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Review

Functions and Toxicity of Nickel in Plants: Recent Advances and Future Prospects

Nickel is an essential nutrient for plants. However, the amount of Ni required for normal growth of plants is very low. Hence, with the level of Ni pollution in the environment increasing, it is essential to understand the functional roles and toxic effects of Ni in plants. We briefly review advances in relevant research over the past 20 years. Based on the available data, two new indirect pathways of Ni toxicity in plants are proposed. These are *(i)* interference with other essential metal ions and *(ii)* induction of oxidative stress. Research should focus on these mechanisms at the protein and molecular levels. Further research should also be directed at plant species that are capable of accumulating Ni at high concentration, so-called hyperaccumulators. Such species can provide model systems to study the mechanisms of Ni tolerance and can also be used for phytoremediation by removing nickel from polluted environment.

Keywords: Heavy metals; Nickel; Plants; Pollution; Toxicity; Accumulation

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1 Introduction

Nickel, first isolated by the Swedish chemist Cronstedt in 1751, is the twenty-second most abundant element in the earth's crust [1, 2], where it occurs in igneous rocks as a free metal or together with iron. It has an atomic number of 28 in the periodic table and an atomic weight of 58.71. Ni is a hard, ductile and silvery-white heavy metal that can take a high polish. In general, naturally occurring concentrations of Ni in soil and surface waters are lower than 100 and 0.005 ppm, respectively [3, 4]. Ni is also released into the environment from anthropogenic activities, such as metal mining, smelting, fossil fuel burning, vehicle emissions, disposal of household, municipal and industrial wastes, fertilizer application and organic manures [5, 6]. Ni is mainly used as a raw material in the metallurgical and electroplating industries, as a catalyst in the chemical and food industry, and as a component of electrical batteries [7]. In recent years, Ni pollution has been reported from across the world, including Asia [8 – 11], Europe [4, 12 – 14] and North America [3, 15, 16]. Pollution mainly results from effluent disposal from mining, smelting and electroplating industries, and from sewage sludge and compost [17 – 19]. Ni^{2+} concentrations may reach 26 000 ppm in polluted soils [4, 5] and 0.2 mg/L in polluted surface waters [20, 21]; 20 to 30 times higher than found in unpolluted areas. Soil and water contamination with Ni has become a worldwide problem [22, 23].

Ni is essential for plants [24 – 26], but the concentration in the majority of plant species is very low (0.05 – 10 mg/kg dry weight) [27]. Further, with increasing Ni pollution, excess Ni rather than a deficiency, is more commonly found in plants [5, 6]. Toxic effects of high concentrations of Ni in plants have been frequently reported, for example inhibition of mitotic activities [28], reductions in plant growth [29] and adverse effects on fruit yield and quality [30]. Extremely high soil Ni concentrations have left some farmland unsuitable for growing crops, fruits and vegetables [31].

Although many reports have focused on the toxic effects of Ni on plants, our knowledge of its toxicity is incomplete, and the detailed mechanisms involved are poorly understood. In this review, we aim to bring together advances made over the past 20 years, paying particular attention to uptake and transport of Ni in plants, its toxic effects, and to the biology of Ni hyperaccumulator species. We also identify aspects that warrant further attention in future research efforts.

2 Uptake of Ni in Plants

Ni has been identified as a component of a number of enzymes, including glyoxalases (family I), peptide deformylases, methyl-CoM reductase and ureases, and a few superoxide dismutases and hydrogenases [32, 33]. Therefore, Ni plays a role in various important metabolic processes, including ureolysis, hydrogen metabolism, methane biogenesis and acitogenesis [26, 34 – 36]. Ni may also have other functions that have yet to be discovered in plants, but that may be revealed with further study and use of new techniques. Since Ni is essential for plant metabolism, its uptake and transport in plants is involved in some important physiological processes.

The uptake of Ni in plants is carried out mainly by root systems via passive diffusion and active transport [37]. The ratio of uptake between active and passive transport varies with species, Ni form and concentration in the soil or nutrient solution [38, 39]. For example, soluble Ni compounds can be absorbed via the cation transport system. Since Cu^{2+} and Zn^{2+} inhibit Ni^{2+} uptake competitively, these three soluble metal ions seem to be absorbed by the same transport system [40 – 42]. In addition, soluble Ni compounds could also be

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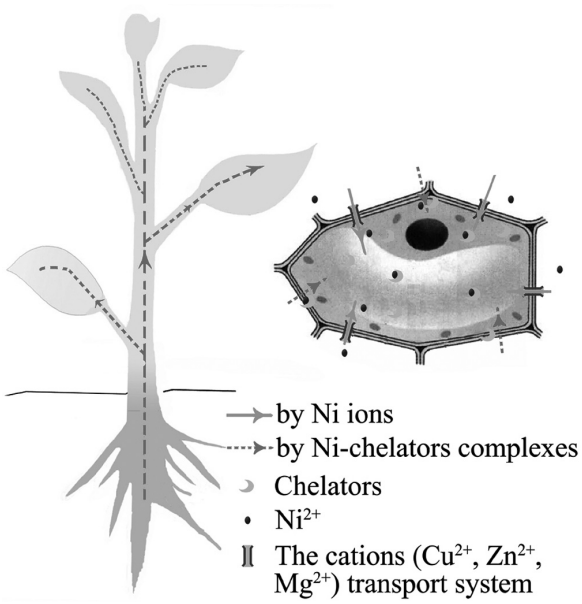

Figure 1. The main pathways of Ni uptake and transport in plants. The chelators include nicotianamine (NA), histidine (His), citrate, organic acids and proteins with various important functions, including permeases, metallothionein (MT), metallochaperones and YS1-like proteins (YSLs).

absorbed via the Mg ion transport system, because of the similar charge/size ratio of the two metal ions [43]. Nevertheless, Mg^{2+} has no inhibitory effect on Ni^{2+} absorption [40, 41]. Secondary active transport of chelated Ni^{2+} is possible, and corresponding proteins that specifically bind Ni^{2+}, such as HoxN (high-affinity nickel transport protein, a permease) [44, 45], metallothionein (MT) [46] and metallochaperones [47 – 49] have been reported (see Fig. 1).

The uptake of Ni by plants depends on Ni^{2+} concentrations [40], plant metabolism [50], the acidity of soil or solution [3, 16, 51], the presence of other metals [52 – 54] and organic matter composition [55, 56]. For example, the uptake of Ni^{2+} by *Lathyrus sativus* reportedly increased with increasing pH up to 5.0, then decreased as pH is increased up to 8.0 [57]. The uptake of Ni^{2+} by *Berkheya coddii* has been found to be inhibited by Ca^{2+} and Mg^{2+} [58]. However, both Ca^{2+} and Mg^{2+} are reportedly non-competitive inhibitors of Ni^{2+} influx in excised barley roots [59]. In these roots, Zn^{2+}, Cu^{2+}, Co^{2+}, Cd^{2+}, and Pb^{2+} inhibited Ni^{2+} influx, whereas Mn^{2+} did not. Amongst these ions, Zn^{2+} and Cu^{2+} were strongly competitive, Co^{2+} was weakly competitively and Cd^{2+} and Pb^{2+} appeared to be non-competitive with Ni^{2+} [59]. The adsorption of Ni^{2+} by *Datura innoxi* was enhanced via the application of ethylenediaminetetraacetic acid (EDTA) to the soil surface [56]. In addition, it was reported that other factors can influence the uptake of Ni^{2+}, such as length of season, method of sowing seed, and soil geochemical properties (aquifer characteristics, surface area, dielectric constant, etc.) [51, 60, 61].

3 Transport and Distribution of Ni in Plants

Ni is transported from roots to shoots [62] and leaves [63] through the transpiration stream [64] via the xylem. This essential element is supplied to meristematic parts of the plants by retranslocation from old to young leaves, and to buds, fruits and seeds, via the phloem [3, 65 – 67]. This transport is tightly regulated by metal-ligand complexes [68 – 73] and proteins that specifically bind Ni [47, 74] (see Fig. 1). Metal ligands, such as nicotianamine (NA), histidine (His) and organic acids (citric acid and malate ions), can act as intracellular chelators, which bind Ni in the cytosol or in subcellular compartments for transport, translocation and accumulation within plants [75 – 78]. For example, there have been reports of Ni-NA complexes in the roots of *Thlaspi caerulescens* [69], Ni-His in the roots of *Alyssum lesbiacum*, *Alyssum montanum* and *Brassica juncea* [75, 77, 79], and Ni-citrate in leaves of *Thlaspi goesingense* and *Thlaspi arvense* [68, 76]. Organic acids, such as citric and malic acids, provide both a source of protons for solubilization and anions for Ni chelation [80 – 82]. Three distinct Ni^{2+} metallochaperones (metalloproteins that aid in the insertion of the appropriate metal ion into a metalloenzyme), including HypB, CooJ and UreE proteins, have been identified in bacteria [47, 49, 83 – 85]. It is likely that similar Ni-binding proteins will be found in plants. Recently, evidence was found indicating that Yellow Stripe-Like Proteins (YSLs) may act as transporters, particularly for Ni-NA, in a metal hyperaccumulating plant [86].

Over 50% of the Ni absorbed by plants is retained in the roots [40]. This may be due to sequestration in the cation exchange sites of the walls of xylem parenchyma cells and immobilization in the vacuoles of roots [37]. Furthermore, a high percentage (over 80%) of Ni in the roots is present in the vascular cylinder, while less than 20% is present in the cortex (see Fig. 2). This distribution suggests a high mobility of Ni in the xylem and phloem [87 – 89]. It is notable that the forms of Ni in xylem exudate are strongly influenced by pH. Notably, Ni is mainly chelated by citrate at pH 5.0, but by histidine at pH 6.5 [89]. In stems and leaves of the Ni hyperaccumulators (*Alyssum bertolonii*, *Alyssum lesbiacum* and *Thlaspi goesingense*), Ni has been found to be distributed preferentially in the epidermal cells, most likely in the vacuoles rather than in the cell wall [90]. However, Krämer et al. [76] reported that 67 to 73% of Ni in the leaves of *Thlaspi goesingense* was associated with the cell wall. This discrepancy may be due to the different Ni concentrations and methods of sample preparation used [90]. The consensus is that Ni in stems and leaves are mainly located in the vacuoles, cell walls and epidermal trichomes associated with citrate [86, 91], malate and malonate [92, 93] (see Fig. 2). However, within cells the Ni contents of different organelles and cytoplasm may differ substantially. Timperley et al. [94] found over 87% of Ni in the cells of leaves of four species located in the cytoplasm and vacuoles, while chloroplasts contained 8 to 9.9% and mitochondria and ribosomes contained only 0.32 to 2.85%.

4 Toxic Effects of Ni on Plants

Although Ni is an essential metal and plays important roles in plant metabolism [24, 95], Ni toxicity has become a particular concern, due to its increased industrial use. Under Ni stress conditions, many common Ni-detoxification responses appear in plants. These responses include the formation of Ni^{2+}-organic acid and Ni^{2+} – NA complexes [76, 90, 96], the overproduction of NA and it's synthase [69, 97, 98], and high levels of free histidine [99]. Other responses include the induction of MTs and thiol glutathione [100, 101], and high concentrations of glutathione, Cys and *O*-acetyl-L-serine (OAS) [102]. In addition, some enzyme activities may be enhanced, such as serine acetyltransferase (SAT) and glutathione reductase [103]. However, under excess Ni conditions, toxicity symptoms in plants will develop.

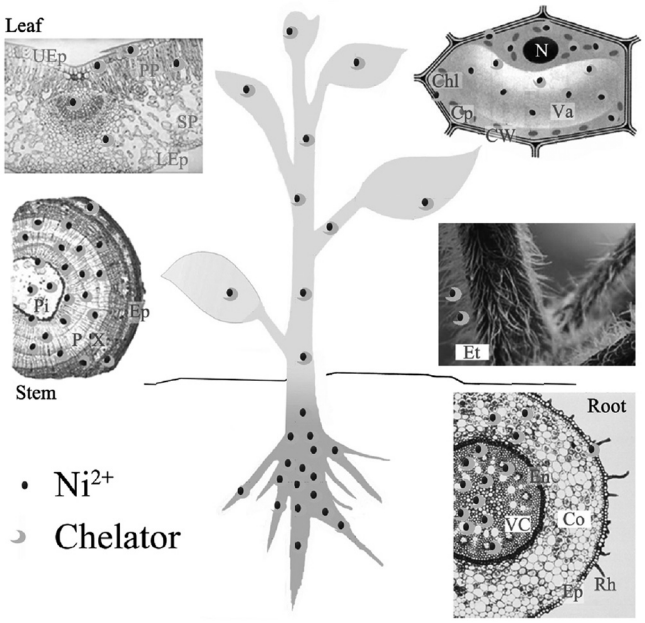

Figure 2. The distribution of Ni in plants. More than 50% of Ni is retained in the roots, and over 80% of the Ni in the roots is present in the vascular cylinder. Ni in stems and leaves are mainly located in the vacuoles, cell walls and epidermal trichomes associated with chelators, such as nicotianamine (NA), histidine (His), citrate, organic acids and proteins with various important functions, including permeases, metallothionein (MT), metallochaperones and YS1-like proteins (YSLs).
Abbreviations in this figure: Cell wall (CW), Chloroplasts (Chl), Cortex (Co), Cytoplasm (Cp), Endodermis (En), Epidermal trichomes (Et), Epidermis (Ep), Lower epidermis (LEp), Nuclear (N), Palisade parenchyma (PP), Phloem (P), Pith (Pi), Root hair (Rh), Spongy parenchyma (SP), Upper epidermis (UEp), Vacuoles (Va), Vascular cylinder (VC), Xylem (X).

Responses to toxicity differ substantially according to plant species, growth stage, cultivation conditions, Ni concentration and exposure time [63, 87, 104–107]. In general, critical toxicity levels are >10 mg/kg dry weight (DW) in sensitive species [13], >50 mg/kg DW in moderately tolerant species [108, 109], and >1000 mg/kg DW in Ni hyperaccumulator plants, such as *Alyssum* and *Thlaspi* species [90, 110]. In sensitive species (for example, barley, water spinach and wheat), chlorosis and necrosis of leaves can appear after plants are treated with Ni at very low concentrations ($\leq$0.2 mM or 11.74 ppm) for less than a week [30, 111, 112]. According to Molas [113], phytotoxicity and accumulation in cabbage decreased in the following order after treatment with different chemical forms of Ni: Ni(II)-Glu > $NiSO_4 \cdot 7H_2O$ > Ni(II)-citrate $\gg$ Ni(II)-EDTA. Plants grown in Ni-contaminated soil and media show various responses and toxicity symptoms including retardation of germination [114], inhibition of growth [28, 30, 115], reduction of yield [28, 116–118], induction of leaf chlorosis and wilting [30, 118], disruption of photosynthesis [29, 30, 116, 119, 120], inhibition of CO_2 assimilation [13, 116], as well as reductions in stomatal conductance [104, 121].

4.1 Growth and Development Inhibition and Reduction of Yield

There have been many reports on the effects of Ni on germination and growth in plants, including the following. The germination of pigeonpea was found to decrease by circa 20% in a 1.5 mM solution of Ni, with the percentage germination related to Ni concentration [28, 114]. Exposure of 42 day-old cabbage plants to 0.5 mM Ni for eight days did not produce any perceptible difference in growth, but their subsequent growth was retarded [118]. The shoot growth of wheat was clearly inhibited when treated with 0.2 mM Ni [30]. The roots of *Nicotiana tabacum* became dark brown within 7 to 10 days of exposure to 0.43 mM Ni and growth of the plants was severely inhibited [115].

Other reports show that accumulation of Ni seriously affects the yield of plants, significantly decreasing the numbers of seeds/pod, 100-seed weight and seed yield per plant [122]. The total dry matter accumulation in roots, shoots and the total biomass may also decrease when plants are stressed by Ni [28, 118], probably due to reductions in leaf blade area and leaf density [116], with accompanying reductions in numbers of flowers and fruits [117]. Overall, reductions in plant yield can be attributed to poor plant development and reduced supply of nutrients to the reproductive parts [10].

4.2 Induction of Leaf Chlorosis, Necrosis and Wilting

Excess Ni has been reported to cause leaf necrosis and chlorosis of plants [3, 37, 87, 123]. Chlorosis and along-vein necrosis appeared in newly developed leaves of water spinach after plants were treated with 0.085 to 0.255 mM (5–15 ppm) Ni for a week [111]. Ni at a concentration of 0.5 mM produced dark brown necrotic spots along the leaf margins and decreased water potential and transpiration rate, resulting in wilting of outer leaves and necrosis of inner leaves of cabbage [118]. Barley grown in 0.1 mM Ni for 14 days showed chlorosis and necrosis of leaves [112]. After three days, treatment at 0.2 mM Ni reduced relative water content of wheat shoots [30]. Rice (*Oryza sativa* L.) grown in a nutrient medium containing 0.5 mM Ni showed a significant decrease in water content [124]. However, these typical visual symptoms of Ni toxicity may also be due to deficiencies of other essential metals, such as Fe, Cu, Zn, and Mn [125, 126].

4.3 Disruption of Photosynthesis

The influence of Ni on photosynthesis is pervasive, occurring both in isolated chloroplasts and whole plants [29, 122, 127, 128]. Ni damages the photosynthetic apparatus at almost every level of its organization, including destroying cells of mesophyll and epidermal tissue [121] and decreasing chlorophyll content (chlorophyll a, b, total chlorophyll and chlorophyll a/b ratio) [10, 30, 63, 116, 118, 120, 129]. Nickel also damages the thylakoid membrane and chloroplast grana structure [29, 119], reducing the size of grana and increasing the number of non-appressed lamellae [116].

At the biochemical level, Ni affects light-harvesting complex II (LHCII) [130, 131] and the amounts of xanthophylls and carotenoids. It also interferes with the photosynthetic electron transport chain [132, 133] and its intermediates (such as cytochromes b6f and b559) in leaves [63, 104]. The inhibition of electron transport is mainly on the donor side of photosystem II (PSII) [127, 132] and the binding site for Q_B, the secondary quinine acceptor of PSII [133, 134]. Further studies on photosynthetic protein complexes have suggested that Ni mainly inactivates photosystem I (PSI) in vivo [127], whereas it primarily targets PSII in vitro [122]. A recent study on spinach leaves in vitro showed that two proteins associated with the oxygen-evolving complex of PSII (the extrinsic 16 and 24 kDa polypeptides) were

depleted following treatment with 1 mM Ni [128]. Taking these studies together, the disruption of photosynthesis by Ni cannot be attributed to any single factor and appears to result from its combined effects on chloroplast structure, chlorophyll content and photosynthetic protein complexes.

5 Toxicity Mechanisms of Ni in Plants

Although Ni toxicity in plants has been extensively reported, the detailed mechanisms involved are still poorly understood. The toxicity of Ni is likely to be caused by indirect mechanisms, because it is not an active or redox metal. Based on analyses of the available data, we propose two mechanisms of Ni toxicity in plants: interference with other essential metal ions and induction of oxidative stress.

5.1 Interference with Other Essential Metal Ions

It is well known that other metals as well as Ni, such as K, Na, Ca, Mg, Fe, Cu, Zn, and Mn are essential for plants [135]. Ni has some similar characteristics to Ca, Mg, Mn, Fe, Cu, and Zn. Therefore, Ni may compete with these metals in absorption and transpiration processes [40 – 42, 136 – 138]. As a result of competition, Ni at high concentrations may inhibit the absorption of these metals, decrease their concentration and even lead to their deficiency in plants [10, 123, 139, 140]. Subsequently, this may affect important physiological processes, and ultimately result in toxic effects [30, 141, 142]. For example, Ni can decrease Mg (or Fe) uptake and its supply to aerial parts via competition, and then induce deficiencies of these elements in plants. This can result in the retardation of germination, growth suppression, and reductions in yields [28, 37, 114, 115]. These inhibitory effects of Ni on the growth of plants can be reduced by supplying additional Mg (or Fe) ions [141 – 143]. Therefore, Ni toxicity in plants is partly due to interference with other essential metal ions. In addition, Ca^{2+} has been shown to reduce the toxic effects of Ni^{2+} on root development in *Alyssum bertolonii* Desv. [144], while Cu seemed to increase Ni toxicity in terms of reduced vitality and growth of Scots pine [145].

Many enzymes, such as superoxide dismutase (SOD) and catalase (CAT), are metalloenzymes containing Fe, Cu, Zn, or Mn in their prosthetic groups. Since excess Ni has been shown to decrease the contents of Fe [118], Cu and Zn [146] in plant tissues, it can be speculated that Ni may reduce the biosynthesis of these metalloenzymes by causing deficiencies of these essential metals [30]. Further studies on photosynthesis in plant leaves suggest that Ni can competitively remove Ca ions from the Ca-binding site in the oxygen evolution complex [128] and replace the Mg ion of chlorophyll [138, 147 – 149], which may eventually inhibit the PSII electron transport chain.

5.2 Induction of Oxidative Stress

Increasing evidence suggests that Ni toxicity in plants is also associated with oxidative stress [28, 30, 115, 150]. Excessive Ni leads to significant increases in the concentration of hydroxyl radicals, superoxide anions, nitric oxide and hydrogen peroxide [115, 120, 151 – 154]. Since Ni is not a redox-active metal, it cannot directly generate these reactive oxygen species (ROS). However, it interferes indirectly with a number of antioxidant enzymes [118, 154 – 158], for example, SOD, CAT, glutathione peroxidase (GSH-Px), glutathione reductase (GR), peroxidase (POD), guaiacol peroxidase (GOPX), and ascorbate peroxidase (APX). Exposure of plants to Ni at low concentrations (= 0.05 mM) and/or for short times has been shown to increase the activities of SOD, POD, GR, and GOPX in order to enhance the activation of other antioxidant defenses and hence lead to the removal (or scavenging) of ROS [102, 158 – 160]. However, excess Ni has been found to reduce the activity of many cellular antioxidant enzymes, both in vitro and in vivo, and plant's capability to scavenge ROS, leading to ROS accumulation and finally oxidative stress in plants [11, 120, 161 – 163].

The activity of antioxidant enzymes may vary with the duration and type of stress treatment, and between plant species (and plant parts). For instance, in experiments by Gajewska and Sklodowska [120] SOD and CAT activities decreased significantly in the leaves of wheat plants in response to 100 μM Ni treatment for 3, 6 and 9 days, whereas GSH-Px, GOPX and APX activities were increased. However, the same authors [158] found that exposure of 14 day old pea plants to Ni (10, 100, 200 μM for 1, 3, 6 and 9 days) resulted in reductions in SOD activities in both leaves and roots, and APX activity in roots, together with increases in APX activity in leaves, increases in glutathione S-transferase (GST) activities in both leaves and roots (most pronounced in roots), while CAT activity generally remained unchanged. Ni at 0.5 mM concentration increased the activities of SOD, GR and POD and decreased the activity of CAT in 6 day old seedlings of pigeonpea (*Cajanus cajan* L. Millspaugh) [28]. CAT and POD activities in leaves decreased significantly after cabbage was treated with 0.5 mM Ni for eight days [118]. The same tendency was found for SOD, CAT and POD activities in leaves of *Hydrocharis dubia* in response to 0.5, 1, 2, 3, 4 mM Ni treatments for three days [14]. Ni has also been shown to increase the plasma membrane (PM) NADPH oxidase, which was shown to be involved in Ni induced ROS generation in roots of 5 day old wheat seedlings (*Triticum durum*) [154].

ROS have been shown to damage cell membrane, proteins, lipids and DNA (causing, inter alia, DNA base oxidation, DNA protein cross-links, DNA gaps and breaks), resulting in lipid peroxidation [115, 156, 157, 159], developmental defects and genetic instability in plant species [43, 164 – 170]. For example, malondialdehyde (MDA, a lipid peroxidation product) content in roots and shoots increased, when pigeonpea plants were treated with 0.5 to 1.5 mM Ni [28]. Similar results have also been reported in corn, wheat and *Alyssum* species [115, 157, 159, 171]. In addition, Ni induced depletion of low molecular weight proteins, such as GSH, may contribute to the induction of oxidative stress in plants [28, 172].

6 Ni Hyperaccumulators

The growing concerns about environmental pollution and interest in phytoremediation have stimulated several recent studies on Ni hyperaccumulator plants, reflecting their potential to survive and sequester high levels of Ni in tissues (from several thousands of mg/kg up to 5% of dry biomass) without exhibiting phytotoxicity [173 – 175]. More than 310 species of Ni hyperaccumulators have been identified [10, 173, 176, 177], including members of the Acanthaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Fabaceae, Flacourtiaceae,Meliaceae, Myristicaceae, Ochnaceae, Poaceae, Rubiaceae, Sapotaceae and Stackhousiaceae [178, 179] (http://en.wikipedia.org/wiki/Hyperaccumulators:_Nickel). The family with the most such species is the Brassicaceae, with more than 80 species which are

capable of accumulating Ni to concentrations as high as 3% of shoot dry biomass [179, 180]. These species have higher requirements for Ni (e.g., up to 500 mg Ni/kg) than normal plants [90]. *Stackhousia tryonii* Bailey (Stackhousiaceae), an herbaceous species from Australia, has been shown to accumulate Ni in dry leaves at concentrations exceeding 4% [181, 182]. In addition, it is notable that many aquatic plants such as *Typha* [183, 184], *Phragmites* [185, 186], *Eichhornia* [187], *Azolla* [188, 189], and *Lemna* [190], have the potential to remove heavy metals from water [191 – 193]. The Ni removal efficiencies of these particular species are 80% higher than those of non-accumulators [183, 190].

Ni hyperaccumulator species are thought to have strategies similar to allelopathy that reduce interspecific plant competition, e.g., increasing Ni availability to other plants by depositing locally Ni rich senescent leaves [194 – 196]. In addition, these species have efficient root absorption mechanisms which allow them to specifically accumulate metals from soils and/or water. After root absorption, Ni can be transported quickly into shoots and leaves of hyperaccumulators and then sequestrated in the vacuole [175]. For these reasons, Ni hyperaccumulators has been extensively used to remove Ni from polluted soils and/or water; a so-called ‚green' technology [23, 38, 176, 195 – 199].

Recent developments of analytical techniques have allowed some of the mechanisms of Ni tolerance in hyperaccumulators to be explored and described. For example, exceptionally high endoDNase activities [200] and elevated concentrations of protective amino acids and proteins, such as free histidine [75], serine decarboxylase (SDC) [201] and metallothionein [46, 101], appear to contribute to the high Ni tolerance of some species, by chelation and/or facilitating the export of Ni from root to shoot in the xylem. In addition, ATP-phosphoribosyltransferase (ATP-PRT) expression has been found to play a major role in regulating the pool of free histidine in such species [202]. ROS and Ca ions have also been demonstrated to participate in Ni induced alterations in the expression of various proteins and genes in animal cells [203, 204].

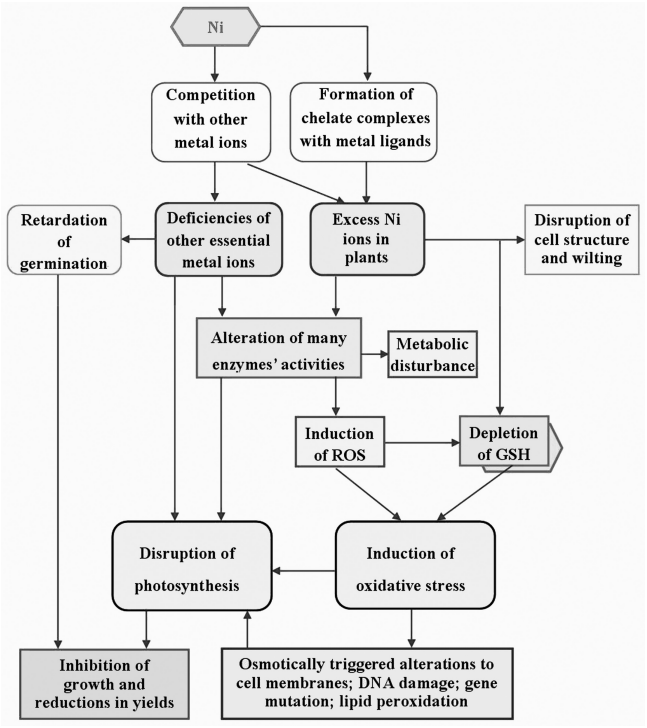

Figure 3. Mechanisms mediating toxic effects of excess Ni in plants. Excess Ni leads to deficiencies of other essential metals in plants via competition and/or the formation of chelate complexes with metal ligands. These processes ultimately result in the retardation of germination, induction of leaf chlorosis and wilting, alteration of enzymes' activities, metabolic disturbance, induction of oxidative stress, disruption of photosynthesis, inhibition of growth and reductions in yields.

7 Summary and Future Prospects

Scientific advances over the past 20 years suggest that Ni is absorbed and redistributed in plants via cation and/or metal-ligand complex transport systems. The toxic effects of nickel in plants reviewed here can be summarized as illustrated in Fig. 3. Briefly, as a result of competition with other essential metals or the induction of oxidative stress, excess Ni inhibits growth and development of plants, induces leaf chlorosis and wilting, and reduces total plant yields. Nickel toxicity also disrupts photosynthesis and alters related enzyme activities. However, the mechanisms operating at both protein and molecular levels that result in these toxicity symptoms remain largely unknown and require further study.

Growing concerns about Ni pollution in the environment have led to research on phytoremediation, i.e., the use of hyperaccumulator or wetland plants to remove and/or sequester Ni from soil and water. However, many such plants have limited utility for phytoremediation, because of their slow growth, difficult propagation, seasonal growth, and low biomass [205, 206]. Solutions to these problems are important and require further research. In addition, although many studies regarding the mechanisms of Ni tolerance in hyperaccumulators have been conducted, further studies are needed to fully understand their details at both biochemical and molecular levels. As an example, unique genes encoding the Ni-chelated proteins in Ni hyperaccumulators could be transferred to fast growing species. This type of genetic modification may allow the development of a plant specifically tailored for Ni phytoremediation with enhanced abilities to tolerate, accumulate and detoxify Ni [207].

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