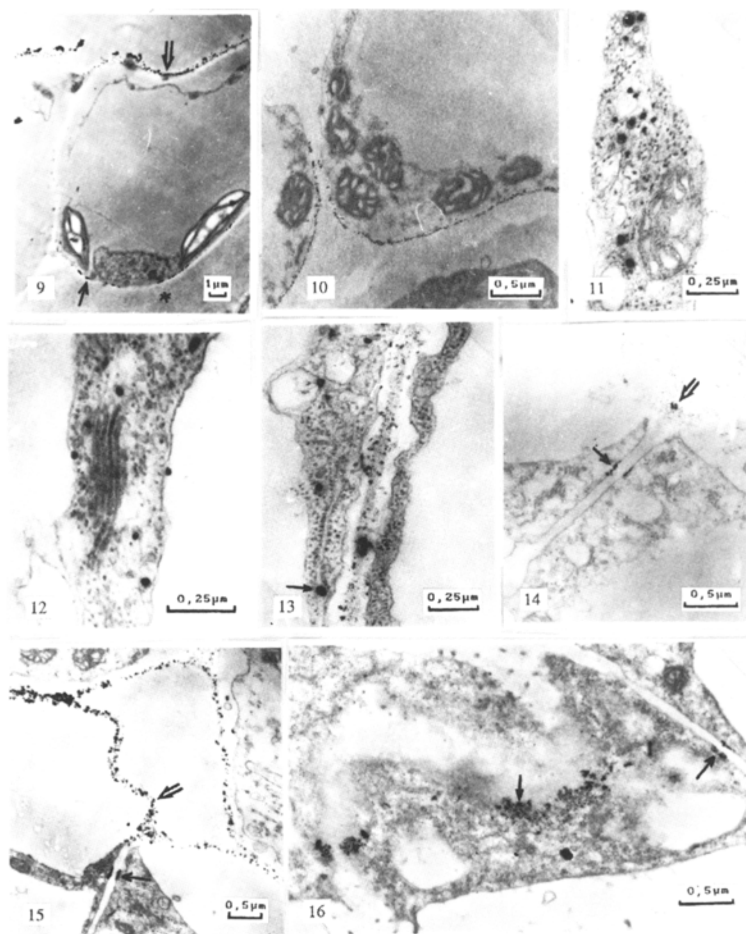
In deeper cell layers lead was observed as small deposits, mostly in the middle lamella, distributed uniformly on the whole cross section surface of the cap. Lead was also found in the lumen of the endoplasmic reticulum (ER) and in dictyosomal vesicles, in most cases at the trans pole of Golgi complex (Fig. 5). Moreover, deposits were localized in vacuoles, in vesicles of unknown origin, in membraneous structures (Fig. 6) and sporadically in plasmodesmata (Fig. 7). After 6 h of exposure lead was localized at the same places as after 2 h. The only observable difference was the increase of lead amount, especially pronounced in the cells of the external layer. In outer tangential and radial walls of this layer the amount of lead was very much higher than after 2 h of exposure (Fig. 8).

Proximal end of the root cap: After 2 h numerous and quite large lead deposits were found on the outer side of the external cell walls of the root cap (Fig. 9, *double arrow*). Small deposits were also sporadically noticed in the radial walls. In some root cap cells the deposits were either observed to be adjacent to the exoplasmic surface of the plasma membrane on the side of inner tangential cell wall, or they were localized in the cell wall near the plasma membrane (Fig. 9, *arrow*).

The cell walls of the epidermis were predominantly free of lead except for inner tangential walls where some deposits were found (Fig. 10). Lead was also localized adjacent to the plasma membrane on the side of the inner tangential cell walls. In epidermis cells lead deposits were present in vesicles in the proximity of Golgi complex. Sporadically lead was found in the swollen endings of endoplasmic reticulum profiles.

In the cortical cells lead was infrequently observed as disorderly distributed deposits in the cell walls. Besides, small deposits were observed occasionally in vesicles (Fig. 11), often Golgi derivated (Fig. 12) and in the lumen of the endoplasmic reticulum (Fig. 13). Lead was also sporadically present in the radial walls of the cell layer adjacent to the endodermis. Large amounts of lead were found in the intercellular spaces external to the endodermis (Fig. 14, *double arrow*). The endodermis itself and the stele cells were basically free of lead deposits except for the Casparian strip regions (Fig. 14, *arrow*). In some cases lead was also observed in the endodermis adjacent to the plasma membrane on the side of external tangential cell walls.

Continued lead exposure resulted in an increase of the amount of lead deposits but their distribution within the root cap cells, the epidermis and the three layers of cortex cells, was very similar after 2 and 6 h of incubation. After 6 h lead was deposited in especially large amounts in the radial walls of the cell layer adjacent to the endodermis, in tangential walls of these cells in the proximity of intercellular spaces, in the intercellular spaces external to the endodermis, and in the region of the Casparian strips (Figs. 15 and 16). Contrary to the 2 h incubation, lead was also present in the cytoplasm of the endodermis and parenchymatous stele cells. Deposits were observed in ER cisternae (Figs. 17 and 18a), in double membraned vesicles



Figs. 9 - 14. II region - proximal end of the root cap. Transverse sections, transmission electron microscope. 2 h of incubation in aqueous lead solution. Fig. 9. Fragment of the root cap which consists (in this region) of only one cell layer. Visible space between the root epidermis and the proximal end of the root cap, normally filled with water (*starlet*). Pb on the outer side of the external cell walls (*double arrow*) and in the inner tangential cell wall near the plasma membrane. Fig. 10. The cells of the root epidermis. Pb in the space between the inner tangential cell wall and the plasma membrane. Fig. 11. The subepidermal cell. Pb in vesicles. Fig. 12. The subepidermal cell. Pb in the dictyosome-derivated vesicles. Fig. 13. The cell of the cortex parenchyma. Pb in the lumen of ER (*arrow*) and in the cell wall. Fig. 14. The endodermis cell. Pb in the intercellular space external to the endodermis (*double arrow*) and in the region of the Casparian strip (*arrow*).

Figs. 15 - 16. II region - proximal part of the root cap. Transverse sections, transmission electron microscope. 6 h of incubation in aqueous lead solution. Fig. 15. Fragment of the endodermis. Pb in the intercellular space external to the endodermis (*double arrow*) and in the region of the Casparian strip (*arrow*). Fig. 16. The endodermis cell sectioned tangentially to the Casparian strip. Pb in the region of the Casparian strip (*arrows*).

and membraneous structures localized in vacuoles (Fig.18a,b), in plasmodesmata (Fig. 19, *arrow*) and in perinuclear space (Fig. 20).

Basal part of the root: The distribution of lead deposits in the basal part of the root and in the region at the proximal end of the root cap was very much alike, but as was shown by the rhodizonate method and confirmed by the electron transmission microscope, lead was present in apoplast of this region as early as after 5 min of exposure. After 30 min of exposure, in case of about 30 % of roots, lead deposits were found also in the vacuoles of the stele cells (Fig. 21). Especially large amounts of lead were observed after the same time period in the intercellular spaces external to the endodermis (Fig. 22) as well as in the surrounding cell walls.

Lead-induced changes of cell ultrastructure: Changes in ultrastructure occurred after 2 to 6 h of exposure to lead, before the appearance of macroscopic toxicity symptoms. In comparison with control plant cells there was an observable increase in the number of membraneous structures, often containing small lead deposits (Figs. 17 and 18a,b). The Golgi complex showed distortion of the dictyosomal cisternae - they became swollen in the middle (Fig. 19). Considerable changes occurred also in endoplasmic reticulum which sometimes formed concentric structures (Fig. 23). The swollen ER cisternae were also frequently observed to form vesicles (Figs. 19 and 24). The vacuoles contained membraneous structures and double membraned vesicles containing lead deposits (Fig. 18a,b). No differences were found in the size of the nucleus, but in several cases, as mentioned above, small lead deposits were observed in the nuclear envelope (Fig. 20).

Discussion

According to many publications, *Lemna minor* is very sensitive to metals (Wang 1986, Smith 1991). This may be due to the rapid absorption and accumulation of metal ions in the plant body. We have established that lead is present in *L. minor* apoplast as early as after 5 min of exposure. Our results agree with the reports of other authors for terrestrial plants. (Wierzbicka 1987a, Woźny 1987). Based on autoradiographic studies (^{210}Pb) it was determined that lead penetrates apoplast of the first four cell layers of the *Allium cepa* adventitious roots within 5 to 15 min of incubation (Wierzbicka 1987b). According to the same author lead is taken up from solution with the same rate along the entire root length. Other authors have reported that lead enters the root through the cells of the root hair zone, protodermal cells of the root tip and peripheric cells of the root cap (Książek and Woźny 1990). The results of our research indicate that in *Lemna minor* roots, three regions favoured in lead uptake can be distinguished. These are: the root tip which comprises only the root cap cells, the region at the proximal end of the root cap, and the basal part of the root. The apical region of the root, favoured in lead uptake in terrestrial plants, is relatively long and reaches from the root tip as far as the root hair zone. As has been stated, in apical region of *Lemna minor* roots, unlike terrestrial plants, lead is taken up by the very end of the root comprising the root cap cell alone, and also by

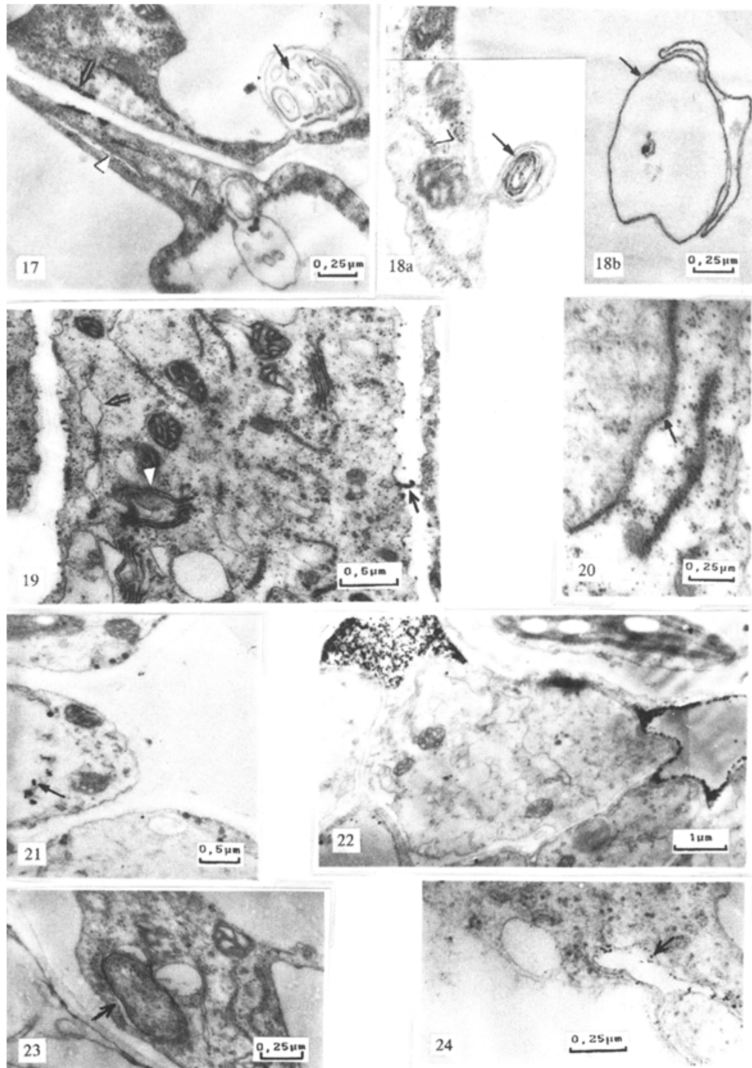


Fig. 17 - 20. II region - proximal end of the root cap. Transverse sections, transmission electron microscope. 6 h of incubation with aqueous lead solution. Fig. 17. The cells of the endodermis. Pb in ER (*white arrow*), in the membraneous structure localized in vacuole (*black arrow*), and in the Casparian strip (*double arrow*). Fig. 18. The cells of the endodermis. Fig. 18 a - Pb in ER (*white arrow*) and in the membranous structure (*black arrow*). Fig. 18 b - double-membraned vesicle (*arrow*) containing Pb. Fig. 19. The cell of the stele parenchyma. Pb in the plasmodesma between the cells of the stele and the endodermis. Swollen ER cisternae (*double arrow*) and the swollen dictyosome (*white arrow*). Fig. 20. The cell of the stele parenchyma. Pb in the perinuclear space (*arrow*).

quite narrow band including proximal end of the root cap together with a respective part of the root. The fact that the basal part of the root takes up lead with such a high rate is also quite surprising. Such an uptake region is unusual for terrestrial plants. *Lemna minor* is an aquatic plant and as such it is characterized by different ecophysiology (Agami and Waisel 1986), which may add to the dissimilarity observed. The lack of continuity in staining of the root by the rhodizonate method poses the question of how lead is transported in the root after it has been taken up. Our observations may suggest that lead is transported vertically in *Lemna minor* roots for only very short distance or is transported in amounts undetectable with an electron microscope. However, several studies on the subject confirm that after lead has been taken up by the roots of terrestrial plants, it moves vertically and horizontally within cortex parenchyma cells (Woźny 1987, Książek and Woźny 1990, Gzyl - unpublished). The endodermis functions as a barrier to the radial apoplastic transport of Pb ions from the cells of the cortex into the central cylinder (Tanton and Crowdy 1971, Książek and Woźny 1990, Punz and Sieghard 1993). Apoplastic Pb can enter the central cylinder 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 the secondary growth (Książek and Woźny 1990). In *Lemna minor* lead is present in the stele at the proximal end of the root cap after 6 h of exposure. Since in this region the endodermis cells have fully developed Casparian strips, it can be inferred that it has been taken up by and transported centripetally in the root tip, where the Casparian strips are absent, and then transported vertically in the central cylinder. Another possible explanation is that lead may enter the symplast of this region by 2 to 6 h of exposure. We hypothesise that this can be possible because of a direct transport from apoplast to vacuoles. Ultrastructural evidence for such a pathway, omitting the cytoplasm, was observed in *Stachys sieboldi* and associated with the storage of carbohydrates within the vacuolar compartment (Auriac and Tort 1985). Invaginations of plasma membrane protruded into the vacuoles and formed "plasma membrane-tonoplast" double membraned vesicles. In the basal part of *Lemna minor* roots lead was observed in the vacuoles of the stele cells after only 30 min of exposure. Such a quick penetration of lead into the vacuoles is an argument in favour of the hypothesis that a direct transport (without participation of the cytoplasm) may be possible. We have also frequently observed double membraned vesicles containing lead deposits in the vacuoles of the stele cells.

The data on ultrastructural changes agree with the results of other authors for plants grown in conditions of heavy metal excess. Enhancement of vacuolisation was observed in response to lead in lupin root cells (Przymusiński and Woźny 1985,

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Fig. 21 - 22. III region - basal part of the root. Transverse sections, transmission electron microscope. 30 min of incubation in aqueous lead solution. Fig. 21. Fragment of the companion cell. Pb in the vacuole (*arrow*). Fig. 22. Pb in the intercellular spaces external to the endodermis.

Fig. 23 - 24. Ultrastructural changes. II region, transverse sections, transmission electron microscope. Fig. 23. The endodermis cell. Concentric configuration of ER (*arrow*). Fig. 24. The endodermis cell. Swollen ER cisternae containing Pb (*arrow*).

Stoyanova and Tchakalova 1993). Lead induced disruption of Golgi complex was clearly demonstrated in cells of the poplar adventitious root tip (Idzikowska 1988). Addition of nickel sulphate to the nutrient medium resulted in degradation of Golgi apparatus in leaves of sunflower seedlings by the second day of exposure (Slivinskaya 1991). Several authors have also reported enlargement of nuclei in meristematic zones of lupin and pea roots in the presence of lead (Przymusiński and Woźny 1985, Romaniuk and Gabara 1988). No such enlargement was observed in the case of *Lemna minor* roots. Concentric configuration of ER, similar to the ones described in this work, were observed in *Lupinus luteus* and *Zea mays* (Woźny 1987, Woźny *et al* 1994), as well as in *Pinus sylvestris* (Idzikowska 1987) and *Funaria hygrometrica* (Krzesłowska - unpublished). The changes in ER, chiefly ER proliferation, formation of vesicles and concentric structures, appear to be one of the most common structural reactions of plant cells to lead. It is not surprising in view of the role of ER in lead ions isolation, which reduces the availability of the toxic metal in the cytosol.

The ultrastructural changes due to the effect of lead bear evidence of disturbances of metabolic processes at the cell level. If the study of these disturbances is to be fully understood, it cannot be discussed apart from the uptake and distribution patterns. Therefore the analysis of these issues should be continued.

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