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GENERAL BIOLOGY

Role of Root and Shoot Tissues of Excluders and Hyperaccumulators in Nickel Transport and Accumulation

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Nickel hyperaccumulators accumulate Ni in shoots, whereas nickel excluders—in roots [1]. Several researchers described Ni distribution in shoots of hyperaccumulators, whereas its distribution in roots of hyperaccumulators and excluders is not essentially studied [2–4].

The main task of this study was to compare Ni distribution in various tissues of excluders (*Zea mays*, *Thlaspi perfoliatum*) and several ecotypes of the hyperaccumulator *T. caerulescens* differing in tolerance to nickel. This work permitted us to elucidate the role of different tissues in Ni accumulation.

Plants were grown on the Hoagland solution in the presence of 100, 150, 200, 300, and 400 μM $\text{Ni}(\text{NO}_3)_2$ (*T. caerulescens*); 10, 20, and 30 μM $\text{Ni}(\text{NO}_3)_2$ (*T. perfoliatum*); and 75 μM $\text{Ni}(\text{NO}_3)_2$ (*Z. mays*). Toxic Ni effects were assessed from plant appearance, root length increment (maize), and changes in fresh and dry weights of roots, leaf blades, and leaf petioles (*Thlaspi*). A dimethylglyoxime method was used for Ni detection [2].

The content of Ni was measured by atomic absorption spectroscopy in roots, leaf petioles, and leaf blades of *T. caerulescens* (ecotypes Felix, Prayon, and Lellingen) and *T. perfoliatum* after 54 days of incubation and also in shoots, apical (the first centimeter from the tip) and basal (the third centimeter from the caryopsis) parts of maize roots after 1, 2, 4, and 5 days of incubation.

Thlaspi. Fresh and dry weights of roots and shoots of *T. caerulescens* were reduced by $\text{Ni}(\text{NO}_3)_2$ concentrations exceeding 300 μM , whereas 20 μM $\text{Ni}(\text{NO}_3)_2$ retarded growth of *T. perfoliatum*. Both species developed lateral roots.

In all ecotypes of *T. caerulescens*, the content of Ni was the lowest in roots, higher in leaf petioles, and still higher in leaf blades. In *T. perfoliatum*, Ni accumulated in roots (Table 1).

Ni was detected in all tissues of the apical root part of *T. caerulescens*. Mature root parts were stained only in the presence of 400 μM $\text{Ni}(\text{NO}_3)_2$, and this staining was weaker than in apical parts. In these mature root parts, the rhizodermis, outer cortex, and tissues of the vascular cylinder were stained brighter than the inner cortex. The endodermis and pericycle were not stained.

In stems of plants incubated with 100–300 μM $\text{Ni}(\text{NO}_3)_2$, Ni was detected only in the protoplasts of large spherical cells of the epidermis; in the presence of 400 μM $\text{Ni}(\text{NO}_3)_2$, it was also found in conducting tissues and in the cells and intercellular space of the cortex.

Ni content in two *Thlaspi* species, $\mu\text{g/g}$ dry wt

$\text{Ni}(\text{NO}_3)_2$ concentration (μM) and the number of plants (n)	<i>T. caerulescens</i> (ecotype Felix)		
	roots	leaf petioles	leaf blades
0 (4)	71 $\pm$ 22	46 $\pm$ 22	18 $\pm$ 5
100 (8)	564 $\pm$ 51	654 $\pm$ 69	1151 $\pm$ 82
200 (6)	1078 $\pm$ 51	1288 $\pm$ 99	2073 $\pm$ 125
300 (8)	1793 $\pm$ 137	2002 $\pm$ 173	3465 $\pm$ 140
400 (4)	2118 $\pm$ 135	2724 $\pm$ 540	3997 $\pm$ 396
<i>T. perfoliatum</i>			
0 (7)	19 $\pm$ 3	12 $\pm$ 1	10 $\pm$ 1
10 (5)	404 $\pm$ 33	26 $\pm$ 1	39 $\pm$ 1
20 (4)	897 $\pm$ 68	50 $\pm$ 2	75 $\pm$ 3
30 (4)	1265 $\pm$ 75	117 $\pm$ 15	131 $\pm$ 8

Note: The mean values and their standard errors are presented. Similar data were obtained for other *T. caerulescens* ecotypes.

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Fig. 1. Ni distribution in (a) lower epidermis of *T. caerulea* (ecotype Prayon) leaf blade; (b) leaf petiole of *T. caerulea* (ecotype Lellingen); (c) lower epidermis of *T. perfoliatum* leaf blade; (d) tissues of the middle part of the *Z. mays* root. (a–c) After 7 weeks and (d) after 48 h of incubation in the presence of (a) 300, (b) 400, (c) 20, and (d) 75 μM $\text{Ni}(\text{NO}_3)_2$. Ni accumulation is seen in *T. caerulea* epidermal cells of (a) the leaf blade and (b) leaf petiole and (d) in *Z. mays* endodermal and pericycle root cells. Ni content in (c) the epidermis of *T. perfoliatum* is below the sensitivity of the dimethylglyoxim method. Designations: E—endodermis; Ep—epidermis; GC—guard cell; IC—inner cortex; Mx—metaxylem; P—pericycle; Pi—pith; Ph—phloem; Px—protoxylem; SC—subsidiary cell; WSC—water storage cell.

In leaf petioles, Ni accumulated mainly in the protoplasts of large epidermal cells (Fig. 1). The content of Ni in the mesophyll was very low. In the leaf blades, the lower epidermis water storage cells were stained much stronger than subsidiary and guard cells of stomatal complex (Fig. 1).

In mature parts of *T. perfoliatum* roots, cortical cells were stained stronger than the tissues of the vascular cylinder. In shoots, low amounts of Ni accumulated in conducting tissues; Ni accumulation in the epidermis was not observed (Fig. 1).

Maize. $\text{Ni}(\text{NO}_3)_2$ (75 μM) suppressed root development by 11 and 50%, respectively, after 1 and 2 days of incubation and completely prevented growth of lateral roots.

In the roots and shoots of the control plants, Ni content did not exceed 30 $\mu\text{g/g}$ dry wt. After 24 h of exposure to 75 μM $\text{Ni}(\text{NO}_3)_2$, Ni content in apical and basal root parts was 673 and 656 $\mu\text{g/g}$ dry wt, respectively. In the basal part, it increased by 1.8 times after another 24 h and by 1.5 times after next 72 h. In the apical part, it remained unchanged after another 24 h. In shoots, Ni

content was 10.2-fold lower than in the basal root part and 5.8-fold lower than in the apical root part.

On the second day, Ni was found in all root tissues. The apical root part displayed the lowest staining. In the meristem cells, the cytoplasm was stained, whereas the nucleus was not. In the middle and basal root parts, the protoplasts of the endodermis and pericycle cells and also the intercellular space in the cortex were most stained (Fig. 1). After 4 days, Ni accumulated in the middle part also in the rhizodermis and after 5 days—in the exodermis.

In shoots, Ni was detected only in conducting tissues, in the endodermis of the mesocotyl, and in the epidermis of the leaf.

DISCUSSION

The results obtained by the histochemical method coincided with Ni quantification, which permits the usage of histochemistry for the assessment of Ni distribution.

Ni penetration into all tissues of the root meristem of all plants tested permits a conclusion that there are no physiological barriers for Ni transport in the meristem.

Above the meristem, Ni distribution in the roots of excluders and hyperaccumulators differed. In excluders, mature root parts accumulated Ni in the endodermis and pericycle, which was not observed in the roots of hyperaccumulators. Thus, the role of different root tissues in Ni transport and accumulation differs in hyperaccumulators and excluders. Ni content in cortical cells of both plant groups was low. However, in excluders, it was clearly higher than in hyperaccumulators, although the latter were grown on the Ni solutions of much higher concentrations. The cortex is important mainly for radial Ni transport. Ni accumulation in the exodermis of the basal part of the maize root permits a supposition that this tissue plays a role of partial barrier limiting Ni transport. In excluders, the endodermis does not function as a barrier, but it is the site of Ni accumulation, whereas in hyperaccumulators, this tissue fulfills neither barrier nor accumulating function.

Due to uneven distribution of plasmodesmata in the maize pericycle [5], this tissue plays a role of a collector for Ni; it is involved in the Ni radial redistribution in the root and simultaneously serves for its accumulation. In hyperaccumulators, the pericycle does not fulfill such functions. Ni accumulation in the maize pericycle suppressed the development of lateral roots.

Since *T. caerulescens* roots do not contain barrier and accumulating tissues, Ni is transported in shoots where it accumulates in the water storage epidermal cells; the presence of these cells is a prerequisite for a capacity of these plants to Ni hyperaccumulation, which is manifested only when roots do not fulfill the barrier function.

The results obtained indicate that the phenomenon of Ni hyperaccumulation observed in several hundreds of plant species could be explained, at least partially, by the specific features of Ni transport in the roots.

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