Nickelophilous plants and their significance in phytotechnologies

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Nickeliferous soils are invaded predominantly by members of the Brassicaceae, Cyperaceae, Cunoniaceae, Caryophyllaceae, Fabaceae, Flacourtiaceae, Euphorbiaceous, Lamiaceae, Poaceae and Violaceae, and many of these plants are metal tolerant. About 300 Ni hyperaccumulating plants been identified. These members exhibit unusual appetite for toxic metals and elemental defense. Hyperaccumulators provide protection against fungal and insect attack. Investigations suggested that Ni-hyperaccumulation has a protective function against fungal and bacterial pathogens in *Streptanthus polygaloides* and *Thlaspi montanum*. Significance of nickelophilous plants and their significance in phytotechnologies are discussed in this paper.

Key words: heavy metal, hyperaccumulators, nickel, phytomanagement, tolerance.

Plantas niquelófilas e sua importância em fitotecnologias: Solos ricos em Ni, niquelíeros, são invadidos predominantemente por membros de Brassicaceae, Cyperaceae, Cunoniaceae, Caryophyllaceae, Fabaceae, Flacourtiaceae, Euphorbiaceous, Lamiaceae, Poaceae e Violaceae, e muitas dessas plantas são tolerantes e metais. Aproximadamente 300 plantas que superacumulam Ni (hiperacumuladoras) já foram identificadas. Estas plantas apresentam capacidade não usual de acumular metais tóxicos e defesa contra eles. O acúmulo excessivo de metais fornece proteção contra o ataque de insetos e fungos. Investigações sugerem que a hiperacumulação de Ni tem como função a proteção contra fungos e bactérias patogênicos em *Streptanthus polygaloides* e *Thlaspi montanum*. A importância de plantas niquelíferas e a sua significância em fitotecnologias são discutidas nesta revisão.

Palavras-chave: fitomanejo, metal pesado, níquel, plantas hiperacumuladoras, tolerância.

INTRODUCTION

Serpentine soils, “hotspots” of metallophyte endemics are a rich source of toxic trace elements. Serpentinized rocks are distributed all over the world viz., western north America; Newfoundland, Mount Albert in eastern Canada; Lizard peninsula, Wales and Scotland; north-east Cuba; Portugal; Italy; Balkan peninsula; Turkey; topical far east; Central Brazil; New Caledonia; south east Asia; Philippines; Japan; Zimbabwe; eastern Transvaal Loweveld of South Africa, New Zealand; greenstone belts of western Australia. (Proctor and Woodell, 1975; Sequeira et al., 1991).

Serpentine soils contain heavy metals including nickel (averaging 10 mg per gram soil), cobalt and chromium, both of the latter being present at lower levels than nickel. Serpentine soils are also characterized by high concentrations of iron and magnesium and low nutrient levels. An interesting ecosystem is established in these biotopes driven by a nickel cycle, in which hyperaccumulating trees extract nickel from deep soil and rock layers and subsequently store it in their leaves (up to 1 % Ni in leaf dry matter). When the leaves are shed from the trees, the nickel is leached out into the surrounding topsoil. The solubilized metal exerts a localized selective pressure on the topsoil microflora, which acquire resistance to high levels of nickel (> 20 mM), as well as on other plant species, which are susceptible to toxic levels of Ni. Interestingly, the microflora which was not found directly beneath the canopy but in the same soil, showed tolerance to lower levels of nickel (3 mM) compared to the resistant population. Thus, the nickel selection pressure exists as a gradient around the hyperaccumulator plants and has a dramatic effect on the composition of the local microbial population (Prasad, 2001).

Hyperaccumulator plants are geographically distributed and are found throughout the plant kingdom (Brooks, 1998; Chaney et al., 1995). To date approximately 450 taxa, ranging in growth habit from annual herbs to perennials are known. Hyperaccumulator plants have been identified on all continents, both in temperate and tropical environments (table 1). Natural occurrences of hyperaccumulators for Ni include New Caledonia, Cuba, Southeast Asia, Brazil, southern Europe and Asia Minor; for Zn and Pb include northwest Europe; and for Cu and Co include south-central Africa. Some families and genera are particularly well documented as Ni hyperaccumulators [Brassicaceae (*Alyssum* and *Thlaspi*), Euphorbiaceae (*Phyllanthus*, *Leucocroton*) and Asterceae, Zn Brassicaceae (*Thlaspi*), and Cu and Co (Lamiaceae, Scrophulariaceae) (Brooks, 1998). There are not many Cr hyperaccumulators in nature, but there are numerous Ni hyperaccumulators. A few Cr hyperaccumulators have been identified, partly because Cr exists predominantly in the 3^+ oxidation state and is very insoluble and much less available for plant uptake.

Some metals may interact competitively for accumulation (e.g., Zn and Ni in calamine and serpentine soils). The number of Ni hyperaccumulator taxa are more than 300 in 35 families (table 1). They commonly have 3-4 % Ni in the dry matter of leaves. *Alyssum betolonii*, which is endemic to serpentine soils, is known for its high concentration of Ni (> 10,000 $mg.kg^{-1}$ in leaves). The fact that serpentine (ultramafic) soils also contain other elements such as Cr has led to the assumption that the preferential accumulation of Ni in many species of *Alyssum* is due to a selective uptake mechanism. *Brassica juncea* (Indian mustard) - a high-biomass producing plant that can accumulate Pb, Cr(VI), Cd, Cu, Ni, Zn, 90 Sr, B, and Se (Palmer et al., 2001; Prasad, 2001) produces biomass of over 20 times that of *Thlaspi caerulescens* (Salt et al., 1998). *Brassica juncea* had the best ability to transport lead to the shoots. Except for sunflower (*Helianthus annuus*) and tobacco (*Nicotiana tabacum*), other non-Brassica plants had phytoextraction coefficients less than one. *B. juncea* cultivars varied widely in their ability to accumulate Pb, with different cultivars ranging from 0.04 % to 3.5 % Pb accumulation in the shoots and 7 to 19% in the roots (Kumar et al., 1995).

Nickel hyperaccumulators - environmental implications

One of the most persuasive ecological explanations for hyperaccumulation of Ni and other toxic metals appears to be the defensive role against herbivores or pathogens (Dudley, 1986; Boyd and Martens, 1988, 1994). This function, which might be similar in other hyperaccumulators, can be improved if the metal is localized in the outer layers of leaves and roots. Like in other Ni accumulators, such as *Hybantus floribundus*, *Senecio coronatus* and *Thlaspi montanum* variety *siskiyouense*, and *A. bertolonii*, Ni has been evidenced in leaf epidermal cells as a red-stained nickel-dimethylglyoxime complex (Boyd, 1988; Farago et al., 1988; Mesjasz-Przybylowicz et al., 1994; Heath et al., 1997; Sanita Di Toppi, 2001). Furthermore, microprobe analysis has shown that leaf hairs have the highest nickel concentrations (Vergano, 1967). Similarly, in *A. lesbiacum*, using a micro-PIXE technique, Ni was found in the epidermis and in leaf trichomes (Gabrielle et al., 1997). The Ni hyperaccumulator *T. montanum* var. *siskiyouense* accumulates the highest Ni concentration at the leaf surface, particularly in the subsidiary cells surrounding the guard cells, and in other elongate epidermal cells, a characteristic that supports the defense hypothesis (Heath et al., 1997; Pollard and Baker, 1997).

Peterson et al. (2003) studied plants, soil, and invertebrates from Portuguese serpentine outcrops whose vegetation is dominated by the Ni hyperaccumulator *Alyssum pintodasilvae*. Peterson et al. (2003) concluded that grasshoppers, spiders, and other invertebrates that fed on these hyperaccumulators spread metals through food chain

Hyperaccumulation of metals is known for about 450 species of flowering plants, which take up, transport and sequester metallic elements, achieving tissue concentrations that are toxic to most organisms (Baker et al., 2000; Reeves and Baker, 2000). Several hypotheses have been advanced to explain the evolution of this trait (Boyd and Martens, 1992), with most attention focused on the hypothesis that hyperaccumulated metals may act as defenses against herbivory (Boyd, 1998; Boyd and Martens, 1998; Pollard, 2000; Pollard et al., 2000). With the exception of recent work by Wall and Boyd (2002), most studies to date have considered interactions between individual plants and herbivores, with little attention being paid to the effects of hyperaccumulators on their communities or ecosystems.

The broader environmental consequences of hyperaccumulation are of practical importance because of developing technologies that would use metal-accumulating plants to cleanse contaminated soil, termed phytoremediation (Schwitzguébel et al., 2002). A relatively unexplored risk of these techniques is that metals sequestered in plant tissues could be consumed by herbivores and thus mobilized into

Table 1. Brassicaceae that accumulate nickel (Ni) (for details refer to Palmer et al., 2001).

Metal (mg.g^{-1} d.wt.)	Taxa	Distribution
1050	*Cardamine resedifolia* L.	Italy
1280	*Alyssum singarense* Boiss. and Hausskn.	Iraq
2000	*Thlaspi bulbosum* Spruner ex Boiss.	Greece
2440	*T. japonicum* H.Boissieu	Japan
3000	*T. epirotum* Halacsy	Greece
3140	*Pseudosempervivum sempervium* Boiss and Balansa) Pobed	Turkey
3420	*Alyssum tenium* Halacsy	Greece
3960	*A. fallacinum* Hausskn	Crete
4000	*Thlaspi ochroleucum* Boiss. and Heldr.	Greece
4480	*Alyssum alpestre* L	Southern Europe
4550	*A. euboeum* Halacsy	Greece
4590	*A. obovatum* (C.A.Mey) Turez	Russia
4900	*A. condensatum* Boiss. and Hausskn.	Iraq, Syria
5530	*Thlaspi montanum* L. var. *montanum*	USA
6230	*Alyssum virgatum* Nyar.	Turkey
6600	*A. smolikanum* Nyar.	Greece
7080	*A. murale* WealdstandKit	Balkans
7290	*A. oxycarpum* Boiss. And Balansa	Turkey
7390	*A. giosnanum* Nyar.	Turkey
7600	*A. peltarioides* subsp.*virgatiforme* Nyar.T.R.Dudley)	Turkey
7700	*A. floribundum* Boiss. and Balansa	Turkey
7860	*A. penjwinensis* T.R.Dudley	Iraq
8170	*A. anatolicum* Nyar.	Turkey
9090	*A. akamasicum* B.L.Burtt	Cyprus
10000	*A. serpylifolium* Desf	Spain
10200	*A. bertolonii* subsp. scutarinum Nyar	Balkans
10200	*A. syriacum* Nyar.	Syria
10400	*A. crenulatum* Boiss	Turkey
10900	*A. callichroum* Boiss. And Balansa	Turkey
11400	*Bornmulleria* sp petri Greuter, Charpipn and Dittrich	Greece
11500	*Alyssum eriophyllum*, Boiss. and Hausskn.	Turkey
11700	*A. discolor* T.R.Dudley and Huber-Morath	Turkey
11800	*Thlaspi tymphaeum* Hausskn.	Greece
11900	*Alyssum trapeziforme* Nyar.	Trukey
12000	*Thlaspi goesingense* Halacsy	Greece
12400	*T. graecum* Jord	Greece
12500	*Alyssum heldreichii* Hausskn.	Greece
12500	*A. robertianum* Bernard ex Godronand Gren	Corsica
13400	*A. bertolonii* Desv.	Italy
13500	*A. cilicium* Boiss. And Balansa	Turkey
13500	*A. corsicum* Duby	Corsica
13500	*A. huber-morathii* T.R.Dudley	Turkey
13600	*Thlaspi kovatsii* Heuffel	Yugoslavia
13700	*Alyssum markgrafii* O.E.Schulz	Albania
14800	*Streptanthus polygaloides* A.Gray	USA
16200	*Thlaspi caerulescens* J.Presl	Greece
16300	*Alyssum chondrogynum* B.L.Burtt	Cyprus
16500	*A. dubertretii* gomb	Turkey
16500	*A. carcium* T.R.Dudleyand Huber-Morath	Turkey
17100	*A. troodii* Boiss.	Turkey
17600	*Pseudosempervium aucheri* (Boiss.) Pobed	Turkey
18100	*Alyssum constellatum* Boiss.	Turkey
18300	*Thlaspi rotundifolium* (L.) Gaudin var. *corymbosum* (Gay)	Central Europe
18900	*Alyssum samariferum* Boiss. and Hausskn.	Samar
18900	*Peltaria dumulosa* Post	Asia
19200	*Bornmuellaria glabrescens* (Boiss and Balansa) Cullen and TR Dudley	Turkey
19600	*Alyssum davisianum* T.R. Dudley	Turkey
20000	*Alyssum cassium* Boiss	Turkey
20800	*Thlaspi elegans* Boiss	Turkey
18300	*T. rotundifolium* (L.) Gaudin var.*corymbosum* (Gay)	Central Europe
18900	*A. samariferum* Boiss. and Hausskn	Samar
21100	*A. pinifolium* (Nyar.)T.R.Dudley	Turkey
21300	*Bornmuellera baldaccii* (Degen) Heywood	Greece
22200	*Alyssum pterocarpum* T.R Dudley	Turkey
22400	*A. lesbiacum* (P.candargy) Rech.f	Greece
23600	*A. cypricum* Nyar	Cyprus
24300	*A. masmenaeum* Boiss	Turkey
26900	*Thlaspi jaubertii* Hedge	Turkey
27300	*T. caerulescens*	Germany/Belgium
29400	*Alyssum argenteum* All	Italy
31000	*Thlaspi sylvium* (as *T. alpinum* subsp. *sylvium*)	Central Europe
31200	*Bornmuellaria tymphea* (Hausskn.) Hausskn	Greece
34400	*Peltaria emarginata* (Boiss.) Hausskn.	Greece
35600	*Thlaspi oxyceras* (Boiss.) Hedge	Turkey, Syria
52120	*Thlaspi cypricum* Bornm.	Cyprus

food chains (Chaney et al., 2000). One way to investigate the possibility of such mobilization is through studies of natural ecosystems whose vegetation is dominated by hyperaccumulating plants.

High Ni concentrations in both grasshoppers and spiders suggest that the presence of hyperaccumulating plants affects the flux of Ni to both herbivore and carnivore trophic levels. This parallels findings recently published by Boyd and Wall (2001) showing that Ni accumulated by a herbivore feeding on hyperaccumulating plants can be passed on to carnivores. In one case, Boyd and Wall (2001) reported the Ni concentration in wild-caught crab spiders (*Misumena vatia*, Araneae: Thomisidae) from *Streptanthus polygaloides* growing on California serpentines.

The consequences and ecological role of metal hyperaccumulation is expanding rapidly. Hyperaccumulation is known for aluminium, copper, cobalt, manganesium, Ni and zinc (Baker and Brooks, 1989). Caledonia, *Sebertia acuminata*, (a tree Sapotaceae) is the classic example capable of concentrating Ni up to 26 % (on a dry matter basis) in the xylem tissue. In Portuguese serpentine ecosystems, *Alyssum serpyllifolium*, a dominant weed, accumulates up to 10,000 ppm of Ni in the leaves. The objective of this paper is to highlight the scope and limitations of Ni tolerant plants and Ni accumulators and their role in promoting phytotechnologies for the environmental cleanup of heavy metals and radionuclides. The below and above-ground biodiversity of Ni tolerant plants/Ni accumulators (alien/indigenous) of metalliferous substrates, is becoming increasingly considered for the phytomanagement of metal contaminated and polluted ecosystems. The Ni tolerant plants/Ni accumulators that accumulate and/or exclude metals have tremendous potential for moving phytoremediation forward. Therefore, for phytomanagement metal-accumulating plants are seeded or transplanted into metal-polluted soil/water. If metal availability were not adequate for sufficient plant uptake, the substrate would require amendment to release or arrest the mobility of metals in the substrate. Synthetic cross-linked polyacrylates (hydrogels) have protected plant roots from heavy metal toxicity and prevented the entry of toxic metals into roots. After sufficient plant growth and metal accumulation, the above-ground portions of the plant are harvested and removed, resulting in the permanent removal of metals from the site. The retention of metals by soil organic matter is also weaker at low pH, resulting in more available metal in the soil solution for root absorption. It is suggested that the phytoextraction process is enhanced when metal availability to plant roots is facilitated through the addition of acidifying agents to the soil. Several researchers have screened fast-growing, high-biomass producing plants (e.g. Poaceae) for their ability to tolerate and accumulate metals in their shoots. The solubilized metal exerts a localized selective pressure on the topsoil microflora, which acquire resistance to high levels (e.g. Ni > 20 mM). Thus, knowledge of how plants can specifically accumulate or exclude essential elements and toxic metals, particularly of Ni tolerant plants or Ni accumulators, is fundamental for selecting species that can be utilized for phytomanagement. This includes knowledge on bioavailability of metals in rhizospheric processes as well as translocation and processing/storage in the above-ground parts of the plant.

Nickelophilous plants phytotechnologies – advantages and limitations

The importance of below and above ground biodiversity is increasingly considered for the phytomanagement of the metalliferous ecosystems. This subject is emerging as a cutting edge area of research and gaining considerable commercial significance in the contemporary field of environmental biotechnology. Globally, metal pollution has increased several thousand-fold (Adriano, 2001). Several microbes, including mycorrhizal and non-mycorrhizal fungi, agricultural and vegetable crops, ornamentals, and wild metal hyperaccumulators and excluders are being tested both under lab and field conditions for cleanup of the metalliferous substrates in the environment. Brassicaceae has the largest number of taxa viz. 11 genera and 87 species. Different genera of Brassicaceae are known to accumulate metals. Ni hyperaccumulation is reported in 7 genera and 72 species, and Zn in 3 genera and 20 species. *Thlaspi* species are known to hyperaccumulate more than one metal i.e *T.caerulescence* for Cd, Ni. Pb, and Zn; *T. goesingense* and *T.ochroleucum* for Ni and Zn and *T.rotundifolium* for Ni, Pb and Zn (Prasad and Freitas, 2003).

Plants that accumulate and exclude metals have tremendous potential for application in remediation of metals in the environment. Significant progress has been achieved in phytoremediation (Vangronsveld and Cunningham, 1998; Glass, 1999; Terry and Bañuelos, 2000; McCutcheon and Schnoor, 2003; Prasad, 2003, 2004a,b). This process involves raising plants hydroponically and transplanting them into metal-polluted waters where the plants absorb and concentrate the metals in their roots and shoots. As they become saturated with the metal contaminants, roots or whole plants are harvested for disposal. The phytoextraction

Table 2. Nickel in plant cell and environment - from adaptive physiology to phytomanagement.
This listed information pertains to Ni and its presence in the environment as a contaminant, and covers topics such as uptake, accumulation, phytotoxicity, physiology and biochemistry of toxicity and tolerance in plants, biochemical chraracterization and phytomanagement.

Function	Authors	Year
Environmental contaminant		
Nickel in rocks, soils, waters and plants adjacent to the Chorchanskaya	Doksopulo	1961
Contamination of road side soil and vegetation	Lagerwerff and Specht.	1970
Impact of nickel contamination on the production of vegetables on an organic soil, Ontario, Canada	Frank et al.	1982
Zinc, copper and nickel concentrations in soil extracts and crops grown on four soils treated with metalloaded sewage sludges	Sanders et al.	1987
Uptake of nickel and cadmium by vegetables grown on soil amended with different sewage sludges	Singh et al.	1989
Nickel in the terrestrial environment	McIlveen and Negusanti	1994
Trace metal bioavailability in municipal solid waste and sewage sludge composts	Pichtel and Anderson	1997
Groundwater composition near the nickel-copper smelting industry on the Kola Peninsula, central Barents Region (NW Russia and NE Norway)	Patrice et al.	1998
Heavy metals in soils and plants of serpentine and industrial sites of Albania	Shallari et al.	1998
Trace elements and precious metals in snow samples from the immediate vicinity of nickel processing plants, Kola Peninsula, northwest Russia	Gregurek et al.	1998
Urinary nickel as bioindicator of Ni exposure of workers in a galvanizing plant in Brazil	Siqueira et al.	1998
Influence of nickel contaminated soils on lettuce and tomatoes	Zdenek Poulik et al.	1999
Clinical toxicology of nickel	Barceloux	1999
Nitrogen transformation and microbial biomass content in soil contaminated with nickel and cadmium from industrial wastewater irrigation	Antil et al.	2001
Contemporary use of Ni and Bi in hot-dip galvanizing	Fratesi et al.	2002
Influence of nickel-contaminated soils on fenugreek (*Trigonella corniculata* L.) growth and mineral composition	Parida et al.	2003
Nnickel speciation in *Sebertia acuminata*, a plant growing on a lateritic soil of New Caledonia	Perrier et al.	2004
Sulphur dioxide adsorption in Scots pine canopies exposed to high ammonia emissions near a Cu-Ni smelter in SW Finland	Derome et al.	2004
Speciation studies of nickel and chromium in wastewater from an electroplating plant.	Jackson et al.	2004
Accumulation		
Accumulators from Western Australia.	Severne and Brooks	1972
Accumulators from from New Caledonia	Kelly et al.	1975
Accumulation by *Rinorea bengalensis* (Wall.)	Brooks et al.	1977
Accumulation in three Australian plants growing on the mineralized sites	Farago et al.	1977
Accumulation by European species of the genus *Alyssum*	Brooks et al.	1978
Selective accumulation of nickel II ions in plants	Still et al.	1980
Accumulation by soybean from sludge-amended soil	Reddy and Dunn	1984
Accumulation by *Psychotria* species from the pacific Basin	Baker et al.	1985
Accumulation by species of *Thlaspi* L., *Cochlearia* L.,	Reeves	1988
Stackhousia tryonii Bailey: accumulator, serpentinite-endemic species of central Queensland	Batianoff et al.	1990
Accumulation mechanisms and tolerance	Gabbrielli and Vergnano	1991
Accumulation by tropical plants growing around an industrial area	Rao and Dubey	1992
Accumulation by serpentine plants.	Reeves	1992
Accumulation in the foliage of plants growing in the vicinity of an oil-fired power plant	William et al.	1993
Accumulation by western North American genera	Reeves et al.	1993
Accumulation in rice plants- effects on mineral nutrition and possible interactions of abscisic and gibberellic acids	Rubio et al.	1994
Accumulation by serpentine species of *Streptanthus* (Brassicaceae): field and greenhouse studies	Kruckeberg and. Reeves	1995
The danger of accumulation of nickel in cereals on contaminated soil	Poulik	1997

Uptake		
Uptake kinetics of nickel using intact soybean seedlings	Cataldo et al.	1978
Nickel uptake by *Alyssum* species	Morrison et al.	1980
Nickel uptake by Californian *Streptanthus* and *Caulanthus* with particular reference to the hyperaccumulator, *S. polygaloides* Gray (Brassicaceae)	Reeves et al.	1981
Metal ion uptake by plants of genus *Aalyssum*	Fiuman et al.	1983
Uptake of nickel by species of *Alyssum bornmuellera* and other genera of Old World Tribus Alyssae	Reeves et al.	1983
Investigation of effects of cadmium, lead, nickel and vanadium contamination on the uptake and transport processes in cucumber plants by TXRF spectrometry	Varga et al.	1999
Chelator (EDTA and HEDTA) effects on Ni uptake by *Helianthus annuus*	Hong and Cutright	2001
Assessment of plant uptake of radioactive nickel from soils	Denys et al.	2002
Transport		
The role of metal transport and tolerance in nickel hyperaccumulation by *Thlaspi goesingense* halacsy	Kramer et al.	1977
Comparative phloem mobility of nickel in nonsenescent plants	Neumann Chamel	1986
Long-distance transport of cobalt and nickel in maturing wheat	Zeller and Feller	1999
Nickel transport systems in microorganisms	Eitinger et al.	2000
Phytotoxicity		
A methodology for establishing phytotoxicity criteria for chromium, copper, nickel and zinc in agricultural and application of municipal sewage sludge	Chang et al.	1992
A comparative analysis of element composition of roots and leaves of barley seedlings grown in the presence of toxic cadmium, molybdenum, nickel and zinc concentratiuons	Brune and Dietz	1995
Tolerance		
Copper and nickel tolerance in *Typha latifolia* clones from contaminated and uncontaminated environments	Taylor and Crowder	1984
Differential tolerance of three cultivars of *Agrostis capillaris* L. to cadmium, copper, lead, nickel and zinc	Symenoides et al.	1985
Comparison of two serpentine species with different nickel tolerance strategies	Gabbrielli et al.	1990
The tolerance of *Empetrum nigrum* to copper and nickel	Monni et al.	2000
Biochemical characterization		
Charcterization of of nickel compounds in *Alyssum bertolonii*	Pelosi et al.	1976
Isolation and identification of a citrate complex of nickel from plants	Lee et al.	1977
The relation between nickel and citric acid in some nickel-accumulating plants	Lee et al.	1978
Nature of nickel complexes in *Psychotria douarrei* and other nickel-accumulating plants	Kersten et al.	1980
The amino acid content of *Hybanthus floribundus*, a nickel accumulating plant and the difficulty of detecting nickel amino acid complexes by chromatographic methods	Farago et al.	1980
Biochemical form of nickel in alfalfa	Theisen and Blincoe	1984
Isolation and partial characterization of nickel complexes in higher plants.	Theisen and Blincoe	1988
Organic constituents and complexation of nickel (II) in soybean xylem exudates	Cataldo et al.	1988
Characterization of the nickel-rich extract from the nickel hyperaccumulator *Dichapetalum gelonioides*	Homer et al.	1991
Bioaccumulation and toxicology of nickel: implications for wild mammals and birds	Outridge and Sheuhammer	1993
Concentration profiles of arsenic, cadmium, chromium,copper, lead, mercury, nickel, zinc, vanadium and polynuclear aromatic hydrocarbons (PAH) in forest soil beside an urban road	Munch	1993
Proton microprobe and X-ray fluorescence investigation of nickel distribution in serpentine flora from South Africa	Mesjasz-Przybylowicz et al.	1994
Localisation of nickel in epidermal subsidiary cells of leaves of *Thlaspi montanum* var. *siskiyouense* (Brassicaceae) using energy-dispersive X-ray microanalysis	Heath et al.	1997
Micro-PIXE as a technique for studying nickel localization in leaves of the hyperaccumulator plant *Alyssum lesbiacum*	Krämer et	1997
Organic costituents and complexation of nickel, iron, cadmium and plutonium in soybean xylem exudates	Cataldo et al.	1998
Nnickel-binding proteins	Watt and. Ludden	1999
The role of histidine in nickel hyperaccumulation in *Thlaspi goesingense* (Halácsy)	Pearsans et al.	1999
Relative Abundance of nickel in the leaf epidermis of eight hyperaccumulators: evidence that the metal is excluded from both guard cells and trichomes	Psaras et al.	2000
Nuclear microprobe studies of elemental distribution in apical leaves of the Ni hyperaccumulator *Berkhya coddii*	Mesjasz-Przybylowicz et al.	2001
Hyphenated technique for investigation of nickel complexation by citric acid in xylem sap of cucumber plants	Gasparics et al.	2002

Nickel contamination affects growth and secondary metabolite composition of St. John's wort (*Hypericum perforatum* L.)	Susan et al.	2003
Organic acid complexation, heavy metal distribution and the effect of ATPase inhibition in hairy roots of hyperaccumulator plant species	Boominathan et al.	2003
Hyperaccumulation		
Hyperaccumulation of nickel by some plants of Southeast Asia	Wither	1977
Hyperaccumulation of nickel by *AlyssumLinnaeua*	Brooks et al.	1979
Comparative studies of nickel, cobalt and copper uptake by some nickel hyperaccumulators of the genus *Alyssum*	Homer et al.	1991
Nickel hyperaccumulated by *Thlaspi montanum* var. *montanum* is acutely toxic to an insect herbivore	Boyd and Martens.	1994
Nickel hyperaccumulation defends *Streptanthus polygaloides* (Brassicaceae) against pathogens	Boyd et al.	1994
The ecological significance of nickel hyperaccumulation: a plant chemical defense	Martens and Boyd	1994
Hyperaccumulation, complexation and distribution of nickel in *Sebertia acuminata*	Sagner et al.	1998
Nnickel hyperaccumulation by Thlaspi montanum var. montanum (Brassicaceae): a constitutive trait	Boyd et al.	1998
The significance of metal hyperaccumulation for biotic interactions	Boyd and Martens	1998
Nickel hyperaccumulation in the Serpentine Flora of Cuba	Reeves et al.,	1999
Metal hyperaccumulation: a model system for co-evolutionary studies	Pollard	2000
The role of root exudates in nickel hyperaccumulation and tolerance in accumulator and non-accumulator species of *Thlaspi*	Salt et al.	2000
Elemental distribution in *Senecio anomalochrous*, a Ni hyperaccumulator from South Africa	Mesjasz-Przybylo-wicz et al.	2001
Rhizosphere characteristics of indigenously-growing nickel hyperaccumulator and excluder plants on serpentine soil	Wenzel et al.	2003
Indicator		
Hybanthus floribundus (Lindl.) F. Muell. indicator and accumulator plant	Cole	1974
Sebertia acuminata: a nickel-indicator and accumulator from New Caledonia	Jaffre et al.	1976
Alyssum bertolonii Desv. a nickel-indicator and accumulator	Vergnano et al.	1977
European species of *Thlaspi* L. (Cruciferae) as indicators of nickel and zinc	Reeves and Brooks	1983
A new nickelophilous species of *Alyssum* (Cruciferae) from Portugal	Dudley	1986
Molecular biology of nickel carcinogenesis	Costa	1998
Elemental defence		
Deterrence of herbivory by zinc hyperaccumulation in *Thlaspi caerulescens* (Brassicaceae)	Pollard and Baker	1997
Aphids are unaffected by the elemental defence of the nickel hyperaccumulator *Streptanthus polygaloides* (Brassicaceae)	Boyd and Martens	1999
Phytoenrichment of soil Ni content by *Sebertia acuminata* in New Caledonia and the concept of elemental allelopathy	Boyd and Jaffré	2001
Responses of generalist predators fed high-Ni *Melanotrichus boydi* (Heteroptera: Miridae): elemental defense against the third trophic level	Boyd and Wall	2001
Spread of metals through an invertebrate food chain as influenced by a plant that hyperaccumulates nickel	Peterson et al.	2003
Interaction with other elements		
Modelling the phytotoxicity of aluminum, cadmium, copper, manganese, nickel, and zinc using the Weibull frequency distribution	Taylor et al.	1991
Modelling the interactive effects of aluminum, cadmium, manganese, nickel and zinc stress using the weibull frequency distribution	Taylor et al.	1992
The effects of nickel on the nutrient fluxes and on the growth of *Elodea Canadensis*	Khknen and Kairesalo.	1998
Metal-metal interactions in accumulation of V^{5+}, Ni^{2+}, Mo$^{6+,}$ Mn^{2+} and Cu^{2+} in under- and above-ground parts of *Sinapis alba*	Fargasov and Beinrohr	1998
Mycorrhizal association		
Response of ectomycorrhizal *Quercus rubra* to soil cadmium, nickel and lead	Dixon	1988
Survival of the indigenous population of *Rhizobium leguminosarum* biovar trifolii in soil spiked with Cd, Zn, Cu and Ni salts	Chaudri et al.	1992
Effects of chromium and nickel on growth of the ectomycorrhizal fungus *Pisolithus* and formation of ectomycorrhizas on *Eucalyptus urophylla* S.T. Blake	Aggangan et al.	1998
Arbuscular mycorrhiza of *Berkheya coddii* and other Ni-hyperaccumulating members of Asteraceae from ultramafic soils in South Africa	Turnau and Mesjasz-Przybylowicz	2003
Physiology and biochemistry		
Nickel in plant growth and metabolism	Mishra and Kar	1974

Is nickel a universal component of plant ureases?	Polacco	1977
Carbohydrate levels and photo assimilate export from leaves of *Phaseolus vulgaris* to excess cobalt, nickel and zinc	Samarakoon and Rauser	1979
Effects of excess cobalt, nickel and zinc on the water relations of *Phaseolus vulgaris*	Rauser et al.	1981
The chemical form and physiological function of nickel in some Iberian *Alyssum* species	Brooks et al.	1981
Effects of heavy metals on the growth and mineral composition of a nickel hyperaccumulator	Varennes et al.	1986
Nnickel-induced stimulation of growth, heterocyst differentiation, 14CO2 uptake and nitrogenase activity in Nostoc muscorum	Rai and Raizada.	1986
Effects of nickel and copper mixtures on tomato in sand culture	Hale et al.	1987
Effects of vanadium, nickel and sulphur dioxide on polar lipid biosynthesis in jack pine	Khan et al.	1987
Impairment of photosystem II activity at the level of secondary quinone electron-acceptor in chloroplasts treated with cobalt, nickel and zinc ions.	Mohanty et al.	1989
Effect of nickel on photosynthesis and the enzymes of the photosynthetic carbon reduction cycle in Pigeon pea (*Cajanus cajan*)	Shoeran et al.	1990
Effect of nickel on the lipid composition, Mg-ATPase activity and fluidity of plasma membranes from rice, *Oryza sativa* cv. Bahia shoots	Ros et al.	1990
Effect of nickel on ethylene biosynthesis in soybean	Pnnazio and Roggero	1992
In vivo and in vitro effects of nickel and cadmium on the plasmalemma ATPase from rice (*Oryza sativa* L.) shoots and roots	Ros et al.	1992
Effect of cadmium and nickel on mobilisation of food reserves and activities of hydrolytic enzymes in germinating pigeon pea seeds	Bishnoi et al.	1993
In vivo response of photosynthetic apparatus of *Phaseolus vulgaris* to nickel toxicity	Krupa et al.	1993
Influence of cadmium and nickel on photosynthesis and water relations in wheat leaves of differential insertion level	Bishnoi et al.	1993
Influence of cadmium and nickel on growth, net photosynthesis and carbohydrate distribution in rice plants	Moya et al.	1993
Treatment of chromium and nickel in wastewater by using aquatic plants	Srivastav et al.	1994
Hydrogen uptake in *Nostoc* strain PCC 73102: Effects of nickel, hydrogen,carbon and nitrogen	Oxelfelt et al.	1995
Free histidine as a chelator in plants that accumulate nickel.	Krämer et al.	1996
Effect of heavy metals on the growth and mineral composition of nickel hyperaccumulation	Verennes A.de et al.	1996
Removal of nickel ions from aqueous solution by biomass and silica-immobilized biomass of *Medicago sativa* (Alfalfa)	Gardea-Torresdey et al.	1996
Phytofiltration of hazardous cadmium, chromium, lead and zinc ions by biomass of *Medicago sativa* (Alfalfa)	Gardea-Torresdey et al.	1998
Phytoremediation	Salt et al.	1998
Influence of nickel on organic acid transport in xylem sap of cucumber	Tat et al.	1999
Influence of Ni supply on growth and nitrogen metabolism of *Brassica napus* L. grown with NH4NO3 or urea as N source	Gerend et al.	1999
Effects of chromium and nickel on germination and growth in tolerant and non-tolerant populations of *Echinochloa colona* (L.)	Grout et al.	2000
Effects of nickel concentration in the nutrient solution on the nitrogen assimilation and growth of tomato seedlings in hydroponic culture supplied with urea or nitrate as the sole nitrogen source	Tan et al.	2000
Effects of chromium and nickel on germination and growth in tolerant and non-tolerant populations of *Echinochloa colona* (L.)	Rout et al.	2000
Effects of nickel concentration in the nutrient solution on the nitrogen assimilation and growth of tomato seedlings in hydroponic culture supplied with urea or nitrate as the sole nitrogen source	Tan et al.	2000
Effect of mixed cadmium, copper, nickel and zinc at different pHs upon alfalfa growth and heavy metal uptake	Peralta-Videa et al.	2002
Phytoremediation of metals using transgenic plants	Pilon-Smits and Pilon	2002
Lead and nickel removal using *Microspora* and *Lemna minor*	Nicholas et al.	2003
Relationship between the chemical form of nickel applied to the soil and its uptake and toxicity to barley plants (*Hordeum vulgare* L.)	Molas and Baran	2004
Phytomining and Phytomanagement		
Nickel phytomining	Nicks and Chambers	1998
Method for phytomining of nickel from soil. US Patent, 5944872	Chaney et al.	1999
Phytomining	Brooks, et al.	1998
Phytomining for nickel	Anderson et al.	1999
The nickel hyperaccumulator plant *Alyssum bertolonii* as a potential agent for phytoremediation and phytomining of nickel	Robinson et al.	1997
The nickel phytoextraction potential of some ultramafic soils as determined by sequential extraction	Robinson et al.	1999
The potential of the high biomass nickel hyperaccumulator *Berkheya coddii* for phytoremediation and phytomining	Robinson et al.	1997
Soil amendments affecting nickel t uptake by *Berkheya coddii*: Potential use for phytomining and phytoremediation	Robinson et al.	1999
The effect of EDTA and citric acid on phytoremediation of Ni from soil using *Helianthus annuu*	Turgut et al.	2004

process involves the use of plants to facilitate the removal of metal contaminants from a soil matrix. In practice, metal-accumulating plants are seeded or transplanted into metal-polluted soil and are cultivated using established agricultural practices. If metal availability in the soil is not adequate for sufficient plant uptake, chelates or acidifying agents would be applied to liberate them into the soil solution. Use of soil amendments such as synthetics (ammonium thiocyanate) and natural zeolites have yielded promising results. Synthetic cross-linked polyacrylates (hydrogels) have protected plant roots from heavy metals toxicity and prevented the entry of toxic metals into roots. After sufficient plant growth and metal accumulation, the above-ground portions of the plant are harvested and removed, resulting the permanent removal of metals from the site. Soil metals should also be bioavailable, or subject to absorption by plant roots. Chemicals that are suggested for this purpose include various acidifying agents, fertilizer salts and chelating materials. The retention of metals to by soil organic matter is also weaker at low pH, resulting in more available metal in the soil solution for root absorption. It is suggested that the phytoextraction process is enhanced when metal availability to plant roots is facilitated through the addition of acidifying agents to the soil. Chelates are used to enhance the phytoextraction of a number of metal contaminants including Cd, Cu, Ni, Pb, and Zn.

Ni tolerant plants/Ni accumulators either accumulate or exclude metals. Hence, plants with a reduced capacity to accumulate toxic metals if edible, should be a concern for human health. In contrast, plants with an enhanced capacity to accumulate toxic metals can help in phytoremediation technologies. Thus, knowledge of how plants can specifically accumulate or exclude essential elements and toxic metals, particularly in case of Ni tolerant plants or accumulators can be exploited for the selection of species that are appropriate for use in phytoremediation. This includes knowledge on bioavailability of metals, rhizospheric processes and root uptake, as well as on translocation to and processing/storage in the above-ground parts of the plant. Use of plants that hyperaccumulate specific metals and control and/or transform organic pollutants is gaining considerable significance in contemporary phytotechnology (table 2).

Ni tolerant plants and Ni accumulators have been found to be useful in phytotechnologies all over the word for transformation and containment of inorganic and organic pollutants including radionuclides (table 2). However, ecosystem design and management, investigations related to rhizosphere biotechnology, processes involved in the evolution of ecosystems and engineering of plant metabolism for enhancing the adaptive ecophysiology still remain a challenging task particularly with regard to the management of the phytomass and recycling (figures 2 and 3).

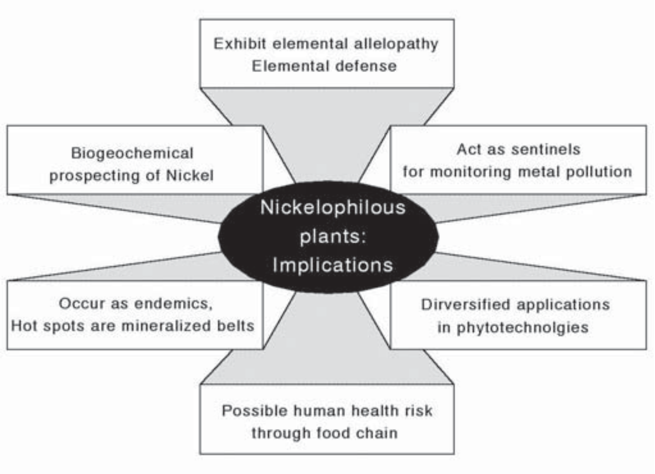

Figure 1. Environmental implications of nickelophilous plants - scope and limitations

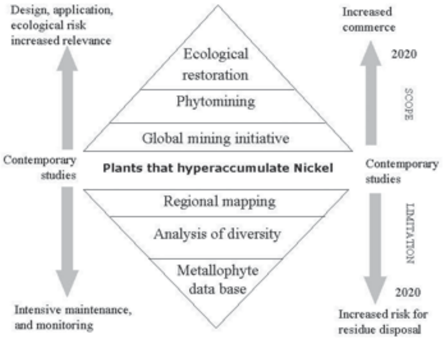

Figure 2. Advantages and limitations of using invasive and non-invasive plants (indigenous and alien) in phytotechnologies. (Based on McCutcheon and Schnoor, 2003).

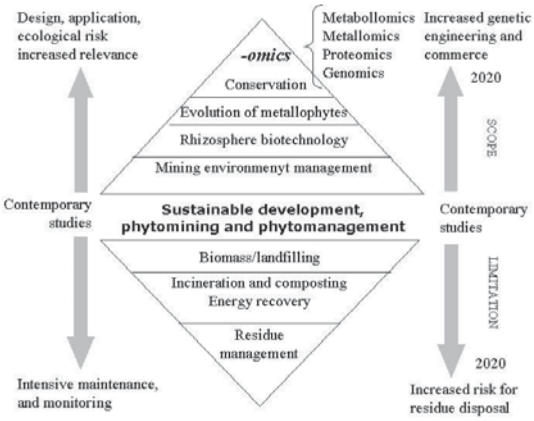

Figure 3. In order to move ahead in phytotechnologies: existing gaps in our knowledge must be thoroughly investigated with the available modern tools (Based on McCutcheon and Schnoor, 2003).

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