Functions of nickel in higher plants - A review

Rudolf R. Kastori, Marina I. Putnik-Delić*, Ivana V. Maksimović

University of Novi Sad, Faculty of Agriculture, Department of Field and Vegetable Crops, Trg Dositeja Obradovića 8, 21000 Novi Sad, Serbia

Corresponding author: putnikdelic@polj.uns.ac.rs

A B S T R A C T

Nickel (Ni) is an essential microelement for higher plants and an important one for many other living organisms. It is present in every part of the biosphere. Higher plants have small requirements towards Ni for their optimal growth and development. That is why its latent and acute deficiencies in nature rarely occur. Soil and water pollution with Ni is a global issue. This is the reason special attention is paid to the effects of higher Ni concentrations on plants metabolism, their organic production, as well as on the possibility of using plants for phytoremediation of Ni contaminated habitats. Depending on the present concentrations, nickel may favourably, unfavourably or not affect the metabolic processes of plants at all (enzyme activity, photosynthesis, respiration, water regime, mineral nutrition, etc.), and thus the growth and development of plants. There are still many questions about the mechanism of Ni influence on the physiological and biochemical processes of plants. Therefore, we believe the presentation of the previous knowledge about the effect of Ni on plants' life processes can contribute to a better understanding of the biotechnical and ecological significance of Ni, and it can indicate further research directions in this field.

Keywords: growth, nickel, physiological processes, plants, toxicity, uptake.

И З В О Д

Никал (Ni) је у малој концентрацији широко распрострањен у биосфери. Главни извор Ni за терестричне биљке је земљишни раствор. У земљишном раствору претежно се налази у виду хидрокси комплекса Ni(OH)+ и јона Ni2+. Растворљивост и тиме мобилност и пиступачност Ni за биљке повећава се са смањењем pH вредности и капацитета земљишта за измену јона. Биљке могу Ni усвајати путем корена и надземних органа. Усвајање се одвија путем дифузије и активног транспорта. При усвајању Ni постоји интеракција са јонима других микроелемената (Zn, Fe, Mn, Cu). Никал је у биљкама добро покретљив у акропеталном и базипеталном правцу. Усвојени Ni се великим делом накупља у корену, у вакуоли и ћелијском зиду. Поједине биљне врсте и генотипови накупљају Ni различитим интензитетом. Хиперакумулатори Ni који већим делом припадају серпентинској флори одликују се нарочито великом способношћу за накупљањем Ni. Ниже концентрације Ni имају значајну улогу и повољно утичу на бројне физиолошке процесе биљака од клијања семена до растења и развића. Више биљке не могу да заврше животни циклус без адекватне обезбеђености Ni стога се он убраја у неопходне микроелементе за биљке. Никал је неопходни састојак ензима уреазе и тиме учествује у метаболизму урее. Поред тога, утиче на садржај пигмената хлоропласта, фотосинтезу, транспорт електрона, дисање, водни режим, минералну исхрану и у крајњој линији на биолошки принос биљака.

Токсичне концентрације Ni изазивају оксидативни стрес повећањем присуства реактивних кисеоничних врста што доводи до поремећаја равнотеже између прооксидативних процеса и антиоксидантног система биљака. Последице оксидативног стреса су липидна пероксидација, оксидативна модификација протеина и ДНК, деградација хлорофила и бројни други поремећаји метаболизмна услед чега ћелије и ткива подлежу некрози уколико не поседују довољно снажне антиоксидантне механизме.

Кључне речи: биљке, никл, раст, токсичност, усвајање, физиолошки процеси.

1. Introduction

Nickel (Ni) is widespread in nature in small concentrations. The share of Ni in the Earth's crust is 0.1%. According to the representation in the Earth's crust, it is on the twenty-second place among the elements. Nickel belongs to the triad of iron, along with cobalt. The elements of this triad are metals that easily transition to a passive state. They are also characterized by the appearance of ferromagnetism. In biological systems, Ni is predominantly found as Ni (II), and may also be present as Ni (I) and Ni (III). Nickel forms stable complexes with certain organic molecules. Based on the knowledge of its effect on life processes, Ni has been considered a necessary microelement for higher plants (Mishra and Kar, 1974; Eskew et al., 1983; Brown et al., 1987a) and some other living organisms (Solomons, 1984) since the late 20th century. The necessity of Ni for plants is especially emphasized after the discovery of Ni being a component of the enzyme urease (Dixon et al., 1975). Depending on its concentration, Ni can have a stimulating or toxic effect on numerous physiological and biochemical processes, and thus on the growth, development and yield of plants. Therefore, understanding its impact on plant life

processes has both theoretical and practical significance. This particularly refers to its toxic effect, having in mind numerous anthropogenic sources of Ni pollutants. Certain plant species and genotypes react differently to the presence of Ni, which should be taken into account in the case of Ni application. As Ni affects nitrogen metabolism, it is essential to take Ni distribution in plants into consideration when applying nitrogen fertilizers.

2. Uptake, Transport and Distribution of Nickel

Terrestrial plants uptake Ni from the soil. Its concentration in the soil primarily depends on its presence in parent rocks, soil forming processes and pollution. On average, the total Ni content in soil varies from 0.2 to 450 mg kg $^{-1}$ (Kabata-Pendias, 2000), while the median for Europe was 14.7 mg Ni kg^{-1} soil (Albanese, 2015). Serpentine soils are particularly known for high Ni levels (Mizuno et al., 2018). Soils formed on serpentines contain from 100 to 7,000 mg kg $^{-1}$Ni. Some endemic species have adapted and acted as Ni hyperaccumulators with the concentration of even 1,000 mg Ni kg^{-1} DW in plant tissue (Milić et al., 2021). The major Ni ores are garnierite and pentlandite. Besides the parent substrate, Ni reaches the soil during the combustion of coal and oil fuels, by the application of mineral fertilizers, especially phosphorus, as well as by waste slit, mines and metal smelters activities (Bogdanović et al., 1997; Kabata-Pendias, 2000). Nickel reaches agricultural soils from the atmosphere too (in Denmark 7 g ha^{-1} per year), and from mineral and organic fertilizers, 4 to 7 g ha^{-1} (Hovmand, 1984). The loss of Ni by removal from the soil by plant yields and leaching is significantly less than the intake, resulting in its accumulation in the soil.

Based on a review of 1,300 published papers worldwide, the average concentration of Ni in the soil is 93 mg kg^{-1} soil (Bogdanović et al, 1997). Ni concentration in the soil depends on the soil type to a large extent. In Vojvodina, in 1,600 tested samples of different soil types, the Ni concentration was between 1.8 and 62.7 mg kg^{-1} soil (Ubavić et al, 1993). The median value of total Ni concentration in the soil under main field crops in Central Serbia was 44.8 mg kg^{-1} (Banjac et al., 2021). Ni is mainly present in the soil in the form of Ni^{2+} ions under anaerobic conditions, which is the most available form to plants (Cempel and Nikel, 2006). In soil solution, Ni is predominantly found in a hydrated form (Yusuf et al., 2011). Nickel is relatively stable in an aqueous solution. In soil solution, Ni may exist as a complex with inorganic and organic ligands, and/or associated with suspended mineral colloids, where the organic complexes may be dominant in soil solution. The solubility, and thus the mobility and availability of Ni for plants, increases with decreasing pH and decreasing ion exchange capacity of the soil. Total Ni content in the soil positively correlates with the content of clay and organic matter, and negatively correlates with fine sand content. The uptake of Ni by plants depends on a number of soil properties, primarily on its form and concentration in the soil, the presence of other metals, the composition of organic matter, and plant metabolism (Chen et al., 2009). Clay soils with high cation exchange capacity are characterized by the lowest transfer coefficient of Ni to plants, due to stronger Ni adsorption in the soil (Rasti

et al., 2020). A higher pH value of the soil solution reduces the uptake of Ni because of the formation of poorly soluble Ni complexes.

Plants can uptake Ni through roots and aboveground organs. Terrestrial plants predominantly uptake Ni through the roots via passive diffusion and active transport. The intensity of Ni uptake largely depends on its concentrations in the nutrient medium. Nickel is translocated to all the tissues of the root via both the apoplast and symplast. Soluble Ni compounds can be taken up through the cation transport systems for Cu^{2+}, Zn^{2+} and Mg^{2+}, due to the similarity of the charge/size ratio, especially Ni and Mg ions. Secondary, active transport of chelated Ni^{2+} is possible (Chen et al., 2009). According to the results achieved through studying the effect of temperature, light intensity, inhibitors of respiration and anaerobic conditions, it can by concluded that, at least partially, the uptake of Ni depends on metabolic processes (Aachmann and Zasoki, 1987; Petrović and Kastori, 1994) (Table 1). In addition to Ni uptake, plant root can also release it into the environment, approximately 5% of the total amount absorbed (Petrović and Kastori, 1979a). Ni can affect the uptake of ions of the other elements, by stimulation or inhibition (Petrović et al., 2003; Rahman et al., 2005; Hasinur et al., 2005; de Queiroz Barcelos et al., 2017). In this regard, however, the results of studies are quite contradictory (Sergin and Kozhavnikova, 2006).

Table 1.
Effect of some respiratory inhibitors on Ni uptake by root segments of young wheat plants (µg Ni/100 g DM/24 hr) (Petrović and Kastori, 1994)

Inhibitor	Control	Treatment		LSD	
		10^{-5}M	10^{-4}M	5%	1%
2.4 DNP	23.0	22.0	19.0	1.8	2.6
KCN	25.8	23.1	18.2	2.0	2.8
Na$_2$HAsO$_4$	29.5	28.0	13.2	2.6	3.7
NaN$_3$	22.3	16.3	13.3	2.3	3.2

Absorbed Ni is largely accumulated in the root (Baccouch et al., 2001), immobilized in vacuoles of root cells and bound to the walls of xylem parenchyma cells (Sergin and Kozhevnikova, 2006). The most part, over 80%, is found in the vascular cylinder, and less than 20% is present in the cortex. Regarding leaves and stem, Ni is predominantly found in the vacuole, cell wall and epidermal trichomes associated with citrate, malonate and malate. According to Timpereley et al. (1973), more than 87% of Ni in leaves is found in cytoplasm and vacuoles, 8-9.9% in chloroplasts, and 0.32-2.85% in mitochondria and ribosomes.

Transport of Ni over longer distances takes place in the xylem and phloem. Nickel shows great mobility there (Page and Feller, 2005). The ascending Ni transport occurs in the xylem under the influence of the transpiration stream. The translocation of Ni in xylem occurs in various forms, most often in the form of citrate and malate complexes. Nickel can be translocated from the xylem to the phloem, as well as redistributed (Zeller and Feller, 1998). Based on the results of experiments with separated roots, both ascendant and descendent transportation of Ni takes place in young wheat plants, as indicated by a relatively high ratio of Ni in the portion of the root placed in the nutritive solution without Ni (Petrović and Kastori, 1979b). When ^{63}Ni was applied in nutrient solution

during the flowering phase of wheat, the root contained 64.4%, stem 1.5%, rachis 2.3%, chaff 4.3%, and grain 22.8% out of the total amount of accumulated Ni (Petrović and Kastori, 1994) (Table2). When applying increasing doses of Ni in triticale by an introduction to the soil, out of the total accumulated amount of Ni 70% was in the grain and only 30% in the vegetative parts of the shoot. The translocation index, describing the translocation of Ni from the vegetative plant parts to the grain, was the highest in Ni, among the ten examined microelements (Kastori et al., 2004). Studies of Banjac et al. (2021) indicated a different accumulation of Ni in the seeds of cultivated species. The median concentration of Ni in wheat and maize seeds was 5.0 mg kg^{-1}, while soybean and sunflower seeds had much higher Ni content, 8.40 and 10.26 mg kg^{-1} median value, respectively. Consequently, the seed bioaccumulation factor ranged from 0.013 in maize to 0.256 in soybeans.

Table 2.

Distribution (%) and translocation of ^{63}Ni after its application to roots and leaves at the stage of flowering and measured at fool maturity (Petrović and Kastori, 1994)

Plant part	Distribution %		Plant part	Distribution %	
	After uptake by roots	After uptake by leaves		After uptake by roots	After uptake by leaves
Root	64.43	18.63	5th & 6th leaf*	0.003	13.00
Stem	1.48	0.73	5th & 6th sheat	1.39	1.43
1st & 2nd leaf	0.01	0.29	Spike	2.29	13.70
1st & 2nd sheath	1.04	0.68	Chaff	4.31	17.30
3rd & 4th leaf	0.001	2.56	Grain	22.79	31.13
3rd & 4th sheath	1.29	0.49	Whole plant	100.00	100.00

*treated leaves

In addition to uptake by the roots, Ni can enter the plants through leaves (Andreeva et al., 2001). When ^{63}Ni was applied at the 6th leaf during the wheat flowering phase, out of the total amount of accumulated Ni app. 62% was translocated ascendingly in ear (31% in grain, 17% in chaff, and 14% in spike), 0,7% in the stem, 19% in leaf and sheet and 19% in the root (Petrović and Kastori, 1994). When ^{63}Ni was applied on sunflower leaves, 37% of the total amount was translocated to other plant organs (Sajwan et al., 1996). During the Ni uptake by the roots and aboveground organs, a significant proportion of Ni is translocated in the edible part of the grain, which can be a problem if the plants are exposed to Ni pollution.

Certain plant species and genotypes accumulate with different intensities (Petrović et al., 2003; Kastori et al., 2010; Sheoran et al., 2016; Rasti et al., 2020). There are about 300 plant species of hyperaccumulators that are characterized by a large accumulation of Ni. Such species mostly belong to the serpentine flora. Maximum Ni concentration (mg kg^{-1} dry matter) in hyperaccumulators Allysum (48 species) ranges from 1,280 to 29,400, Phyllanthus (41 species) from 1,090 to 60,170, Thlaspi (23 species) from 2,000 to 31,000, and Hybanthus (5 species) from 3,000 to 17,600 (Seregin and Kozhevnikova, 2006).

3. Results and Effect of Nickel on physiological Processes Various Enzyme Activities

Most plant physiological processes depend on enzyme activity. Essential macro- and microelements can directly (metalloenzymes) and/or indirectly participate in or influence the enzymatic activity of plants. In their review article, Li and Zamble (2009) studied in great detail the enzymes that require Ni for their catalytic function, listing the enzymes: (NiFe)-hydrogenases, superoxide dismutase, carbon monoxide dehydrogenases, methyl-CoM reductase, glyoxilase I, acireductone dehydrogenases and ureases. According to Drzewiecka et al. (2012), Ni is an important metal in plant metabolism and a co-factor of numerous metalloenzymes. Urease is considered to be the most important Ni-metalloenzyme in higher plants (Polacco et al., 2013). Urease occupies a significant place in the history of biochemistry, as it was the first enzyme ever to be crystallized (1926).

Among enzymes containing Ni, urease, its catalytic and non-catalytic properties (Kappaun et al., 2018), as well as its structure and catalytic mechanism (Mazzei et al. 2020), have been studied in great detail. The role of Ni in urease function (urea amidohydrolase, ED 3.5.1.5) was determined by Dixon et al. (1975). This gave a great impetus to the study of the Ni role in the life processes of plants, which ultimately resulted in Ni being one of the essential microelements for higher plants (Brown et al., 1987a; Poonkothai and Vijayavathi, 2012). This was to be expected since Ni has been located around the argon-carbon-argon line in the periodic table of elements, on the nutrient line or the life line, in the vicinity of the biogenic elements iron and cobalt. According to the understanding in the field of bioinorganic chemistry, the place of an element in the periodic table may indicate its biogenicity to some extent.

The presence of urease has been found in numerous organisms, including higher plants, algae, fungi, prokaryotes, as well as invertebrates (crabs, mussels), while its presence has not been detected in vertebrates. Urease is a significant protein, especially in the seeds of Cucurbitaceae, Fabaceae, Asteraceae and Pinaceae families (Bailey and Boulter, 1971). It is also present in the leaf tissues of all plants to a lesser extent (Hogan et al., 1983), which allows the volatilization of ammonia from the surface of plants. Ammonia released by plants is thought to be connected with reactions producing NH$_3$. Different values for ammonia volatilization by plants are reported in the literature, as it depends on a number of factors: supply of plants with nitrogen, ecological conditions, plant species, stages of plant development, etc. (Kastori, 2004).

Ureases are ubiquitous metalloenzymes that catalyze the transformation of urea. Enzymatic hydrolysis of urea proceeds in two phases. First, urea is hydrolyzed to ammonium carbonate: $(NH_2)_2CO + 2H_2O \rightarrow (NH_4)_2CO_3$, which is then decomposed into ammonia, carbon dioxide and water: $(NH_4)_2CO_3 + H_2O \rightarrow 2NH_3 + CO_2 + 2H_2O$. The decomposition of urea to ammonium carbonate occurs under the effect of the enzyme urease, while further transformation proceeds without the participation of the enzyme. The formation of urea in the animal and plant world is identical. Urea is formed from arginine by the enzyme arginase, which also produces ornithine. The seeds of many plants contain arginine as a reserve source of nitrogen. Arginine is also a significant source of nitrogen during leaf aging. Urease isolated from jack bean was studied in great detail. It was found that it consists of six subunits and each of them contains two Ni atoms (Marschner, 2012).

Nickel plays an important role in the nitrogen metabolism of plants (Gerendas and Sattelmacher, 1999; Follmer, 2008; Gajewska and Sklodowska, 2009), especially in plants where ureids, e.g. allantoin, are represented to a greater extent. In addition, Ni has a role in providing plants with urea (Bai et al., 2006). This could explain the particularly beneficial effect of Ni in legumes, where ureides accumulation occurs. The majority of higher plants contain urease, even when the nitrogen source is NH_4^+, NO_3^- or N_2. This indicates the necessity of urease in the metabolism of ureides (uric acid, allantoin, allantoic acid, and urea) and guanidine (arginine, cannavalin and agmatine) (Bai et al., 2006, 2008). Ureides and guanidines are used by higher plants as a transport form of nitrogen or they represent compounds for nitrogen accumulation. The utilization of nitrogen from the mentioned compounds for anabolic purposes takes place through urea, which is why there is a need for urease. For example, soybean uses ureides to transport nitrogen as well. In conditions of Ni deficiency, urease activity decreases and urea concentration increases, as a result of which its concentration in top of leaves can reach 2.5% in dry matter, causing tissue necrosis. Ni deficiency not only reduces the activity of urease, but also of the other enzymes involved in nitrogen metabolism, like nitrate-reductase. Therefore, it adversely affects protein synthesis and total nitrogen content (Brown et al., 1990). Contrary to the above, Gajewska and Sklodowska (2007) documented a slight increase in protein content in wheat leaves when applying Ni, while Gopal and Nautiyal (2012) and Maksimović et al. (2012) recorded a significant accumulation of proline. According to Oliveara et al. (2013), the activity of urease in lettuce leaves increased with the application of Ni, regardless of whether the applied form of nitrogen was urea or ammonium-nitrate. A positive correlation was found in pecan between Ni levels in the leaves and urease activity (Ojeda-Barrios et al., 2016).

In addition to its role in nitrogen metabolism in plants, urease also has a non-catalytic biological effect, regardless of the ureolytic activity (Follmer et al., 2001). Urease plays a role in cell-to-cell communication. Plant urease has insecticidal and fungicidal effects, and a role in soybean nodulation. Jack bean urease indicates interaction with cell membrane lipids, which may be the basis for non-enzymatic, biological properties of urease (Kappaun et al., 2018).

Urease also plays a significant role in the transformation of urea in the soil (Kumar and Wagenet, 2018) in solid, liquid and mineral fertilizers (urea, calcium-cyanamide), as well as in the loss of nitrogen from the soil in the form of ammonia. Urease is synthesized in the soil by a large number of bacterial species (*Micrococcus ureae*, *Sarcina urea*, *Urobacillus pasteuri*, *Urobacterium miqueli*), as well as by a number of fungi and actinomycetes. Urease enters the soil mostly as extracellular urease bound to humic substances and clay.

Increased concentrations of heavy metals, among which Ni is classified, tend to cause phytotoxicity. One of the primary effects of phytotoxic amounts of heavy metals in higher plants is the inhibition of enzyme activity. Two mechanisms of enzyme inhibition predominate: a) binging of the metal to functional groups of the enzyme, such as sulfhydryl group, involved in the catalytic action or structural integrity of enzymes, and b) deficiency of an essential metal in metalloproteins or metal-protein complexes, eventually combined with substitution of the toxic metal for deficient element (Van Assche and Clijsters, 1990). At molecular and cellular levels, Ni ions bind strongly to sulphur, oxygen and nitrogen atoms and show a high affinity for sulfhydryl and disulphide groups. This leads to damage of the secondary protein structure, manifests itself in the activity of enzymes, and thus in metabolic processes (Siedlecka and Krupa, 2002).

Oxygen is found in the atmosphere in an inactive form (O_2), which can be activated physically or chemically to form reactive oxygen species. Oxygen activation occurs not only in the external environment, but also in plants, causing oxidative stress. Abiotic and biotic stress, including high concentrations of heavy metals, cause oxidative stress in plants, and accumulation of reactive oxygen species (Gratao et al, 2005; Popović and Štajner 2008; Sachan and Lal, 2017). Increasing the Ni concentration reduces the activity of antioxidant enzymes capable of reducing the presence of reactive oxygen species, which results in their accumulation, thereby causing oxidative stress in plants (Bhalerao et al., 2015; Georgiadou et al., 2018). Oxidative stress is a balance disturbance between prooxidative processes and the antioxidant system of the organism. High concentrations of Ni ions promote the formation of reduced oxygen forms, hydrogen peroxide, superoxide radical, hydroxyl radical and nitric oxide.

All aerobic organisms are exposed to oxidative stress. Reactive oxygen species are continuously developed in cells exposed to aerobic conditions. Peroxisomes also play an important role in detoxification. Peroxide compounds are formed in numerous metabolic processes of plants, which in larger quantities can be very harmful for cells. The antioxidant enzyme catalase found in plants, predominantly located in peroxisomes, decomposes peroxide into water and oxygen, and thus releases the cell from hydrogen peroxide, which is a strong oxidant.

The electron configuration of the oxygen molecules in the ground state enables the gradual reduction of oxygen atoms. Ions of transition metals, such as Mn^{2+}, Cu^{2+}, Cr^{3+} and Fe^{2+} with the exception of Ni^{2+} may participate in this process. However, numerous publications indicate that it can affect their presence indirectly through the activity of the antioxidant enzymes catalase, peroxidase, superoxide dismutase,

glutathione peroxidase, ascorbate peroxidase and guaiacol peroxidase. Based on numerous studies, it is considered that both redox active and non-redox-active metals can induce the accumulation of reactive oxygen species, and so does Ni. The antioxidative defense enzymes, guaiacol peroxidase, ascorbate peroxidase, and glutathione reductase, showed increased activity in Ni-treated drought sensitive durum wheat seedlings (Pandolfini et al., 1996). As stated by Ilin et al. (2000), the lower Ni concentrations increased the activity of superoxide dismutase, while the higher concentrations decreased its activity in both wheat and maize leaves. Consequently, the quantity of oxygen radicals was significantly lower at lower Ni concentrations. In order to survive in the presence of higher concentrations of heavy metals, plants developed antioxidant defence systems to counteract oxidative damage from reactive oxygen species. Exposing plants to low concentrations of Ni or for a shorter period of time may increase the activity of antioxidant enzymes (Gomes-Junior et al., 2006; Kumar et al., 2012; Gopal and Nautiyal, 2012), which leads to a decrease of oxygen radicals. Yan et al. (2008) found an increase in the activity of the antioxidant enzymes, superoxide dismutase, peroxidase, catalase and phenylalanine ammonia-lyase at lower concentrations of Ni. These authors believe that this has a primary role in regulating the levels of reactive oxygen species in the presence of higher concentrations of Ni. However, activated antioxidant enzymes were not sufficient enough to combat Ni toxicity-induced oxidative stress.

In addition to antioxidant enzymes, plants contain non-enzymatic antioxidant compounds (tripeptide glutathione, phenolic acids, flavonoids, carotenoids, terpenes, L-ascorbic acid, etc.) that also protect them from the harmful effects of oxygen radicals. Silicon has been found to play a positive role in protecting against the negative effects caused by abiotic stressors, heavy metals including Ni (Khalig et al., 2015). Silicon application to Ni-stressed mustard plants increased the activity of antioxidant enzymes and enzymes associated with the ascorbate glutathione cycle and glyoxalase systems, as well as flavonoid and total phenol content (Abd-allah, 2019). Flavonoids and phenols help plants to withstand the adverse effects of metal stress. Oxidative stress caused by the presence of a higher Ni concentration can be modified by the interference between Ni and Fe (Nishida and Mizuno, 2011, Lešková et al., 2020).

4. Photosynthesis and Respiration

Higher Ni concentrations can inhibit photosynthesis directly or indirectly in a number of ways: by disorganizing the chloroplast ultrastructure through limiting biosynthesis or intensifying the degradation of chloroplast pigments; by inhibiting photosynthetic electron transport chain and Calvin cycle enzymes; by an insufficient supply of carbon dioxide due to reduced stomatal conductance; by induction of oxidative stress; by peroxidation of membrane lipids, etc. (Bhalerao et al., 2015; Parlak, 2016; Sachan and Lal, 2017).

Regarding the cellular organelles, chloroplasts are exposed to oxidative stress to the greatest extent. Depending on the applied concentration, nickel can reduce the number and size of chloroplasts, lead to disorganization of the organelle ultrastructure by reducing the number of thylakoids, changing the composition of membrane lipids and their peroxidation, by induction of oxidative stress (Molas, 1997; Parlak, 2016). Numerous studies have found a decrease in the concentration of chloroplast pigments, chlorophylls and carotenoids, in the presence of higher Ni concentrations (Milošević et al., 2002; Petrović et al., 2003; Drazkiewicz and Baszynski, 2010; Parlak, 2016), whereby an increase in the carotenoids/chlorophyll ratio occurs (Gopal and Nautiyal, 2012). Heavy metals are believed to reduce chlorophyll content by its enzymatic degradation, as higher chlorophyllase activity has been demonstrated in plants treated with heavy metals and inhibition of chlorophyll biosynthesis at the protochlorophyllide level, acting on protochlorophyllide reductase (Kastori et al., 1997). The decrease in the intensity of Ni-stress-induced photosynthesis is the result of a decrease in chlorophyll content and reduced light absorption by chloroplasts (Khan et al., 2016). The possibility of replacing magnesium in the chlorophyll molecule with heavy metals, including Ni, has been documented. Studies showed that the replacement of magnesium in the chlorophyll molecule by heavy metals, including Ni, occurred *in vivo*, which prevented the altered chlorophyll molecules from absorbing light energy. Moreover, it has prevented electron transfer in the photosynthetic chain, which led to disruption of photosynthesis (Küpper et al., 1996). Chlorosis caused by higher Ni concentrations can be the consequence of the antagonism between Ni and iron, and thus its deficiency, as well as the lack of magnesium, and inhibition of chlorophyll biosynthesis (Seregin and Kozhevnikov, 2006; Lešková et al., 2017). Ni ions in chloroplast thylakoids reduce the content of ferredoxin, plastocyanin, cytochromes b6f and b559 which adversely affects the efficiency of the electron transport chain (Siedlecka and Krupa, 2002). In photoautotroph cyanobacteria Cylindrospermum, application of Ni resulted in growth inhibition, oxygen release and uptake, chlorophyll fluorescence and Hill activity (Singh et al., 1989). The reaction centre PSII is located on the inner (oxidation) side of the thylakoid membrane, and is connected to the enzyme complex where the photolysis of water occurs, i.e. water-splitting. Treatment with Ni affects water-splitting (Boisvert et al., 2007). The enzyme complex where water photolysis takes place contains manganese, calcium and chlorine. It is believed that heavy metals can replace manganese in the complex, which plays a significant role in water-splitting (Mallick and Mohn, 2003). According to Ghasemi et al. (2012), higher Ni concentrations adversely affect the photosynthetic protein complexes and the Hill reaction. The effect of Ni on photosynthesis includes its effect on stomatal and mesophyll conductance for CO_2, as well as the carboxylation capacity. Velikova et al. (2011) found a significant decrease in photosynthesis in black poplar, depending on the applied Ni concentration, caused by a decrease in stomatal and mesophyll conductance and metabolism impairment. Long-term Ni exposure (25 or 50 µM) decreases leaf pigment (SPAD index), the efficiency of PSII, and induces lipid peroxidation and membrane damage (Kumar, et al., 2015). Freitas et al. (2018) stated the beneficial effect of 0.5 mg Ni/kg soil on photosynthesis in soybean genotypes. Nickel can reduce the symptoms of Asian soybean rust caused by a pathogen *Phakopsora pachyrhizi* by increasing

concentrations of carotenoid, chlorophyll and ethylene, and photosynthetic capacity during the infectious process (Einhardt et al., 2020).

Nickel can affect not only the circulation of matter, but also the energy. Lower concentrations of Ni stimulate, while higher reduce the intensity of respiration. Miller et al. (1970) discovered that a Ni concentration of 0.08 mM maximally increased the intensity of respiration in the mitochondria of maize. Lower Ni concentrations, from 10^{-7} to 10^{-6} M in the conditions of water cultures, significantly increased the intensity of respiration at the roots and in the aboveground part of the pea, while the higher concentrations inhibited it (Petrović et al., 2003). Higher plants can use various organic acids as a substrate for respiration, not only from the citric acid cycle, but also the others. Since Ni affects the metabolism of organic acids, it can also affect respiration indirectly. According to Bai et al. (2006), nickel deficiency disrupted carbon metabolism and the citric acid cycle, the second stage of respiration.

5. Nitrogen and Organic Acid Metabolism

Besides being the constituent of the urease molecule, nickel also affects the nitrogen metabolism of plants. A large number of proteins contain Ni (Thomson, 1982). Numerous studies have shown an increase in the proline content in the presence of a higher concentration of heavy metals, as well as Ni (Parlak, 2016; Abd-Allah et al., 2019). The accumulation of free amino acids, especially proline, can contribute to the stabilization of molecules of proteins and membranes, as well as osmoregulation. It can also represent a reserve of carbon and nitrogen in plant metabolism (Hare and Cress, 1997). With increasing concentration of Ni in the nutrient solution where mustard was grown, Gopal and Nautiyal (2012) found an increase in proline and glycine betaine concentrations, and a decrease in soluble proteins. Latif (2010) discovered a significant decrease in radish total protein with an increasing concentration of nickel-sulphate. The decrease in protein content is thought to be the result of increased protease activity under stressful conditions. Treatment of wheat seedlings with 100 μM Ni led to the decrease of NR and NiR activities (Gajewska et al., 2009a). Nickel can also affect the uptake of nitrate ions indirectly, by acting on H^+-ATPase proton pump and on H^+/NO_3^- symporter, since it changes hydrolytic and transporting activities of the plasma membrane bound H^+-ATPase (Janicka-Russak et al., 2008). Stress caused by Ni also reduces the activity of GS and NADH-GOGAT (Yusuf et al., 2011). Both excess and lack of Ni have an effect on nitrogen metabolism. Lack of Ni in young pecan leaves disrupts the metabolism of ureides, amino acids and organic acids, leads to the accumulation of xanthine, allantoic acid, ureidoglycolate, and citrulline, and decreases the concentration of total ureides, urea, and urease activity (Bai et al., 2006). The level of Ni in the leaves also affected the distribution of some free amino acids. Ni deficiency increased the accumulation of glycine, valine, isoleucine, tyrosine, tryptophan, arginine and total content of free amino acids, and decreased the concentration of histidine and glutamic acid. The efficiency of atmospheric nitrogen fixation largely depends on hydrogenase activity. In some legumes, Ni is necessary for root nodule growth, hydrogenase

activation and nitrogen metabolism (Dalton et al., 1985; Cammack, 1995; Freitas et al., 2018).

Organic acids play multiple roles in plant life processes. In ryegrass and maize, Yang et al. (1997) found an increase in the concentration of certain organic acids in shoots and roots in the presence of Ni. Moreover, they discovered the link between the organic acid and Ni accumulation, as well as translocation. According to studies by Bai et al. (2006), in pecan sufficiently supplied with Ni, foliage contained dominant organic acids, including lactic, oxalic, citric, and diglycolic acid, while tartaric, formic, malic and acetic acid pools were very low. Ni-deficient foliage had increased lactic and oxalic acid, but reduced maleic acid. The total concentration of organic acids was about 2 times higher in Ni-deficient than in Ni-sufficient foliage. Nickel is predominantly bound to citrates, hence correlation with Ni accumulation (Hossain et al., 2012).

6. Water Relations

The anatomic and morphologic changes caused by heavy metals stress affect the water relations in plants. Nickel caused a decrease in the water potential, relative water content, osmotic and turgor potential in two durum wheat cultivars with different sensitivity to water stress (Pandolfini et al., 1996). High concentrations of heavy metals, including Ni, increased stomatal diffusive resistance, but reduced transpiration intensity, and total and relative water content (Kastori et al., 2000). In rice, the concentration of 0.5 mM Ni in the nutrient medium significantly reduced the water content (Lamas et al., 2008), while the treatment with 0.2 mM Ni decreased the relative water content in wheat shoots after three days (Gajewska et al., 2006). The reductions in total and relative water content at reduced transpiration indicate that excess heavy metal concentrations greatly curtail plants' water uptake. A three-day treatment with 0.2 mM Ni reduced the relative water content in wheat shoots (Gajewska et al., 2006). The presence of Ni in plants increases the level of abscisic acid (ABA), which induces stomatal closure (Bishnoi et al., 1993). Excessive concentrations of heavy metals cause xeromorphic changes in plants, a decrease in leaf area and the size of epidermal cells, while stomatal density increases (Breckle, 1991; Kastori et al., 2000). In poplar leaves, stomatal and mesophyll conductance largely decreased by Ni stress (Velikova et al., 2011). In mustard plants, leaf relative water content and transpiration rate decreased with increasing concentrations of Ni, and electrolyte leakage increased with Ni stress in comparison to the control (Abd-Allah et al., 2019). The toxic effect of Ni decreased the area of leaf blades, the major transpiring surface (Chen et al., 2009).

7. Seed Germination

Seed germination and seedlings growth are very important stages in plant life, as those stages greatly affect their further successful growth, development and organic production. Niethammer (1930) was among the first to notice the influence of Ni on seed germination. He found that a lower concentration of Ni salt (0.1% solution) has a stimulating effect, while higher (0.5 to 1.0%) has an inhibitory effect. Higher concentrations of $NiSO_4$ acted less inhibitory than

NiNO$_3$. Later Mishra and Kar (1974) and Das et al. (1978) also discovered the beneficial effect of low Ni salt concentration on seed germination of different plant species. According to Borwn et al. (1987a), barley plants grown for three generations without Ni in a nutrient medium produced grain with a very low percentage of germination. However, the grain of plants grown in the presence of 1.0 μM Ni had a germination rate of 94%. These authors believe that the lack of Ni reduces the ability of plants to form viable grain, or that Ni is necessary in embryo metabolism during germination. It is believed that the vitality of Ni-deficient seed cannot be repaired by treating it with Ni, as it is necessary for seed formation and development (Brown et al., 1987a). It is assumed that the effect of Ni on seed germination is also based on the mobilization of reserve seed nitrogen compounds during the germination by the enzyme urease, as it is its essential ingredient. The use of urease PPD (phenyl phosphorodiamidate) inhibitors leads to loss of seed viability. Necrosis caused by the urea accumulation occurs on the leaves of plants that have been developed from seeds produced from Ni-deficient plants (Brown et al., 1987b). In soybeans grown from seeds enriched and externally provided with Ni, growth was improved and there was no urea damage to the leaves (Kutman et al., 2012). Dorogházi et al. (2010) studied the effect of maize seed imbibition in solutions with different Ni concentrations (0 to 10^{-2} mol Ni/L) and found that Ni is intensively transferred to the root and shoot of young plants during seed germination. The applied Ni concentrations did not show an effect on the examined germination parameters, except for the highest concentration, which significantly increased the share of atypical seedlings and non-germinating seeds and reduced germination energy and seed viability. Shweti et al. (2018) found a positive effect of the application of low NiCl$_2$ concentrations (5 mg L^{-1}) on seed germination and production of fresh and dry matter seedlings in nine wheat cultivars. However, higher concentrations had adverse effects, reducing studied parameters, but not to the same extent in all tested cultivars. Other researchers also cited the adverse effect of higher Ni concentrations on seed germination and seedling growth (Rao and Sresty, 2000; Farooqi et al, 2009; Yusuf et al., 2011; Pavlova et al., 2018). Higher Ni concentrations directly affect the activity of amylases, proteases and ribonucleases, and thus affect the decomposition and mobilization of nutrients, reserve substances of seeds during germination (Ahmad et al., 2011). In addition to reducing the activity of hydrolytic enzymes, the unfavourable effect of high Ni concentrations on seed germination is also explained by a decrease in the elasticity of cell walls and disturbed cell proliferation. Based on the previous knowledge, it can be concluded that the influence of Ni on seed germination and seedling growth primarily depends on the applied concentration and type of Ni salt, as well as on the method of its application, plant species and genotype.

8. Effect of Nickel on Growth and Development

Nickel affects physiological processes, cell biomolecules, the function and composition of cell membranes, the structure of the cell wall and cell organelles, cell division and the development of tissues and organs, and thus the growth, development and accumulation of plant organic matter.

Based on numerous authors' study results, it can be concluded that Ni affects macro biomolecules of cells, i.e. nucleic acids (Kastori et al., 1978). Lower Ni concentrations increase their content, especially DNA, stabilize DNA structure and affect the structural stability of ribosomes. On the other hand, higher concentrations increase ribonuclease activity and affect membrane functionality (Lamas et al., 2008). Phosphorus incorporation into certain groups of nucleic acids plays a significant role in plant metabolism. The low concentration of Ni (1 μg L^{-1}) in the leaves of young maize plants has significantly increased the incorporation of ^{32}P in certain groups of nucleic acids, while a high concentration (104 μg L^{-1}) decreased it noticeably (Kastori et al., 1978). There was increased cytosine methylation in 18S rDNA by NiCl$_2$. Li et al. (2015) assumed that plant nucleus variation and 18S rDNA methylation can serve as an indicator of soil and plant pollution with Ni.

Nickel affects the properties of biomembranes and the structure of the cell wall. Oxidative stress caused by higher concentrations of Ni leads to lipid peroxidation of cell membranes, thus affecting their composition and function (Molas, 1997; Gopal and Nautiyal, 2012; Parlak, 2016). Nickel may play a cofactor role in the metabolic processes of precursors in the synthesis of lignin, a component of the cell wall (Wood and Reilly, 2006). As a result, Ni-deficient supply can significantly reduce its formation. Nickel can contribute to host resistance to infections by increasing enzyme activity and lignification of leaf tissues (Einhardt et al. 2020). Lešková et al. (2020) stated that genes involved in cell wall modification significantly inhibit high Ni concentrations. Nickel binds efficiently in the cell wall of the root cell to carboxyl groups, hydroxycinnamic and polygalacturonic acids (Meychik et al., 2014). As a result, the cell wall represents a significant compartment for Ni binding, thus contributing to the tolerance of plants to high concentrations of Ni.

Higher Ni concentrations disturb the integrity and orientation of microtubules, and induce root gravitropic defects in Arabidopsis (Lešková, et al., 2020). Among other things, microtubules enable the movement of chromosomes and provide the structural orientation of organelles. Chromosome stickiness, anaphase bridges, laggards and extrusion of nuclear material into cytoplasm were observed in tip cells of the root in *Plantago lanceolata* treated with Ni (Pavlov, 2017). Higher concentrations of Ni reduced the size of chloroplasts and led to a change in their structure (Molas, 1997). Nickel induced changes in the structure of the nucleus and nucleolus in root cells (Robertson and Meakin, 1980). Application of NiCl$_2$ in root tip cells brought deformity and damage to the nucleolar structure and significantly increased the number of cells with abnormal nucleoli (Li et al., 2015).

Nickel can inhibit cell division and elongation. With increasing Ni concentration (0-0.1 mM) and treatment duration, the mitotic index of root-meristem cells, chromosome bridges and stickiness decreased significantly, and the number of abnormally divided cells increased (Pavlova, 2017). The unfavorable effect of higher Ni concentration on mitotic activity is a consequence of the nucleolar structure damage, aberrations in chromosome integrity and abnormalities during mitosis. Demchenko et al. (2005) described the

effect of Ni on the growth, proliferation, and differentiation of root cells in wheat seedlings. High Ni concentrations in endoderm and pericycle cells block cell division in the pericycle, resulting in the inhibition of root branching (Seregin and Kozhevnikova, 2005). According to Kozhevinkova et al. (2009), Ni in maize roots inhibited cell division to a greater extent than their elongation. In the presence of calcium, the effect of Ni on root growth was smaller due to less accumulation of Ni in the apical part of the root. Accumulation of metals in the zone of elongation can lead to reduced cell elongation, especially if Ni-competing ions are not present. It is believed that heavy metals can also reduce cell elongation by altering the cell wall plasticity, induced by indole-3-acetic acid.

The effect of Ni on cell division and elongation reflects on the development of certain plant tissues. Excess Ni decreased the mesophyll thickness in the leaves of young wheat plants (Kovačević et al., 1998). The number of cortical cell layers increased in the roots of maize seedlings of Ni treated plants, although the other measured anatomical parameters were not significantly affected (Maksimović et al. 2007). Kozhevnikova et al. (2009) stated a significant reduction in the rate of cell production in the meristem of maize seedlings roots, and thus decreased the size of the meristem.

Plant growth is determined by cell division and elongation. Nickel has an effect on these two processes, thus affecting the growth of individual branches and the whole plant. Nickel had a significant adverse effect on total root length and primary seminal root length, while the number of nodal roots increased in treated maize seedlings (Maksimović et al., 2007). A reduction in the growth of maize seedling's root in the presence of Ni was also recorded by Kozhevnikova et al. (2009). Its unfavorable effect was alleviated by the presence of calcium. Therefore, in the absence of calcium, Ni accumulated to a greater extent in the apical part of the root where cell division is intense. However, in the presence of Ca, Ni accumulated in the basal part and hence interfered less with cell division. Lešková et al. (2017) also stated the adverse effect of Ni on root elongation, which is explained by the inhibitory effect of excessive Ni concentration on auxin distribution between shoots and roots, by rapidly inhibiting the auxin transporter PIN2, which is very sensitive to the presence of Ni (Lešková et al., 2020).

9. Essentiality of Nickel in Plants

So far, numerous authors have pointed out the necessity of Ni in the life processes of higher plants and thus their growth and development (Eskew et al., 1983; Brown et al., 1987a; Wood et al., 2006a; Yusuf et al., 2011). Nickel is necessary for the majority of higher plants in small concentrations. Depending on the plant species, the critical, required Ni concentration in the shoot ranges from 0.01 to 10 μg g^{-1} dry matter (Marschner, 2012), or, from 0.01 to 5 μg g^{-1} dry matter (Rizwan et al., 2017).

Wood et al. (2006) described in detail the symptoms of Ni-deficiency in certain organs of woody plants. The leaves are characterized by the following: chlorosis, reduced size and altered shape, transitory dark green zone at the leaf tip, tip necrosis, cupping and wrinkling of leaves, absence of laminar development and winged petiole. Shoot and root characteristics include: loss of apical dominance and rosetting, internodes and tree size is increasingly diminished, buds shape tends to become increasingly distorted and bud break tends to be delayed, the shoots and limbs are noticeably brittle, the root systems are reduced. In reproduction organs a small percentage of flowers will develop to ripening. In soybeans, the lack of Ni due to reduced urease activity leads to the accumulation of toxic urea concentrations in the leaves (Eskew et al., 1983). In tomatoes, the young leaves are chlorotic and the meristem necrotizes (Checkai et al., 1986). In conditions of Ni deficiency, barley does not form germinating grains due to the disturbed process of grain filling. Therefore, barley is not able to complete its life cycle in the absence of Ni, while its application eliminates the symptoms of deficiency (Brown et al., 1987a).

Ni-deficiency is more common on dry and cold soil in the early stages of plant development. It can be induced by the presence of higher concentrations of Zn, Fe, Mn, Mg, Ca and Cu, and root damage by nematodes (Wood, 2006). Plants such as pecan, which use the ureide transporting mechanism, have a special need for Ni for urea metabolism. Ni-deficiency in these plants affects the catabolism of urea, and thus the availability of nitrogen for growth and development processes (Bai et al., 2006). Urease activity in pecan leaves was positively correlated with Ni concentration (Ojeda-Barrios et al. (2016). In case of insufficient urease activity, urea accumulates in the leaves and necrosis occurs in the top part of the leaves.

In the past numerous authors have found a beneficial effect of Ni on the growth, development and organic production of plants, which confirms its necessity for higher plants. Roach and Barclay (1946) recorded an increase in potato yield during foliar fertilization with Ni. Yang et al. (1996) found that Ni concentrations up to 60 μM in maize and white clover stimulate, while in the case of cabbage and English ryegrass reduce the mass of dry matter. Dry matter mass of above-ground parts and roots in pea cultivars in water culture conditions significantly increased with lower Ni concentrations, 10^{-8} and 10^{-7} M (Petrović et al., 2003). Nickel fertilization under greenhouse and field conditions with 0.5 mg Ni kg^{-1} soil resulted in greater grain yield in soybean genotypes (Freitas et al., 2018). In a pot experiment, the shoot yield of wild marigold was significantly increased by the application of vermicompost and Ni up to 30 ppm, as compared to control. The plant height and the number of branches per plant were significantly increased by the application of 10 ppm Ni alone (Chand et al., 2015). It is considered that foliar application of Ni is more favorable than its introduction into the soil due to its more efficient use by plants. Foliar application of Ni affects the growth and yield components of barley. Plant height, leaf greenness index, number of tillers, ears, number of grains per ear, straw yield, grain yield and weight of 1000 grains was the maximum with three foliar applications of 0.2% of NiSO$_4$·7H$_2$O at 20, 40 and 60 days after sowing (Kumar et al., 2018). Based on the results of examining the effect of Ni on the growth, development and yield of plants, it can be concluded that it depends on numerous factors, primarily on the applied concentration and form of Ni, the method of its application, plant species and genotype, and levels of Ni in plants.

10. Toxicity of Nickel in Plants

Soil pollution with heavy metals (Cd, Pb, Zn, Cr, Ni) is a large problem in intensive plant production (Bošković-Rakočević et al., 2014). During the late 19th century, Hasselhoff (1893) noticed that Ni could be toxic to plants. Under natural conditions, toxic effects of Ni can occur on soils formed from serpentine (ultramorphic) minerals and other soils rich in Ni (Mizuno et al., 2018). In the ash of some plant species, which grow on soils formed on serpentine rocks, the Ni content can be up to 10%. Due to the widespread use of Ni in various areas, soil enrichment with Ni can also occur from anthropogenic sources, by pollution (Turan et al., 2017). According to a number of authors, the toxic content of Ni for most plant species ranges from 10 to 100 ppm in dry matter (Kabata-Pendias, 2000).

High concentrations of Ni can adversely affect the growth, development and production of dry matter of plants through various non-specific mechanisms (Maksimović et al., 2012) (Table 3). Those mechanisms include the production of free radicals and oxidative stress, inhibition of enzyme activity, and cation and anion uptake, changes in membrane permeability and water relations, decline in photosynthesis and respiration, morphological and anatomical changes, inhibition of seed germination and growth and development. These physiological and morphological changes caused by excessive concentrations of Ni are manifested by various symptoms of injury, including chlorosis, necrosis and wilting of leaves, stunted growth and dry matter production. Corn roots became brown after Ni treatment (Baccouch et al., 2001). The browning may indicate the oxidation of phenolic compounds to cytotoxic quinones. Some authors recorded a significant decrease in growth and dry matter production in the presence of higher Ni concentration, including Petrović et al. (2003) in different pea cultivars, Pandey and Pathak (2006) in mung bean, and Pandey and Gopla (2010) in eggplant. However, Pavlova et al. (2018) found a decrease in seed germination of Allyssum species. While increasing Ni concentrations in mustard, Gopal and Nautiyal (2012) found a greater decrease in dry matter yield in leaves and stem than in root, although Ni accumulation in root was higher. Gajewska et al. (2009) recorded a decrease in fresh wheat root mass in the presence of 100 μM Ni and a reduction of shoot length by 40% at a Ni concentration of 200 μM (Gajewska et al. 2006). In cabbage, 0.5 mM Ni caused the appearance of dark brown necrotic spots and wilting of the outer leaves, and necrosis of the inner leaves (Panday and Sharma, 2002). Chlorosis and along-vein necrosis occurred on newly formed leaves of water spinach in the presence of 0.085 to 0.255 mM Ni over four weeks (Sun and Wu, 1998). The presence of 0.1 mM Ni caused chlorosis and necrosis on the leaves of barley during two weeks of growth (Rahman et al., 2005). In sugar beet plants, chlorotic and necrotic spots caused by excess Ni (29.8 mg/kg dry matter) first appear along the perimeter of the oldest leaves. Over time, chlorosis turns into necrosis, and necrotic spots spread within the intercostal part of the leaf. At the same time, it is noticed that middle-aged leaves turn yellow and wither (Kastori et al., 1996). In general, it can be said that the symptoms of certain elements' excess are less typical than those caused by their lack.

Table 3.
Dry weight and total leaf area of different Brassicaceae grown in the presence of Ni (Maksimović et al., 2012)

Plant species	Treatment	Dry weight (mg plant^{-1})			Leaf area (cm^2)
		leaf	stem	root	
Brassica napus L.	Control	78.07	63.46	6.84	485.65
	Ni	52.48	41.38	7.06	205.83
Brassica alba L.	Control	103.76	103.13	19.60	511.27
	Ni	35.14	25.35	12.22	95.55
Brassica nigra L.	Control	92.60	51.16	15.21	605.09
	Ni	38.66	23.48	7.08	147.15
Brassica rapa L.	Control	116.08	45.45	9.55	594.85
	Ni	40.98	15.54	4.56	130.15

With toxic Ni concentrations, biochemical and physiological functions can cause symptoms of a deficiency of other essential metals, due to nickel antagonistic effect toward other essential metals (Fe, Mg, Cu, Zn and Mn) during their transport (Hasinur et al., 2005). Therefore, for example, excess Ni causes chlorosis on the leaves similar to iron deficiency (Leškova et al., 2017). Chlorosis is very pronounced if the ratio of Ni:Fe concentration in plants is 6:1 or higher, while it is insignificant at a ratio of 1:1. In some plant species, the Ni:Cu ratio can also affect the intensity of chlorosis. In tomato, higher Ni concentrations decreased the concentration of macroelements N, P, K, Ca and Mg in leaves, fruits and root, while the concentration of microelements was reduced in leaves and fruits. However, concentrations of Fe, Zn, Cu and Ni were increased in the root (Kumar et al., 2015). Increasing the pH value of the soil, for example by calcification, reduces the uptake of Ni by plants and thus alleviates its adverse effects. Also, in some plant species, Ca, Mg, Mo, and Co can mitigate the adverse effects of higher Ni concentrations on the growth and development of plants, due to their antagonistic effects toward Ni.

Some plant species show different tolerance to high concentrations of Ni. Based on LC50 more tolerant plants may include *Panicum miliaceum* and *Cucumis sativum*, while less tolerant include *Lolium perene*, *Panicum maximum*, *Zea mays*, *Lactuca sativa* and *Chloris gayana* (Seregin and Kozhevnikova, 2006). Poplars (Populus) are resistant to the presence of Ni and have the ability to accumulate significant amounts

of this pollutant in the plant (Đelić et al., 2018). Higher tolerance to high concentrations of Ni is characteristic for Ni hyperaccumulating plant species, which can be used for phytoremediation of Ni contaminated soils.

11. Conclusions

The main source of nickel in terrestrial plants is soil solution, where Ni is mostly found in a hydrated state. The solubility, and therefore the availability of Ni for plants, increases with decreasing pH and soil ion exchange capacity. Higher plants can absorb and redistribute Ni via cation and/or metal-ligand complex transport systems. Transport of Ni at greater distances takes place in the xylem and phloem. Nickel exhibits great mobility in the acropetal and basipetal directions, both when absorbed through the roots, and when introduced through aboveground organs. During the uptake of Ni, there is an interaction with the ions of other microelements (Fe, Zn, Mn, and Cu). Absorbed Ni largely accumulates in the vacuole and cell wall. Some plant species and genotypes accumulate Ni with different intensities. Ni hyperaccumulators are characterized by a great ability to accumulate Ni. They mostly belong to the serpentine flora. Lower Ni concentrations play a significant role or favorably affect numerous plant physiological processes, from seed germination to growth and development. Moreover, it has been found that plants cannot complete their life cycle normally without an adequate nickel supply. These findings led to the inclusion of Ni in the group of essential microelements for higher plants. Individual plant species have different needs for Ni. Circumstantial evidence indicates that ureide-transporting species possess a higher Ni requirement than amide-transporting species. Acute deficiency of Ni is recognizable by several morphological symptoms. Under natural conditions, Ni-deficiency is rare as in most cases the soil is sufficiently provided with plant-available Ni. Ni-deficiency can be successfully eliminated by the introduction of Ni into the nutrient substrate or by treating the aboveground organs with a dilute solution of Ni salt.

High Ni concentrations have a phytotoxic effect, and induce oxidative stress resulting in increased generation of reactive oxygen species (ROS) and activation of antioxidant enzymes. However, activated antioxidant enzymes are not sufficient enough to combat Ni-induced oxidative stress. Therefore, large quantities of ROS inhibit cell division and elongation, damage many cellular organelles, oxidise proteins and lipids, inhibit photosynthesis, alter water relations and degrade chlorophyll molecules, consequently minimizing biological yield of plants.

References

Abd-Allah, E.F., Hashem, A., Alam, P., Ahmad, P. (2019). Silicon alleviates nickel-induced oxidative stress by regulating antioxidant defense and glyoxalase systems in mustard plants. *Journal of Plant Growth Regulation,* 38, 1260-1273.

Albanese, S., Sadeghi, M., Lima, A., Cicchella, D., Dinelli, E., Valera, P., Falconi, M., Demetriades, A., De Vivo, B. (2015). GEMAS: Cobalt, Cr, Cu and Ni distribution in agricultural and grazing land soil of Europe. *Journal of Geochemical Exploration,* 154, 81-93.

Andreeva, I.V., Govorina, V.V., Vinogradova, S.B., Yagodin, B.A. (2001). Nickel i plants. *Agrokhimiya*, 3, 82-94.

Baccouch, S., Chaoui, A., El Ferjani, E. (2001). Nickel toxicity induces oxidative damage in Zea mays roots. *Journal of Plant Nutrition*, 24, 1085-1097.

Bai, C.C., Reilly, C.C., Wood, B.W. (2006). Nickel deficiency disrupts metabolism of ureides, amino acids, and organic acids of young pecan foliage. *Journal of Plant Physiology*, 140, 433-443.

Bai, C.C., Reilly, C.C., Wood, B.W. (2008). Insights into the nutritional physiology of nickel. *Acta Horticulturae,* 772, 365-368.

Bailey, C.J., Boulter, D. (1971). Urease a typical seed protein of the Leguminosae. In: Harborne, J.B. et al. (eds.) *The Chemotaxonomy of the Leguminosae.* Academic Press, New York, pp. 485-502.

Banjac, D.D., Ninkov, J.M., Milić, S.B., Jakšić, S.P., Živanov, M.S., Radović, B.I., Malićanin, M.V. (2021). Nickel content in field crop seeds and agricultural land of Central Serbia. *Matica Srpska Journal for Natural Sciences*, 141, 81-93.

Bhalerao, S.A., Sharma, A.S., Poojari, A.C. (2015). Toxicity of nickel in plants. *International Journal of Pure and Applied Bioscience,* 3, 345-355.

Bishnoi, N.R., Sheoran, I.S., Singh, R. (1993). Influence of cadmium and nickel on photosyntheis and water relations in wheat leaves of different inseration level. *Photosynthetica*, 28, 473-479.

Bogdanović, D., Ubavić, M., Hadžić, V. (1997). Teški metali u zemljištu. In: Kastori, R. (ed.) Teški metali u životnoj sredini. Naučni institut za ratarstvo i povrtarstvo, Novi Sad, pp. 97-143.

Boisvert, S., Joly, D., Leclerc, D., Govindachary, S., Harnois, J., Carpentier, R. (2007). Inhibition of the oxygen-evolving complex of photosystem II and depletion of extrinsic polypeptiedes by nickel. *Biometals,* 20, 879-889.

Bošković-Rakočević, Lj., Pavlović, R., Bogdanović, D. (2014). Effect of fertilization on available cadmium level in soil and lettuce. *Acta Agriculturae Serbica*, 19(37), 3-14.

Breckle, S.W. (1991). Growth under stress: Heavy metals. In: Waisel, Y. et al.(eds.) *Plant Roots: The Hidden Half.* Marcel Dekker, New York, pp. 351-373.

Brown, P.H., Welch, R.M., Cary, E.E. (1987a). Nickel: a micronutrient essential for higher plants. *Plant Physiology*, 85, 801- 803.

Brown, P.H., Welch, R.M., Cary, E.E., Checkai, R.T. (1987b). Beneficial effects of nickel on plant growth. *Journal of Plant Nutrition*, 10, 2125-2135.

Brown, P.H., Welch, R.M., Madison, J.T. (1990). Effect of nickel deficiency on soluble anion, amino acid and nitrogen levels in barley. *Plant and Soil*, 125, 19-26.

Cammack, R. (1995). Splitting molecular hydrogen. *Nature*, 373, 556-557.

Cempel, M., Nikel, G. (2006). Nickel a review of its sources and environmental toxicology. *Polish Journal of Environmental Studies*, 15, 375-382.

Chand, S., Kumari, R., Patra, D.D. (2015). Effect of nickel and vermicompost on growth, yield, accumulation of heavy metals and essential oil quality of Tagetes minuta. *Journal of Essential Oil-Bearing Plants*, 18, 767-774.

Checkai, R.T., Norvell, W.A., Welch, R.M. (1986). Investigation of nickel essentiality in higher plants using recirculating resin-bufferd hydroponic system. *Agronomy Abstracts*, 195.

Chen, C., Huang, D., Liu, J. (2009). Functions and toxicity of nickel in plants: recent advances and future prospects. *Clean*, 37, 304-313.

Dalton, D.A., Evans, H.J., Hanus, F.J. (1985). Stimulation by nickel of soil microbial urease activity and urease and hydrogenase activities in soybeans grown in a low-nickel soil. *Plant and Soil*, 88, 245-258.

Das, P.K., Kar, M., Mishra, D. (1978). Nickel nutrition of plants: I. Effect of nickel and some oxidase activities during rice (*Oryza sativa* L.) seed germination. *Zeitschrift für Pflanzenphysiologie*, 90, 225-233.

de Querioz Barcelos, J.P., de Souza Osorio, C.R.W., Leal, A.J.F., Alves, C.Z., Santos, E.F., Reis, H.P.G., dos Reis, A.R. (2017). Effects of foliar nickel (Ni) application on mineral nutrition status, urease activity and physiological quality

of soybean seeds. *Australian Journal of Crop Science*, 11, 184-192.

Demchenko, N.P., Kalimova, I.B., Demchenko, K.N. (2005). Effect of nickel on growth, poliferation, an differentiation of root cells Triticum aesativum seedlings. *Russian Journal of Plant Physiology*, 52, 220-228.

Dixon, N.E., Gazola, C., Blakeley, R.L., Zerner, B. (1977). Jack bean urease (EC 3.5.1.5), a metalloenzyme. A simple biological role for nickel? *Journal of American Chemical Society,* 97, 4131-4133.

Djelić, G., Timotijević, S., Simić, Z. (2018). Uptake and distribution of metals in *Populus nigra* and *Populus tremula*. Acta *Agriculturae Serbica*, 23(46), 167-176.

Doroghází, O.T., Kastori, R.R., Maksimović, I. (2010). Nickel translocation from seed during germination and growth of young maize plants. Matica *Srpska Journal for Natural Sciences,* 119, 17-25.

Drazkiewicz, M., Baszynski, T. (2010). Interference of nickel with the photosynthetic apparatus of Zea mays. *Ecotoxicology and Environmental Safety*, 73, 982-986.

Drzewiecka, K., Mleczek, M., Gasecka, M., Magdziak, Z., Golinski, P. (2012). Chamges in Salixviminalis L. cv. Cannabiana morphology and physiology in response to nickel ionshydroponic investigations. *Journal of Hazardous Materials*, 218, 429-438.

Einhardt, A.M., Ferreira, S., Hawerroth, C., Valadares, S.V., Rodrigues, F.A. (2020). Nickel potentiates soybean resistance against binfection by Phakopsora pachyrhizi. *Plant Pathology*, 69, 849- 859.

Eskew, D.L., Welch, R.M., Norvell, W.A. (1983). Nickel, an essential mironutrient for legumes and possibly all higher plants. *Science*, 222, 621-623.

Follmer, C. (2008). Insights into the role and structureb of olant ureases. *Phytochemistry*, 69, 18-28.

Follmer, C., Barcellos, G.B., Zingali, R.B., Machado, O.L.T., Alves, E.W., Barja-Fidalgo, D. (2001). Canatoxin, a toxic protein jack beans (*Canavalia ensiformis*), is a variant from of urease (EC.3.5.1.5): biological effects of urease independent of its ureolytic activity. *Biochemical Journal*, 360, 217-224.

Freitas, D.S., Rodak, B.W., Reis, A.R., Reis, F.B., Carvalho, T.S., Schulze, J., Carneiro, M.A.C., Guitherme, L.R.G. (2018). Hidden nickel defficiency ? Nickel fertilization via soil improves nitrogen metabolism and grain yield in soybean genotypes. *Frontiers in Plant Science*, 9, 614.

Gajewska, E., Sklodowska, M. (2007). Effect of nickel on ROS content and antioxidative enzyme activities in wheat leaves. *BioMetals*, 20, 27-36.

Gajewska, E., Sklodowska, M. (2009). Nickel-induced changes in nitrogen metabolism in wheat shoots. *Journal of Plant Physiology*, 166, 1034-1044.

Gajewska, E., Sklodowska, M., Slaba, M., Mazur, J. (2006). Effect of nickel on antioxidative enzymes activities, proline and chlorophyll content in wheat shoots. *Biologia Plantarum*, 50, 653-659.

Gajewska, E., Wielanek, M., Bergier, K., Skoldowska, M. (2009a). Nickel induced depression on nitrogen assimilation in wheat roots. *Acta Physiologiae Plantarum*, 31, 1291-1300.

Georgiadou, E.C., Kowalska, E., Patla, K., Kulbat, K., Smolinska, B., Leszcynska, J., Fotopoulos, V. (2018). Influence of heavy metals (Ni, Cu and Zn) on nitro-oxidative stress responses, proteome regulation and allergen production in basil (*Ocimum basilicum* L.) plants. *Frontiers in Plant Science*, 9, 862-873.

Gerendas, J., Sattelmacher, B. (1999). Influence of Ni supply on growth and nitrogen metabolism of *Brassica napus* L. grown with NH4NO3 or urea as N source. *Annals of Botany*, 83, 65-71.

Ghasemi, F., Heidari, R., Jameii, R., Purakbar, L. (2012). Effect of Ni^{2+} toxicity on Hill reaction and membrane functionality im maize. *Journal of Stress Physiology and Biochemistry*, 8, 55-61.

Gomes-Junior, R.A., Moldes, C.A., Delite, F.S., Gratao, P.L., Mazzafera, P., Lea, P.J., Azevedo, R.A. (2006). Nickel elicits a fast antioxidant response in Coffea arabica cells. *Plant Physiology and Biochemistry*, 44, 420-429.

Gopal, R., Nautiyal, N. (2012), Growth, antioxidant enzymes activities, and proline accumulation in mustard due to nickel. *International Journal of Vegetable Science*, 18, 223-243.

Gratao, P.L., Polle, A., Lea, P.J., Azevedo, A. (2005). Making the life of heavy metal- stressed plants a littel essier. *Functional Plant Biology*, 32, 481-494.

Hare, P.D., Cress, W.A. (1997). Metabolism implications of stress-induced proline accumulation in plants. *Plant Growth Regulation*, 21, 79-102.

Hasinur, R., Shamima, S., Shah, A., Shigenao, K.W. (2005). Effect of nickel on growth and composition of metal micronutrients in barley plants grown in nutrient solution. *Journal of Plant Nutrition*, 28, 393-404.

Hogan, M.E., Swift, I.E., Done, J. (1983). Urease assay and ammonia release from leaf tissues. *Phytochemistry*, 22, 663-667.

Hossain, M.A., Piyatida, P., Silva, J.A.T.D., Fujita, M. (2012). Molecular mechanism of heavy metal toxicity and tolerance in plants: Centrale role of glutathion in detoxification of reactive oxigen species and methylglyoxal and in heavy metal chelation. *Journal of Botany*, 12, 37-45.

Hovmand, M.F. (1984). Cycling of Pb, Cd, Cu, Zn and Ni in Danish agriculture. In: Berglund, S. (eds.) *Utilisation of sewage sludge on land: Rates of application and long-term effects of metals*. Springer, pp. 166-185.

Ilin, S.Z., Kastori, R., Malenčić, Đ.R. (2000). The effect of nickel on superoxide dismutase activity, lipid peroxidation intensity and oxygen radical quantity in young plants of wheat and maize. *Matica Srpska Journal for Natural Science,* 98, 39-44.

Janicka-Russak, M., Kabala, K., Bruzynski, M., Klobus, G. (2008). Response of plasma membrane H+-ATPase to heavy metal stress in Cucumis sativus roots. *Journal of Experimental Botany*, 59, 3721-3728.

Kabata-Pendias, A. (2000). *Trace Elements in Soil and Plants*. Third Edition. CRC Press, Boca Raton, Florida.

Kappaun, K., Piovesen, A.R., Carlini, R.C., Ligabue-Braun, R. (2018). Ureases: Historical aspects, catalytic, and non catalitic properties- A review. *Journal of Advanced Research*, 13, 3-17.

Kastori, R. (2004). Nitrogen volatilization from plants. Matica Srpska *Journal for Natural Science*, 107, 111-118.

Kastori, R.R., Maksimović, I.V., Marinković, R.Z., Zeremski-Škorić, T.M., Ninkov, J.N., Putnik-Delić, M.I. (2010). Genetic variability of concentration of microelements in wild sunflower species and hybrids. Matica Srpska *Journal for Natural Science*, 118, 69-77.

Kastori, R., Grujić, S., Kandrač, J., Petrović, N. (1978). Effect of nickel on incorporation of 32P into several types of nucleic acids in young corn leaves. *Agrochimica*, 22, 61-68.

Kastori, R., Petrović, N., Arsenijević-Maksimović, I. (2000). Effect of excess Cd, Pb, Cu and Ni concentrations on plant water relations. ESNA XXX Annual Meeting, Keszthely, Hungary, Book of abstracts, 88.

Kastori, R., Petrović, N., Kovačev, L. (1996). Neparazitne bolesti i oštećenja šećerne repe. Institut za ratarstvo i povrtarstvo, Novi Sad , Jugošećer D. D. Beograd.

Kastori, R., Petrović, N., Maksimović-Arsenijević, I. (1997). Teški metali i biljke. U: Kastori, R. (ed.) *Teški metali u životnoj sredini*, Naučni institut za ratarstvo i povrtarstvo, Novi Sad.

Khan, M.I.R., Khan, N.A., Masood, A., Per, T.S., Asgher, M. (2016). Hydrogen peroxide alleviates nickel- inhibited photosynthetic responses through increase in use-efficiency of nitrogen and sulfur, and gluthatione production in mustrad. *Frontiers in Plant Science,* 7, 44-54.

Kovačević, G., Kastori, R., Markulov, Lj. (1998). Effect of excess heavy metal concentrations on leaf anatomy of wheat plants. The 11th Congress of the Federation of European Societies of Plant Physiology. Bulgarian Journal of Plant Physiology Special issue, 198.

Kozhevnikova, A., Seregin, I., Bystrova, E., Belyaeva, A., Kataeva, M., Ivanov, V. (2009). The effect of lead, nickel,

and strontium nitrates on cell division and elongation in maize roots. *Russian Journal of Plant Physiology,* 56, 242-250.

Kumar, H., Sharma, D., Kumar, Y. (2012). Nickel-induced oxidative stress and role of antioxidant defence in barley roots and leaves. *International Journal of Environmental Biology*, 2, 121-128.

Kumar, O., Singh, S.K., Latare, A.M., Yadav, S.N. (2018). Fertilization of nickel affects growth, yield component and micronutrient status of barley (*Hordeum vulgare* L.) grown on low nickel soil. *Archives of Agronomy and Soil Science*, 64, 1407-1418.

Kumar, P., Rouphael, Y., Cardarelli, M., Colla, G. (2015). Effect of nickel and grafting combination on yield, fruit quality, antioxidative enzyme activities, lipid peroxidation, and mineral composition of tomato. *Journal of Plant Nutrition and Soil Science*, 178, 848-860.

Küpper, H., Küpper, F., Spilling, M. (1996). Environmental relevance of heavy metal-substituted chlorophylls using the example of water plants. *Journal of Experimental Botany*, 47, 259-266.

Kutman, B.Y., Kutman, U.B., Cakmak, I. (2012). Nickel-enriched seed and externally supplied nickel improve growth and alleviate foliar urea damage in soybean. *Plant and Soil*, 363, 61-75.

Lamas, A., Ulrich, C.I., Sanz, A. (2008). Ni2+toxicity in rice: Effect on membrane functionality and plant water content. *Plant Physiology and Biochemistry*, 46, 905-910.

Latif, H.H. (2010). The influence of nickel sulphate on some physiological aspects of two cultivars of *Raphanus sativus* L. *Archives of Biological Sciences Belgrade*, 62, 683-691.

Lešková, A., Giehl, R.F.H., Hartmann, A., Fragašová, A., von Wirén, N. (2017). Heavy metals induced iron deficiency responses at different hierarchic and regulatory levels. *Plant Physiology*, 174, 1648-1668.

Lešková, A., Zvarik, M., Araya, T., Giehl, R.F.H. (2020). Nickel toxicity targets cell wall-related processes and PIN2-mediated auxin transport to inhibit root elongation and gravitropic responses in Arabidopsis. *Plant and Cell Physiology*, 61, 519-535.

Li, Y., Zamble, D.B. (2009). Nickel homeostasis and nickle regulation. *Chemical Reviews*, 109, 4617-4643.

Li, Z., Chen, X., Li, S., Wang, Z. (2015). Effect of nickel chloride on Arabidopsis genomic DNA and methylation of 18S rDNA. *Electronic Journal of Biotechology*, 18, 51-57.

Maksimović, I., Kastori, R., Krstić, L., Luković, J. (2007). Steady presence of cadmium and nickel affected root anatomy, accumulation and distribution of essential ions in maize seedlings. *Biologia Plantarum*, 51, 589-592.

Maksimović, I., Putnik-Delić, M., Kastori, R., Zeremski, T., Marjanović-Jeromela, A., Gani Novaković, I. (2012). Growth and chemical composition of camelina under heavy metals stress. Abstracts, Plant Biology Congress, Freiburg 2012, jointly organised by FESPB and EPSO, 29 July-3 August 2012, 373.

Mallick, N., Mohn, F.H. (2003). Use of chlorophyll fluorescence in metal-stress research: a case study with the green microalga Scenedesmus. *Ecotoxicology and Environmental Safety*, 55, 64-69.

Marschner, P. (ed.) (2012). Marschner's Mineral Nutrition of Higher Plants. Third Edition, Academic Press, London.

Mazzei, L., Musiani, F., Ciurli, S. (2020). The structure-based reaction mechanism of urease enzyme: tale of a long dabats. *Journal of Biological Inorganic Chemistry*, 25, 829-845.

Meychik, N., Nikolaeva, Y., Kushunina, M., Yermakov, I. (2014). Are the carboxyl groups of pectin polymers the only metal-binding sites in plant cell walls ? *Plant and Soil,* 381, 25-34.

Milić, D., Bubanja, N., Ninkov, J., Milić, S., Vasin, J., Luković, J. (2021). Phytoremediation potential of the naturally occurring wetland species in protected Long Beach in Ulcinj, Montenegro. *Science of the Total Environment*, 797, 148995.

Miller, R.J., Dumford, S.W., Koeppe, D.E., Hanson, J.B. (1970). Divalent cation stimulation of substrate oxidation by corn mitochondria. *Plant Physiology*, 45, 649-653.

Milošević, N., Govedarica, M., Kastori, R., Petrović, N. (2002). Effect of nickel on wheat plants, soil microorganisms and enzymes. *Studia Universitatis Babes-Bolyaj, Biologia* XLVII, 1, 79-84.

Mishra, D., Kar, M. (1974). Nickel in plant growth and metabolism. *Botanical Review,* 40, 395-452.

Mizuno, T., Nakahara, Y., Fujimori, T., Yoshida, H. (2018). Natural revegetation potential of Japanese wild thyme (Thymus quinquecostatus Celak) on serpentine quarries. *Ecological Research*, 33, 777-788.

Molas, J. (1997). Changes in morphological and anatomical structure of cabbage (*Brassica oleracea* L.) outer leaves and in ultrastructure of their chloroplasts caused of nickel. *Photosynthetica*, 34, 513-522.

Niethammer, A. (1930). Landwirtschaftliche-biologische Studien mit Nickel und Cyanverbindungen. *Archiv fur Pflanzenbau*, 4, 607-634.

Nishida, S., Tsuzuki, C., Kato, A., Aisu, A., Yoshida, J., Mizuno, T. (2011). ATIR1, the primary iron uptake transporter in the roots, mediates excess nickel accumulation in Arabidopsis thaliana. *Plant and Cell Physiology,* 52 (8), 1433-42.

Ojeda-Barrios, D.L., Sánchez-Chávez, D.L., Sida-Arreola, J.P., Valdez-Cepeda, R., Balandran-Valladers, M. (2016). The impact of foliar nickel fertilization on urease avtivity in pecan trees. *Journal of Soil Science and Plant Nutrition*, 16, 237-247.

Page, V., Feller, U. (2005). Selective transport of zinc, manganese, nickel, cobalt and cadmium in the root system and transfer to the leaves in young wheat. *Annals of Botany*, 96, 425-434.

Pandey, N., Pathak, G.C. (2006). Nickel alters antioxidative defense and water status in greengram. *Indian Journal of Plant Physiology*, 11, 113-118.

Pandey, V.K., Gopal, R. (2010). Nickel toxicity effects on growth and metabolism of eggplant. *International Journal of Vegetable Science*, 16, 351-360.

Pandolfini, T., Gabbrielli, R., Ciscato, M. (1996). Nickel toxicity in two durum wheat cultivars differing in drought sensivity. *Journal of Plant Nutrition*, 19, 1611-1627.

Parlak, K.U. (2016). Effect of nickel on growth and biochemical characteristics of wheat (*Triticum aesativum* L.) seedlings. NJS – Wagen. *Journal of Life Science*, 76, 1-5.

Pavlova, D. (2017). Nickel effect on root-meristem cell division in *Plantago laceolata* (Plantaginaceae) seedlings. *Australian Journal of Botany*, 65, 446-452.

Pavlova, D., Vila, D., Vila, K., Bani, A., Xhaferri, B. (2018). Effect of nickel on seed germination of Alyssum species with potential for phytomining in Albania. *Fersenius Environmental Bulletin*, 27, 1345-1352.

Petrović, N., Kastori, R. (1979a). Uptake and traslocation of 63Ni in young wheat plants. Mineral Nutrition of Plants. Proceedings of the First International Symposium on Plant Nutrition. Sofia, Vol. 2, 324-327.

Petrović, N., Kastori, R. (1979b). A nickkel (^{63}Ni) eloszlása és retranszlokációja fiatal napraforgó növényekben. *Agrokémia és Talajtan,* 28, 157-166.

Petrović, N., Arsenijević-Maksimović, I., Kastori, R. (2003). Uticaj koncentracije nikla na masu suve materije i mineralne ishrane graška. *Zbornik radova, Naučni institut za ratarsvo i povrtarstvo*, Novi Sad, 38, 91-100.

Petrović, N., Kastori, R. (1994). Uptake, distribution and tranlocation of nickel (^{63}Ni) in wheat. *Journal of Food Physiology Supplement,* 1, 71-73.

Petrović, N., Maksimović, I., Sekulić, P., Ralev, J., Kastori, R. (2003). Coefficient of Zn, Cu, Cd and Ni accumulation in some cultivated plants. Proceedings of The 10th Symposium on Analytical and Environmental Problems, SZAB, Szeged, 151-154.

Polacco, J.C., Mazzafera, P., Tezotto, T. (2013). Opinion- Nickel and urease in plants: Still many knowledge gaps. *Plant Science,* 199-200, 79-90.

Poonkothai, M., Vijayavanthi, B.S. (2012). Nickel as an essential element and toxicant. *Journal of Environmental Science*, 1, 285-288.

Popović, B., Štajner, D. (2008). Oksidativni stres kod biljaka. Poljoprivredni fakultet, Novi Sad.

Rahman, H., Sabreen, S., Alam, S., Kawai, S. (2005). Effect of nickel on growth and composition of metal micronutrients i barley plants grown in nutrient solution. *Journal of Plant Nutrition*, 28, 393-404.

Rao, M.K.V., Sresty, T.V. (2000). Antioxidative parameters in the seedlings of pigeonpea (*Cajanus cajan* (L.) Millspaugh) in response to Zn and Ni stresses. *Plant Science,* 157, 113-128.

Rasti, S., Rajabzadeh, M.A., Khosravi, A.R. (2020). Controlling factors on nickel uptake by plants growing on Ni-laterites: A case study in biogeochenical exploration from the Mazayejan area, SW Iran. *Journal of Geochemical Exploration*, 217, 1-11.

Rizwan, M., Imtiaz, M., Dai, Z., Mehmood, S., Adeel, M., Liu, J., Tu, S. (2017). Nickel stressed responses of rice in Ni subcellular distribution, antioxidant production , and osmolyte accumulation. *Environmental Science and Pollution Research*, 24, 20587-20598.

Roach, W.A., Barclay, C. (1946). Nickel and multiple trace element deficiencies in agricultural crops. *Nature*, 157, 696-699.

Robertson, A.I., Meakin, M.E.R. (1980). The effect of nickel on cell division and growth of *Brachystegia spiciformis* seedlings. *Kirkia*, 12, 115-125.

Sachan, P., Lal, N. (2017), An overview of nickel (Ni²⁺) essentiality, toxicity and tolerance strategies in plants. *Asian Journal of Biology*, 2, 1-15.

Sajwan, K.S., Ornes, W.H., Youngblood, T.V., Alva, A.K. (1996). Uptake of soil applied cadmium, nickel and selenium by bush beans. *Water, Air, and Soil Pollution*, 91, 209-217.

Seregin, L.V., Kozhevnikov, A.D. (2006). Physiological role of nickel and its toxic effects in higher plants. *Russian Journal of Plant Physiology*, 53, 257-277.

Sheoran, V., Sheoran, A.S., Poonia, P. (2016). Factors affecting phytoexrtaction: a review. *Pedosphere*, 26, 148-166.

Shweti, D., Kumar, A., Verma, J.S. (2018). Effects of nickel chloride on germination and seedling growth of different wheat (*Triticum aesativum* L. em Thell.) cultivars. *Journal of Pharmacognosy & Phytochemistry*, 7, 2227-2234.

Siedlecka, A., Krupa, Z. (2002). Functions of enzymes in heavy metal treated plants. In: Prasad, M.N.V., Strazatka, K. (Eds.) *Physiology and Biochemistry of Metal Toxicity and Tolerance in Plants.* Kulwer Akademic Publishers, Dordrecht / Boston / London.

Singh, D.P., Punam, K., Bisen, P.S. (1989). Effect of Ni²⁺, Hg²⁺ and Cu²⁺ on growth, oxygen evolution and photosynthetic electron transport in Cylindrospermum IU 942. *Journal of Plant Physiology*, 132, 406-412.

Sun, E.J., Wu, F.Y. (1998). Along-vein necrosis as indicator symptom on water spinach caused by nickel in water culture. *Botanical Bulletin of Academia Sinica,* 39, 255-259.

Turan, V., Ramzani, P.M.A., Ali, Q., Abbas, F., Iqbal, M., Irum, A., Khan, W.D. (2017). Allewation of nickel toxicity and an improvement in zinc bioavailability in sunflower seed with chitosan and biochar application in pH adjusted nickel contaminated soil. *Archives of Agronomy and Soil Science*, 64, 1053-1067.

Ubavić, M., Bogdanović, D., Dozet, D. (1993). Teški metali u zemljištima Vojvodine. In: Kastori, R. (ed.). *Teški metali i pesticidi u zemljištu*. Poljoporivredni fakultet, Institut za ratarstvo i povrtarstvo, Novi Sad, 31-47.

Van Assche, F., Clijsters, H. (1990). Effect of metals on enzyme activity in plnats. *Plant, Cell and Environment*, 13, 195-206.

Velikova, V., Tsonev, T., Loreto, F., Centritto, M. (2011). Changes in photosynthesis, mesophyll conductance to CO_2, and isoprenoid emissions in *Populus nigra* plants exposed to excess nickel. *Environmental Pollution*, 159, 1058-1066.

Wood, B.W., Reilly, C.C., Nyczepir, A.P. (2006). Field deficiency of nickel in trees: Symptoms and causes. *Acta Horticulturae*, 721, 83-97.

Wood, W.B., Reilly, C.C. (2006a). Nickel and plant disease. International Plant Nutrition Institute <http:// www. Nuitricaodeplantas.agr. br/sitedownloads/unesp-jaboticabal/Niquel-doencas-BruceWood.pdf>

Yan, R., Gao, S., Yang, W., Cao, M., Wang, S., Chen, E. (2008). Nickel toxicity induced antioxidant enzyme and phenylalanine ammonia-lyase acvtivities in *Jatropha curcas* L. cotyledons. *Plant, Soil and Environment*, 54, 294-300.

Yang, X.E., Baligar, V.C., Froster, J.C., Martens, D.C. (1997). Accumulation and transport of nickel in relation to organic acids in ryegrass and maize with different nickel levels. *Plant and Soil*, 196, 271-276.

Yusuf, M., Fariduddin, Q,. Hayat, S., Ahmad, A. (2011). Nickel: An overview of uptake, essentiality and toxicity i plants. *Bulletin of Environmental Contamination and Toxicology*, 86, 1-17.

Zeller, S., Feller, U. (1998). Redistribution of cobalt and nickel in detached wheat shoots: Effect of steam-girdling and of cobalt and nickel supply. *Biologia Plantarum*, 41, 427-434.