Adaptation of plants to an environment polluted with heavy metals

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Abstract

This paper presents the problem of tolerance of plants to heavy metals. Induction, development and stability of tolerance are described. Multiple and co-tolerance are presented in the context of specificity of acquired tolerance to heavy metals. Phenomena involved in the uptake and distribution of metals in plant tissues along with the mechanisms of exclusion and accumulation are discussed. The problem of tolerance development in plants is presented also in the light of the nutritional conditions that plants most often encounter in contaminated environments.

Key words: heavy metals, tolerance, plants

INTRODUCTION

Man's activities are responsible for creating whole areas with significantly elevated levels of heavy metals. These metals are highly toxic and therefore present a danger to the life and health of mankind (Schubert 1973). These contaminated areas are mainly dump sites for steel mill and technological wastes, areas affected by industrial fallout and automotive exhausts, as well as old metal miner or excavation sites (Bradshaw 1975, Rauser and Winterhalder 1985, Fabiszewski 1986, Baker 1987). Fertilizers are also contaminated with heavy metals and because of this, compounds containing them pass into the soil and into the food produced on it (Mengel and Kirkby 1983).

No biological function has yet been established for such heavy metals as lead or mercury. Many others, however, including zinc and copper, are micronutrients required by living organisms as part of coenzymes or prosthetic groups of

enzymes belonging to numerous metabolic pathways. In large amounts, however, these metals are also harmful (Tomsett and Thurman 1988).

With time, contaminated areas are gradually populated by plants which have developed a resistance to the metals in the soil. These are, however, slow processes. If large-scale cultivation of varieties of plants that are resistant to heavy metals was possible, then rapid recultivation of ever increasing contaminated areas would become a reality. For this reason it is important to recognize and understand the processes involved in the appearance and establishment of tolerance in plants. Many problems of heavy metal tolerance in plants were reviewed in recent years, among them evolutionary and genetical aspects (Antonovics et al. 1971, Walley et al. 1974, Bradshaw 1975, MacNair 1981b, Baker 1987), methodology (Wilkins 1978, Baker 1987) or mechanisms of tolerance on the cellular level (Thurman 1981, Brown and Shrift 1982, Foy 1983a, Stavarek and Rains 1984, Borkowska 1988, Tomsett and Thurman 1988, Tukendorf 1989). This paper presents problems involved in heavy metal tolerance on the level of the whole plant — cellular tolerance mechanisms are excluded from the scope of this review.

TOLERANCE AND ITS CLASSIFICATION

Plants considered to be resistant to metals are those which show only slight, if any, growth reduction at the concentrations of metals in the environment at which susceptible, unresistant plants die or show very stunted growth (Bradshaw 1975, Thurman 1981). It is believed that a population of plants must have considerable genetic variability in order to adapt to an environment rich in heavy metals (Antonovics and Bradshaw 1970, Bradshaw 1975, Karatagliis 1980). Plants which develop tolerance are those whose normal populations have tolerance genes. If such a population is subjected to a high concentration of heavy metals, individuals lacking tolerance die, the remaining resistant ones give rise to a tolerant population (Bradshaw 1975, Walley et al. 1974). It is therefore seen that tolerance may develop suddenly in several or even in one generation. However, it takes several or even over ten years to form a stabilized population that is tolerant to the given metal (Bradshaw 1975, Wu et al. 1975a). For example, a 4-year-old population of *Agrostis tenuis* resistant to copper exhibits an average tolerance level of 21%, a 7-year-old population — 32%, a 15-year-old population — 42% (Bradshaw 1975).

The following types of tolerance are recognized (Tomsett and Thurman 1988):

Constitutional tolerance — refers to plants growing in unpolluted areas. It is therefore assumed that these plants had never previously been in contact with the metal but nonetheless exhibit a high tolerance to a potentially toxic level of this metal.

Co-tolerance — is found when a tolerance developed towards one metal may confer tolerance to a different metal/metals with which the plant had never been in contact with before.

Multiple tolerance — is when a population of plants has a tolerance to two or more metals whose levels in the soil have been elevated.

The concept of constitutional tolerance has evoked a certain degree of controversy. Its existence in respect to such toxic metals as lead, zinc, copper and cadmium has been questioned (Antonovics et al. 1971). According to these authors, species do not have constitutional tolerance to heavy metals — their resistance begins to develop when the plants come into contact with them in a polluted environment.

However, the use of tolerance tests to compare species has shown distinct differences in the resistance of plants to metals, although they did not grow on metallic soils. For example, from among four studied species of plants from unpolluted areas (Kroez et al. 1989), the most resistant to aluminum was *Arnica montana*, followed by *Antennaria dioica* and *Viola canina* with *Filago minima* — the least tolerant. However, the differentiation of resistance to manganese was slightly different. *Filago minima* was the least resistant while the tolerance of the remaining three species was rather high and similar to each other. It was also found that the resistance to aluminum of *Arnica montana* growing on contaminated soil was just as high as that of an Al-tolerant plant — *Deschampsia flexuosa* from a region with an elevated aluminum level. Other authors have also carried out comparative studies on the tolerance of plants that had never been in contact with heavy metals. Hutchins et al. (1986) compared the resistance of five species of conifer seedlings to aluminum, Alliot et al. (1983) studied the resistance of five species of algae to heavy metals: Cd, Cr, Cu, Hg, Ni, Se, Tl, Benac (1976) investigated the resistance of corn and peanuts to Mn, Horst (1985) — of three cereal species to aluminum. In all of these cases more or less pronounced differences in tolerance to metals were found. Reeves and Baker (1984) also come out in favor of the existence of constitutional tolerance in their study on the uptake of metals by two *Thlaspi goesingense* populations. Nothing yet is known, however, about the mechanism of constitutional tolerance or on how it is related to the remaining types of tolerance. It may be possible, though, that the described differences in the tolerance of plants from non-polluted areas can be the result of the various capabilities for physiological adaptation of various plant species within the limits set by their genotype. It has also not been ruled out that the resistance of plants growing in an unpolluted area may be acquired, eg. by crossing with resistant plants growing in other areas — either during the present generation or during preceding ones. Karatagliis (1986) and Karatagliis et al. (1986) have described examples of increasing the resistance to metals of plants growing on unpolluted soil by crossing them with resistant plants growing near the grounds of an old mine. This is explained by gene flow on the assumption that tolerance has a genetic basis (Urqurt 1970,

Gartside and McNeilly 1974, Hertstein and Jäger 1986, Karataglis 1980a, b, c, 1986).

Another problem related to the remaining two types of tolerance — co-tolerance and multiple tolerance — is the question of the specificity of tolerance. An elevated level of two or more metals in the environment is the stimulus inducing the development of specific multiple tolerance to them in the plant species growing on such a site (Jowett 1958, Walley et al. 1974, Bradshaw 1975, Karataglis 1980b, Fisher 1981). In addition, this tolerance is greater the higher the concentration of the metal/metals in the soil (Karataglis 1982, Hertstein and Jäger 1986). It has been found, however, that plants exhibit tolerance to only those metals found in relatively large amounts in the soil (Ernst 1975, Mathys 1975, Karataglis 1978, 1980b, 1982). Under natural conditions, a specific metal is often accompanied by others as admixtures, multiple tolerance therefore develops. This type of tolerance has been found in very many plant species. It has been described in *Festuca rubra*, *Agrostis tenuis* and *Arrhenatherum elatius* by Hertstein and Jäger (1986) to cadmium, zinc, lead and copper, in *Deschampsia cespitosa* to copper, nickel and cadmium by Cox and Hutchinson (1981), in *Agrostis capillaris* and *Festuca rubra* to lead and zinc by Karataglis et al. (1986), in *Agrostis tenuis* to lead, zinc and copper (Karataglis 1980a, b, 1982) as well as to numerous metals in *Silene burchelli*, *S. cobalticola*, *Agrostis gigantea*, *Deschampsia cespitosa*, *Hordeum jubatum*, *Poa compressa* and *Melilotus alba* (Miller 1982, Baker et al. 1983, Rauser and Winterhalder 1985) and in algae to copper and nickel by Stokes (1981).

The concept of the specificity of tolerance was related to the suggestion that tolerances to different metals were independent of each other both genetically and physiologically (Coughtrey and Martin 1979). Walley et al. (1974) have shown that 1-2 % of a normal, non-tolerant population of *Agrostis tenuis* survives on soil rich in copper as well as in zinc. Tests conducted on these plants showed that they developed full tolerance to copper but a significantly lower tolerance to zinc. These authors' studies led them to put forth their hypothesis that tolerances to various metals are independent of each other.

However, the existence of co-tolerance would contradict specificity of tolerance developed to a given metal. *Deschampsia cespitosa* growing in the vicinity of a nickel and copper plant developed multiple tolerance to nickel, copper and aluminum present in the soil in higher amounts, but additionally developed resistance to lead and zinc, in spite of the fact that the soil lacked these metals (Cox and Hutchinson 1979). Environmentally induced tolerance to zinc, copper, lead and cadmium in *Festuca rubra*, *Agrostis tenuis* and *Arrhenatherum elatius* was accompanied by the appearance of tolerance to Ni, whose level in the soil was not elevated (Hertstein and Jäger 1986). Co-tolerance was found not only in higher plants (Gregory and Bradshaw 1965, Cox and Hutchinson 1980, 1981, Symeonidis et al. 1985, Verkleij and

P r a s t 1989) but also in the algae *Scenedesmus acutiformis* and *Chlorella fusca*, which, inhabiting a lake polluted with nickel and copper — also exhibited tolerance to silver which was not present in the environment (Stokes et al. 1973 — cited according to C o x and H u t c h i n s o n 1979). This would suggest the existence of certain physiological tolerance mechanisms which can reduce sensitivity to other metals to such a degree as to make the plant resistant to a different metal, not present in its environment (C o x and H u t c h i n s o n 1979, H e r t s t e i n and J ä g e r 1986). Studies on the tolerance of four grass species to copper, nickel and zinc when only the soil levels of copper and nickel were elevated showed the presence of co-tolerance only in *Deschampsia cespitosa*, while it was lacking in *Agrostis gigantea*, *Hordeum jubatum* and *Poa compressa*. The occurrence of co-tolerance may therefore be a characteristic trait for a given species (R a u s e r and W i n t e r h a l d e r 1985).

THE STABILITY OF TOLERANCE

What happens when plants growing on contaminated soil are transplanted to unpolluted soil and cultivated on it for some time? The tillers of the grass, *Holcus lanatus*, resistant to cadmium were collected from a contaminated site, rooted and cultivated for five years on unpolluted soil. Its tolerance level was tested every year. A significant drop in tolerance was found after only one year of cultivation on clean soil (B a k e r 1984). We are therefore dealing with a changeable, environmentally induced, reversible response of plants to an elevated soil cadmium level which would indicate that, in this case, tolerance was not directly determined genetically.

However, the studies by S i m o n (1977) on *Agrostis tenuis* and *Festuca ovina* gave contradicting results. Resistance was retained, which the author attributed to the genetic basis of the tolerance of these species. Similar results were obtained for Cu-tolerant *Agrostis tenuis* (K a r a t a g l i s 1980a) and zinc and Pb-tolerant forms (B r a d s h a w 1952) — tolerance did not diminish after two years of growth on uncontaminated soil.

How then can such diametrically different results be explained? The paper by B a k e r et al. (1986) provides interesting results. Comparative studies on diminishment of tolerance were conducted on Cd-tolerant *Holcus lanatus*, a grass collected from the grounds of an old mine and from sites contaminated mainly by atmospheric pollution. These plants were grown for 3 years on unpolluted soil. It was found that the populations which came from the mine grounds were more stable in respect to tolerance to cadmium than those from the sites with atmospheric pollution, in which tolerance diminished. In the case of the plants from the mine grounds, strong selection forces in the form of high concentrations of cadmium, almost reaching toxic levels, were at work from the very start. These concentrations are high enough to rapidly cause permanent genotypic changes in the population, leading to tolerance to the metal. On the other hand, it is

suggested that in areas subjected to atmospheric pollution causing gradual contamination, the concentrations with which plants come in contact increase gradually, selection also develops gradually since selection initially causes only a small number of the plants least able to adapt to die. Only with time, as the metal concentration in the soil's surface layer increases the forces of selection increase, and therefore only those individuals with a high degree of tolerance will survive (Baker et al. 1986). In a population gradually poisoned with rising concentrations of metals, physiological adaptation within genotypically defined limits probably occurs in many individuals and such plants die only after their adaptation limit is surpassed while their genotype remains unchanged. Such plants will surely be found among those which lose their tolerance when transplanted to unpolluted soil.

TISSUE CULTURES IN TOLERANCE STUDIES

Cell cultures have also been used in the study of tolerance of plants to heavy metals. Much valuable information on the mechanisms involved in tolerance has been gained from the comparison of results of studies using cell cultures and parent plants.

Explanted tissues of cauliflower, lettuce, potato and carrot were subjected to zinc, copper, mercury and lead. All of these tissues showed growth inhibition and their response to the same level of metal was similar to that of their parent plant (Barker 1972). Similar results were obtained by Wu and Antonovics (1978) in studies on zinc and copper tolerance of whole plants and *Agrostis stolonifera* callus. These authors concluded that tolerance to these metals is determined genetically and operates on a cellular level. Ojima (Ojima et al. 1984, Ojima and Ohira 1985, 1988) investigated tolerance to aluminum of tolerant and non-tolerant carrot cell lines. He then carried out the regeneration of plants from both callus lines. After bringing them to flower and self-pollination, he obtained seeds from which he grew Al-tolerant seedlings.

Studies on Zn- and Pb-tolerant and Zn- and Pb-sensitive populations of *Anthoxanthum odoratum* also showed that the tolerance of the parent plant is maintained in the callus. The callus initiated directly from a tolerant parent plant was resistant to Pb and Zn (no growth reduction), while addition of Cu and Ni, to which it was not resistant, inhibited its growth. It can be concluded from this that tolerance to metals is not dependent on the presence of differentiated tissues (Qureshi et al. 1981). Although no difference was found between the tolerance of callus and its parental plant (as determined by growth ability), a distinct difference was found between the amounts of accumulated metal. Plants tolerant to zinc and lead accumulate significantly more metal than non-tolerant ones, whereas in both resistant and sensitive lines the amounts of zinc and lead in callus tissues increase with the increase in their external concentration. A similar situation is found in respect to copper and nickel. Therefore, in spite of retaining

a similar tolerance as in its paternal plant, the metabolism of metals in the entire plant is somewhat different than in callus. It can therefore be concluded that the usefulness of tissue cultures in studies on tolerance to heavy metals is limited. They can be used in controlling those mechanisms functioning at the cellular level which are not dependent on the structure of the whole plant (e.g. shoot-root interactions) or related to functions affecting the whole plant (e.g. photosynthesis, transport in the plant) (Stavarek and Rains 1984).

INDUCTION OF TOLERANCE UNDER LABORATORY CONDITIONS

Studies on the various processes involved in tolerance to metals are best done using two populations of the same species — tolerant and sensitive. An inferior approach is to carry out studies on different populations with different tolerances. Tolerant and sensitive populations of the same species are usually collected from polluted and unpolluted sites inhabited by the species in question. However, plants tolerant to metals can be obtained by inducing tolerance under laboratory conditions. In most cases this is achieved by administering low concentrations of the metal over an extended period before giving a higher, more toxic dose. In this way, a tolerant population of *Medicago sativa*, resistant to aluminum, was obtained (Campbell et al. 1988). Similarly, by exposing a *Holcus lanatus* population to low concentrations of cadmium, a rise in its tolerance to this metal was achieved (Brown and Martin 1981, Baker et al. 1986). A Cd-resistant *Euglena gracilis* line was also obtained using this method — wild cells were cultivated for 6 months in the presence of 5×10^{-4} M CdCl_2 (Bariand and Mestre 1984).

Experiments of this type have also been carried out on cell cultures. By subjecting *Nicotiana tabacum* cells to long-term exposition to increasing concentrations of cadmium (Huang and Goldsbrough 1988, Domazlicka and Opatrny 1989) or potato cells to aluminum (Wersuhn et al. 1986), cell lines were obtained that were capable of growth in concentrations of metals that were lethal to the initial lines. Al-resistant callus cell lines obtained from carrot hypocotyls were selected from a suspension by subjecting it to a 4 mM solution of AlCl_3 (Ojima and Ohira 1988).

Another method of obtaining cell lines resistant to metals under laboratory conditions is the mutagenization method. It was used on the callus of *Petunia hybrida* (Colijn et al. 1979). An Hg-resistant callus line was obtained by mutagenization of initial callus cells using 1-methyl-3-nitro-1-nitrosoguanidine followed by selection with 20 $\mu\text{g/ml}$ HgCl_2 .

THE "NEED" HYPOTHESIS

Studies on tolerant plants have shown that they often grow better on soil enriched with metals than in an uncontaminated environment (Bradshaw 1952, Antonovics et al. 1971, Mathys 1975, Coughtrey and Martin

1977, Simon 1977, Cox and Hutchinson 1980). Not only has growth stimulation been observed, but also a positive correlation between the soil content of heavy metals and the dry weight of resistant plants (Bradshaw 1952, Coughtrey and Martin 1977, Cox and Hutchinson 1981, Rauser and Winterhalder 1985). This is true also for germination. *Deschampsia cespitosa* seeds collected from metallurgic plant grounds contaminated with copper and nickel germinate better on soil containing these metals than they do on control, unpolluted soil (Cox and Hutchinson 1980).

The above observations led to the formulation of the "need hypothesis" which suggests that the evolution of tolerance to metals is accompanied by the phenomenon of increased requirement of tolerant plants for higher levels of the metal to which it has adapted (Antonovics et al. 1971). Grime and Hodgson (1969) have, however, proposed a different explanation of this phenomenon. It is probable that in resistant plants, the efficiency of metal detoxication mechanisms is so high that access to the metal internally becomes difficult for the plant until the point when its internal concentration becomes sufficiently high.

It is not known, however, if this phenomenon applies only to those metals needed by the plant as micronutrients participating in the normal growth and development of the plant or if it also applies to such metals as Pb and Hg.

TOLERANCE AND THE AMOUNT OF METAL IN THE PLANT

Plants growing on sites contaminated by heavy metals accumulate various amounts of them in their tissue. They differ in their abilities to accumulate metals both in respect to the amount which may be stored in tissues without causing them harm as well as in their ability to selectively take up metals from the soil. This is manifested in the ratio between the amount of metal in the plant's tissues and its concentration in the soil. This served as the basis for classifying plants into three groups (Baker 1981), differing in their plant/soil relationship in respect to metal concentration (Fig. 1).

Fig. 1. Three ways in which the response of plants to increasing soil metal levels may be reflected by the metal concentrations in aerial plant parts (Baker 1981)

Accumulators — accumulate metals both at low and high soil metal levels, mainly in their above-ground parts (Fig. 1a). The following plants belong to this group exhibiting a high tendency for accumulation of metals: *Thlaspi alpestre*, *Minuartia verna* and *Psychotria douarrei* (Kersten et al. 1980, Baker 1981). Reeves and Baker (1984) described exceptionally high accumulation of nickel, zinc, cobalt and manganese by *Thlaspi goesingense*, and Reeves (1988) reported intense accumulation of zinc and nickel by the species *Thlaspi* and *Cochlearia*. Studies on plants growing on sites rich in selenium showed that most of the accumulators found there belonged to the genus *Astregalus* (Brown and Shrift 1982). Other plants characterized by hyperaccumulation of metals are, among others, endemic species growing on serpentine soils, that is, especially rich in nickel, but also in zinc, cobalt, chromium. These are e.g. *Alyssum serpylliforum* (Brooks et al. 1981) and *Serbertia acuminata* which accumulate up to 25% nickel in their cytoplasm, expressed in relation to dry weight (Jaffre et al. 1976). Intense accumulation of copper has in turn been described in the above-ground parts of *Becium homblei*, in which no mechanism limiting the uptake of the metal has been found. Regular fires of the bush, where this plant grows, destroy its stems and leaves. This probably prevents the plant from becoming poisoned from its unlimited accumulation of the metal (Reilly and Stone 1971).

Indicators — uptake and transport of metals to shoots is regulated so that the metal's internal concentration is a reflection of its external level (Fig. 1b). Proportionality between the concentration of a metal in a plant and its concentration in the substrate has been observed, among others, in respect to cadmium in *Brassica napus* (Lehn and Bopp 1987), zinc in *Triodia pungens* (Nicolls et al. 1965), *Minuartia verna*, *Festuca ovina* and *Agrostis tenuis* (Barry and Clark 1978) and in other herbal species (Fabiszewski 1986, Babalonas et al. 1987, Van Erp and Van Lune 1989).

Excluders — the concentration of a metal in the shoots is maintained on a low level in spite of its high concentration in the environment. However, after a certain level is surpassed, the mechanisms excluding metal from the shoots cease to function, transport to the shoot becomes unchecked and may lead to the death of the plant (Fig. 1c). These plants accumulate large amounts of metal in their roots. Very many plants, including both herbs and crop plants, belong to this group. Among them are *Silene maritima* after administration of zinc (Baker 1978), *Anthoxanthum odoratum* after zinc and lead (Qureshi et al. 1985), *Agrostis tenuis* after cadmium (Hertstein and Jäger 1986), *Agrostis stolonifera* after copper (Wu et al. 1975b), *Medicago sativa* after aluminum (Campbell et al. 1988), corn after cadmium, lead, copper and zinc (Lelova et al. 1986).

It must be noted here that the same plant can be an accumulator in respect to one metal and, at the same time, be an indicator or excluder in respect to others. For example, *Triodia pungens* (Nicolls et al. 1965) is an indicator for zinc while

an excluder for lead and copper, *Thlaspi alpestre* is an accumulator in respect to zinc and cooper but an excluder for lead, *Minuartia verna* is an accumulator for zinc and an excluder for lead and copper (Ernst 1974 — cited according to Baker 1981, Barry and Clark 1978).

EXCLUSION AND ACCUMULATION MECHANISMS

The three different types of plants described above have certain mechanisms functioning on the level of the entire organism which allow them to tolerate large amounts of metal in their tissues. These include the mechanism of exclusion which functions to protect the stem from excess concentrations of metal ions, in which the roots play the main role in storage of metals. The mechanism of accumulation allows plants to store large amounts of metals in their shoots (Bartuska and Unger 1980, Tingey et al. 1982). The fact that metals are preferentially stored in various parts of plants without harm to them suggests that tolerance mechanisms did not evolve accidentally on the cellular level in particular plant parts.

Exclusion is the mechanism most frequently encountered in tolerant plants. These are the plants which accumulate mainly in their roots the heavy metals which they have taken up and strictly control the amount of metal transported to the above-ground parts. It is thought that they possess a mechanism which limits the translocation of metals to shoots (Wu and Antonovics 1975, Wu et al. 1975b, Thurman 1981, Qureshi et al. 1985). Using Zn-tolerant and sensitive *Silene maritima* clones, Baker (1978) showed that up to 0.5 ppm, the Zn content in the roots and stem was similar in both populations. Above this concentration its amount in the roots of tolerant plants equalled 70-80% of the total zinc content in the plant, while in the not-tolerant population, 30-50%. It was concluded that tolerance to zinc is manifested here in the general reduction of uptake, limited transport to shoots and accumulation in roots. Qureshi et al. (1985) studied the tolerance to zinc, lead and copper of *Anthoxanthum odoratum* populations from regions with elevated zinc and lead levels and in control populations. Clones from the contaminated regions were tolerant only to Zn and Pb and exclusion of metals from shoots was observed in them. There was, however, no tolerance to copper and its accumulation in plant parts was the same in both populations. Tolerance to cadmium in *Agrostis tenuis*, *Festuca rubra* and *Arrhenatherum elatius* is, according to Hertstein and Jäger (1986) related to its concentration in shoots — it is lower in more tolerant populations. The main difference among the populations was the degree of pollution of the soil needed to reach the same cadmium concentration in the shoots of two tolerant *Agrostis tenuis* populations. It was estimated to be 4-5 times higher than in not tolerant populations. It has also been shown that the exclusion mechanism found in *Silene burchelli* var. *angustifolia* and *S. cobalticola* is more effective in respect to

cobalt than copper (Baker et al. 1983). Limited transport of heavy metals from roots to shoots in tolerant species manifesting itself in preferential accumulation in roots has also been observed in other plants, including *Holcus lanatus* after administration of zinc, cadmium and lead (Coughtrey and Martin 1979), *Medicago sativa* and other plants after aluminum (Foy 1983a, Campbell et al. 1988), *Mimulus guttatus* after Cu (MacNair 1981a), the genus *Silene* from Zair after Cu and Cd (Baker et al. 1983) and *Silene vulgaris* after cadmium (Verkleij and Prast 1989), corn and peanuts after Mn (Benac 1976).

Excluders and accumulators represent extreme types of physiological responses to heavy metals — the distribution of these metals is organized differently inside the organism. In both cases the tolerance mechanisms are "internal" in the active detoxification of metal ions in the cell itself (Baker 1981). The difference lies in the different location in which inactivation takes place — in the roots of excluders while in the stems of accumulators. For instance, *Thlaspi goesingense* accumulates nickel mainly in its above ground parts (Reeves and Baker 1984), similarly as *Becium homblei* — copper (Reilly and Stone 1971) or *Thlaspi cepeaefolium* — zinc (Rascio 1977). It should, however, be remembered that since the same plant can be both an accumulator and excluder at the same time in respect to different metals, the detoxification mechanisms should be specific for each of the metals.

A hitherto unexplained physiological phenomenon observed by Rascio (1977) is related to the accumulation of metals in the roots or above ground parts of plants. He showed that excluders — *Biscutella laevigata* and *Anthyllis vulneraria* which have accumulated very large amounts of zinc in their roots, release it in the autumn and transport it to their shoots. Similarly — lead accumulated in the root of winter rape was transported to the shoot in the winter (Lehn and Bopp 1987). It is not known how common this phenomenon is in plants and it therefore needs more study.

As I have mentioned before, exclusion mechanisms (stem protection) and accumulation are related to the different distribution of active processes involved in resistance to metals. It must also be added that there are still other parts of plants that are highly protected from accumulation of metals. These are the regions of the quiescent center in the root and shoot apical meristems (Lane and Martin 1977, Sieghardt 1981, 1984, Przymusiński and Woźny 1985, Wierzbička 1987) and seeds (Baumhardt and Welch 1972, Koeppe 1981, Godzik 1984, Garcia et al. 1979). The mechanisms involved in these protective barriers have not yet been explained. Only the seeds of plants growing on soils rich in nickel contain large amounts of this metal (Reeves and Baker 1984). After they germinate on normal soil, the Ni in the plants which develop from them gradually becomes diluted, similarly as in the case of seedlings growing on serpentine soil and transplanted to normal soil. This suggests that nickel is not lost at all, or only to a very slight degree, through the roots.

The uptake of metals from soil is influenced by numerous factors, among which the most important are pH, temperature, soil ions and organic matter content of the soil. Metal ions that are complexed with organic matter are usually less accessible to plants, thus the concentration of metal ions available to roots is decreased (Ernst 1975, Garcia et al. 1979). Even a case of lack of tolerance to zinc and lead in *Festuca rubra* growing on soil enriched with these metals but also containing a high calcium level has been reported. This plant did not develop tolerance because at high soil levels of calcium in the form of CaCO_3 accompanying heavy metals, these metals may form insoluble or poorly soluble carbon salts with it. The lack of unbound toxic metal ions in the environment around the roots made selection of plants for tolerance to them impossible and these sites are inhabited by species sensitive to these metals (Karatagliis 1981).

Mining excavation sites or industrial waste dump sites do not provide a favourable environment for plants growing there, not only because these sites are contaminated with metals, but because of their low fertility, frequently low, less often, high pH, hard soil texture and low water content. There is therefore another important factor associated with contaminated sites — nutrition, which determines which species can inhabit the given area (Bradshaw 1975, Foy 1983b, Tomsett and Thurman 1988). Species inhabiting contaminated areas can be divided into two groups (Baker 1987). The first group includes plants characteristic for shallow, poor soils — *Minuartia verna*, *Koeleria macrantha*, *Festuca ovina*, *Hieracium pilosella*, *Thymus praecox* ssp. *arctius* are its chief representatives. Plants such as *Dactylis glomerata* or *Arrhenatherum elatius*, which require more fertile soils containing more organic matter are found in the second group.

In addition to unfavorable environmental conditions, heavy metals themselves have an adverse effect on plant nutrition. Depending on the type of metal and species of plant, they inhibit the uptake and transport of macro- and microelements to above-ground plant parts, lower the mineral content of plants (Foy 1983a, b, Burzyński and Grabowski 1984, Foy and Oakes 1984, Horst 1985, Thornton et al. 1986, 1987, Biddappa et al. 1987, Burzyński 1987).

Tolerance to heavy metals often manifests itself in inhibiting the processes listed above. Resistant lines often show, in comparison with sensitive ones, a significantly less depressed mineral content, increased mineral uptake, increased resistance to certain mineral deficiencies and reduced nutritional requirements as well as the appearance of the capability to absorb and utilise mineral compounds in the presence of heavy metals. And so, Jowett (1959) demonstrated that Pb-tolerant *Agrostis tenuis* from the site of a lead mine is concomitantly adapted to low soil calcium and phosphorus levels, which was not

found in this plant growing on an unpolluted pasture. The reduction of the tissue calcium content of Al-sensitive *Vigna unguiculata* is much deeper than in its resistant genotypes (H o r s t 1985). Al-tolerant wheat is also more efficient in taking up magnesium than its Al-sensitive form (F o y 1983b). Greater magnesium and potassium uptakes were also found in Al-tolerant potatoes (F o y et al. 1978). B a u m g a r t n e r et al. (1976) found that the Al-tolerant Santa Cruz Kada tomato has a lower nutritional calcium and phosphorus requirement than the more sensitive Ronita. It was also shown that tolerance of plants to aluminum is concurrent with their tolerance to phosphorus deficit (F o y et al. 1978) and in peas it is related to the ability to take up and utilise phosphorous in the presence of Al, in contrast to the Al-sensitive line (K l i m a s h e v s k i et al. 1979). There is also evidence that Al-tolerant plants are more efficient in absorbing calcium and phosphorus when the concentration of these elements is low in the substrate (F o y 1983b). H a n s o n and K a m p r a t h (1979) have shown, however, that in spite of the fact that in Al-sensitive and tolerant soybean the level of metabolic intermediates is the same, after administration of the metal, the ATP and pyruvate levels rise in the resistant line.

It is well known that the pH of the substrate has a very significant effect on the availability of metals to plants. Aluminum is especially toxic at low pH values (5.0) when its solubility rises steeply (F o x 1979, F o y 1983a, b, F o y and C a m p b e l l 1984, F o y and O a k e s 1984, B l a m e y et al. 1987, T h o r n t o n et al. 1987). Raising the soil pH is a good way of preventing the harmful effects of aluminum, as well as of lead and copper, on plants (H o r s t 1985, M e r r y and T i l l e r 1986, K a r a t a g l i s 1987). It has been demonstrated that the uptake of other metals, such as lead, copper, zinc nad mercury, also rises as the soil pH drops (Z i m d a h l 1976, H o r s t 1985, L a m e r s d o r f 1989, L e h t o n e n 1989), thereby increasing the availability of these metals. A decrease in the soil organic matter content along with a rise in the amount of phosphorus compounds also causes an increase in the lead content in plant tissues (Z i m d a h l 1976). Thus, plants growing on acidic, contaminated soils should exhibit not only tolerance to metals, but also to low pH (F o y and C a m p b e l l 1984). S o l i m a n (1976) examined the effect of low substrate pH on the growth of two lines of *Mimulus guttatus* — tolerant and sensitive to copper. She demonstrated that the tolerant line was also tolerant to low pH while the sensitive line grew better at a higher pH.

Another way in which tolerant plants handle metals in acidic soil was discovered. Al-tolerant wheat is characterized by more efficient utilisation of NO_3^- (in the presence of NH_4^+) as a nitrogen source, increasing in this way the soil pH, which, in turn, decreases the availability of Al (F o y et al. 1978). However, nitrification is inhibited in highly acidic soils and NH_4^+ ions become the main source of nitrogen. Many Al-tolerant plants growing on these soils also tolerate NH_4^+ ions which are toxic to Al-sensitive plants. The former even prefer NH_4^+ over NO_3^- as their nitrogen source (F o y 1983a).

It should be added, however, that in spite of increased solubility of cadmium compounds at low pH, it has been shown that in such plants as *Dactylis glomerata*, *Lactuca sativa*, *Lolium perenne*, *Rorippa nasturtium-aquaticum*, an increase in the total tissue cadmium content is observed as the substrate pH rises. The inhibition of cadmium absorption by roots at low pH values is caused by increased competition with hydrogen ions (Hatch et al. 1988).

When investigating the problem of tolerance of plants to heavy metals, it should therefore be kept in mind that plants growing in contaminated areas must be adapted not only to toxic amounts of metals in the soil, but also to very difficult nutritional conditions, very often unfavorable soil pH and bad water conditions.

Summarizing the information presented above, a question arises about the basic problems which are the subject of current and future scientific investigations. One of them is the problem of induction and stability of tolerance in view of the fact that its genetic basis has become accepted. Inconsistencies in the results describing the loss as well as the retention of tolerance during cultivation of plants on uncontaminated soil, makes it necessary to determine what constitutes the induction of tolerance and what is the reason for its loss. The next problem is to establish the nature of constitutional tolerance and its role in the induction of permanent and transient tolerance. A subsequent important and unsolved question is the source of the observed specificity of tolerance in plants. It also remains unclear how "internal" (cellular) mechanisms of plant tolerance cooperate with those mechanisms which decide where detoxification of the metal inside the plant mainly occurs. Therefore in spite of the wealth of information collected so far, much more still remains to be explained in order to fully understand the basis of tolerance in plants.

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Przystosowanie roślin do środowiska skażonego metalami ciężkimi

Streszczenie

Praca przedstawia problem tolerancji roślin na metale ciężkie. Opisano w jaki sposób tolerancja jest indukowana, jak się rozwija i jak długo utrzymuje. Tolerancja wielokrotna i ko-tolerancja jest omawiana w świetle problemu specyficzności nabytej odporności na metale ciężkie. Opisano zagadnienia związane z pobieraniem metalu przez rośliny i jego rozmieszczeniem w tkankach oraz związane z tym mechanizmy wykluczania i akumulacji. Problem rozwoju tolerancji u roślin został przedstawiony także w świetle warunków pokarmowych z jakimi stykają się one najczęściej na terenach skażonych.