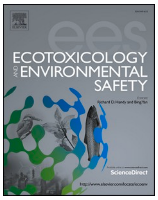
Ecotoxicology and Environmental Safety 289 (2025) 117669

Contents lists available at ScienceDirect

Ecotoxicology and Environmental Safety

journal homepage: www.elsevier.com/locate/ecoenv



Review

Microbial assisted alleviation of nickel toxicity in plants: A review

Xinyu Mao[a], Bilal Ahmad[b], Sabir Hussain[c], Farrukh Azeem[d], Muhammad Waseem[c],
Yousef Alhaj Hamoud[e], Hiba Shaghaleh[f], Amany H.A. Abeed[g], Muhammad Rizwan[c,*],
Jean Wan Hong Yong[h,*]

[a] College of Agricultural Science and Engineering, Hohai University, Nanjing 210098, China
[b] Molecular, Cellular, and Developmental Biology, Kansas State University, Manhattan, KS 66506, USA
[c] Department of Environmental Sciences, Government College University Faisalabad, Faisalabad 38000, Pakistan
[d] Department of Bioinformatics and Biotechnology, Government College University Faisalabad, Faisalabad 38000, Pakistan
[e] College of Hydrology and Water Resources, Hohai University, Nanjing 210098, China
[f] College of Environment, Hohai University, Nanjing 210098, China
[g] Department of Botany and Microbiology, Faculty of Science, Assiut University, Assiut 71516, Egypt
[h] Department of Biosystems and Technology, Swedish University of Agricultural Sciences, Alnarp 23456, Sweden

ARTICLE INFO

Edited by Dr R Pereira

Keywords:
Nickel
Phytotoxicity
PGPB
Phytoremediation
Geno-remediation
Metal transporters
Chelators

ABSTRACT

Nickel (Ni) is required in trace amounts (less than 500 $\mu g\ kg^{-1}$) in plants to regulate metabolic processes, the immune system, and to act as an enzymatic catalytic cofactor. Conversely, when nickel is present in high concentration, it is considered as a toxic substance. Excessive human nickel exposure occurs through ingestion, inhalation, and skin contact, ultimately leading to respiratory, cardiovascular, and chronic kidney diseases. Due to anthropogenic activities, the nickel concentrations in various environmental scenarios have progressively risen to levels as high as 26,000 ppm in soil and 0.2 $mg\ L^{-1}$ in water; surpassing the established safety threshold limits of 100 ppm for soil and 0.005 ppm for surface water. Nickel is required by various plant species for facilitating biological processes; in the range of 0.01–5 $\mu g\ g^{-1}$ (dry weight). When present in excess, nickel toxicity in plants (10–1000 $mg\ kg^{-1}$ dry weight mass) causes many disrupted metabolic processes; leading to lower growth, altered development, hindered seed germination, chlorosis, and necrosis. To tackle any metal-linked pollution issues, various remediation approaches are employed to remove heavy metals (especially nickel) and metalloids including physicochemical, and biological methods. Based on literature, the physicochemical methods are not commonly used due to their costly nature and the potential for producing secondary pollutants. Interestingly, bioremediation is considered by many practitioners as an easy-to-handle, efficient, and cost-effective approach, encompassing techniques such as phytoremediation, bioleaching, bioreactors, green landforming, and bio-augmentation. Operationally, phytoremediation is widely utilized for cleaning up contaminated sites. To support the phytoremediative processes, numerous nickel hyperaccumulating plants have been identified; these species can absorb from their surroundings and store high concentrations of nickel (through various mechanisms) in their biomass, thereby helping to detoxify nickel-contaminated soils via phytoextraction. The microbe-assisted phytoremediation further optimizes the nickel detoxification processes by fostering beneficial interactions between microbes and the nickel-hyperaccumulators; promoting enhanced metal uptake, transformation, and sequestration. Microbe-assisted phytoremediation can be categorized into four subtypes: bacterial-assisted phytoremediation, cyanoremediation, mycorrhizal-assisted remediation, and rhizoremediation. These diverse approaches are likely to offer more effective and sustainable remediative strategy to ecologically restore the nickel-contaminated environments.

Abbreviations: DWM, Dry Weight Mass; ACD, Allergic Contact Dermatitis; NRAMP, Natural Resistance-Association Macrophage Protein; ZIP, Zinc-Iron Permease; YSL, Yellow-Stripe 1-like; HMA, Heavy Metal ATPase; CDF, Cation Diffusion Facilitator; CAX, Cation exchanger proteins; ABC, ATP-binding cassette transporters; ROS, Reactive Oxygen Species; AO, Ascorbate Oxidase; POD, Peroxidase; CAT, Catalase; SOD, Superoxide Dismutase; GR, Glutathione Reductas; ETC, Electron Transport Chain; AMF, Arbuscular Mycorrhizal Fungi; H^+-ATPase, Hydrogen Ion Proton ATPase; PM, Plasma Membrane; NA, Nicotinamide; IAA, Indole Acetic Acid; PGPB, Plant Growth-Promoting Bacteria; PGPR, Plant Growth Promoting Rhizobacteria; LMWOA, Low Molecular Weight Organic Acids.

* Corresponding authors.
E-mail addresses: mrazi1532@yahoo.com (M. Rizwan), jean.yong@slu.se (J.W.H. Yong).

https://doi.org/10.1016/j.ecoenv.2025.117669
Received 30 October 2024; Received in revised form 16 December 2024; Accepted 1 January 2025

1. Introduction

Lithogenic and anthropogenic activities are continuously contaminating the biosphere with noxious gases, organic/inorganic chemicals, heavy metals/metalloids, pesticides, fungicides, excessive or long-term use of agrochemicals (e.g. superphosphate fertilizers, urea), and synthetic dyes (Adil et al., 2023; Clemens and Ma, 2016; Khaliq et al., 2024; Liu et al., 2012; Shaghaleh et al., 2024; Wang et al., 2020; Wei et al., 2024). These pollutants are irreversible and non-degradable, which induce notably negative impacts on the quality of soil and water reservoirs (Alamgir et al., 2024; Fayiga and Saha, 2016). Simultaneously, human population has also been exposed to environmental pollution, which may cause neurological disorders, instability, immune system suppression, induce cancer, skin diseases, and water or airborne diseases (Tan et al., 2010; Wu et al., 2023). Nowadays, heavy metal contamination in soil has become an important environmental and nutritional concern throughout the world. Approximately 0.5 million land sites in the European Union countries have been reported as uncontrolled contaminated sites, affecting a significant portion of agricultural land. The total area of contaminated land in the EU is substantial, with many of these sites impacting cultivable soil and agricultural productivity. In Greece, Portugal, Ireland, India, Poland, and North America, extensive agricultural lands have been reported to exhibit heavy metal-polluted soil. Literature reported that approximately 40 % of fertile land in China has also been affected by heavy metal pollution (Qin et al., 2021; Wen et al., 2022).

Heavy metals or metalloids found in the periodic table with a relatively high atomic density greater than 4 g/cm^3 , about five times higher than water (Ejaz et al., 2023). The high atomic density of heavy metals makes the remediation process from soil very challenging. Unplanned industrialization and urbanization, irrigation practices, metal mining, industrial effluents, military explosives, automobiles, combustion processes, electroplating processes, etc., are major anthropogenic agents to accumulate heavy metals in soil and ultimately enter our food chain (Bauddh et al., 2015; Maurya et al., 2019; Rashid et al., 2023; Sharma et al., 2023; Singh et al., 2009; Willey, 2008). Heavy metals are categorized into three groups: toxic, precious, and radionuclide (Bishop, 2002). Certain heavy metals are essential for proper regulatory functioning of living cells, including zinc (Zn), iron (Fe), cobalt (Co), manganese (Mn), molybdenum (Mo), nickel (Ni), and copper (Cu). However, several metals or metalloids, especially cadmium (Cd), mercury (Hg), chromium (Cr), boron (B), aluminum (Al), lead (Pb), and arsenic (As) are toxic and potentially lethal to plant and animal cell physiology, considered as non-essential heavy metals (Rashid et al., 2023; Song et al., 2019; Tang et al., 2015; Tow et al., 2019; Van der Ent et al., 2013; Yong et al., 2010). The concentration of essential or non-essential heavy metals is important for plant cells in trace amounts (de Bang et al., 2021; Marschner, 2011). However, the occurrence of heavy metals in plant tissues above a certain threshold level can induce negative effects upon many essential physiological processes: photosynthesis, nutrient uptake, biosynthesis of hormones, and agglomeration of reactive oxygen species (ROS); and consequently lowering plant growth (Clemens and Ma, 2016; Gangwar et al., 2011; Kachenko et al., 2008; Kramer et al., 2000; Li et al., 2024; Sharma et al., 2016; Merian, 1984).

2. Nickel and its sources in the environment

Nickel, with the symbol "Ni" in the periodic table, has an atomic number of 28 and an atomic mass of approximately 58.69 at. mass units. Nickel exhibits several oxidation states, including $^{-}1$, $^{+}1$, $^{+}2$, $^{+}3$, and $^{+}4$. However, its most abundant oxidation state is $^{+}2$ (Denkhaus and Salnikow, 2002). Nickel possesses a hard, cubic crystalline structure and silvery-white appearance. It is characterized by its ductility, corrosion resistance, and magnetic properties at temperatures below 345℃. Additionally, nickel is an excellent conductor of heat (Musiani et al., 2015).

It is a trace element, naturally present in ultramafic soil, released into the surroundings by natural processes and anthropogenic activities. Nickel occurs in atmosphere as particles (0.1–0.2 μm diameter) and amalgamates with chlorides, sulfurs, and nitrites (Kabata-Pendias, 2000; Mustafa et al., 2023). Nickel and its salts occur naturally in the earth's crust at a concentration of 80 μg g^{-1}. In ultramafic rocks, such as peridotite or serpentine soil, the abundance of nickel is estimated to be as high as 2000 μg g^{-1}. Because of its chalcophilic characteristics, nickel is naturally found in association with sulfides, antimonides, and arsenides (Sigel et al., 2007). The concentration of nickel in soil ranges from 5 to 500 μg g^{-1} and can vary across different geographical areas. Moreover, its uptake in plant tissues has been reported between 0.5 and 5 μg g^{-1}, with variations depending on the plant species. In animal tissues, nickel accumulation falls within the range of 0.1–5 μg g^{-1}, while freshwater sources generally contain nickel concentrations ranging from 5 to 100 μg L^{-1} (Maurya et al., 2019; Schrenk et al., 2020).

2.1. Nickel concentration in air (airborne nickel)

Nickel and its compounds are constantly released into the atmosphere as a result of natural processes and human activities. Each year, approximately 8.5 million kg of nickel is discharged into the atmosphere through lithogenic sources, including waste incineration, windblown dust, and volcanic eruptions. Interestingly, anthropogenic emissions contribute to nickel release at a rate about five times higher than that of natural sources (Begum et al., 2022) shown in Fig. 1.

Nickel sulfate occurs in the ambient air, primarily due to its leachable nature. Approximately 20–80 % of nickel sulfate emissions have been attributed to coal combustion, while around 90 % of other nickel salts are released into the ambient air from oil combustion. Nickel oxides, sulfates, nitrates, and sulfide ores like pentlandite (FeNi)9S8, as well as nickel species found in the garnierite zone (silicate-oxide), also play a role in air pollution. Each year, the input of nickel into the atmosphere amounts to approximately 150,000 to 180,000 metric tons, originating from both natural sources and human activities. These activities include industrial effluents, fossil fuel consumption, and the disposal of nickel compounds or alloys (Kasprzak et al., 2003).

2.2. Nickel levels in soil

Nickel is an essential trace element that occurs naturally in various forms, including inorganic metallic crystalline form, complexed organic or inorganic cations, water-soluble free ions, or metal-chelated complexes. In the Earth's geochemical makeup, nickel is normally found in combination with iron, sulfur, and cobalt. The deposition of nickel salts from the atmosphere to the soil occurs through different transferring processes like dew, fog, and rain. The estimated concentration of nickel in various soils falls within the range of 4–80 ppm. On average, nickel constitues approximately 0.008 % of the Earth's crust (Tian et al., 2012).

In naturally occurring soils, the concentration of nickel is typically around 50 mg kg^{-1} in sandstones or acidic igneous rocky soil. However, in argillaceous rocks (such as shales, siltstone, and mudstone) or basic rocks, the reported nickel concentration is approximately 500 mg kg^{-1}. In serpentine soils, the nickel content can be even higher, exceeding 1000 mg kg^{-1} (Kierczak et al., 2021; Reeves et al., 1996).

Nickel is introduced into water bodies through diverse natural and human activities. Mechanisms, including chemical weathering and direct leaching, may lead to a substantial increase in the dissolved nickel in water bodies (Friberg et al., 1979). Typically, the concentrations of nickel in seawater and drinking water were found to be 0.1–0.5 μg L^{-1} and < 10 μg L^{-1} respectively. Drinking water generally serves as the primary source of nickel intake for humans (Sigel et al., 2007).

3. The role of nickel in biological systems

Nickel serves as an essential catalytic cofactor for enzymes in various

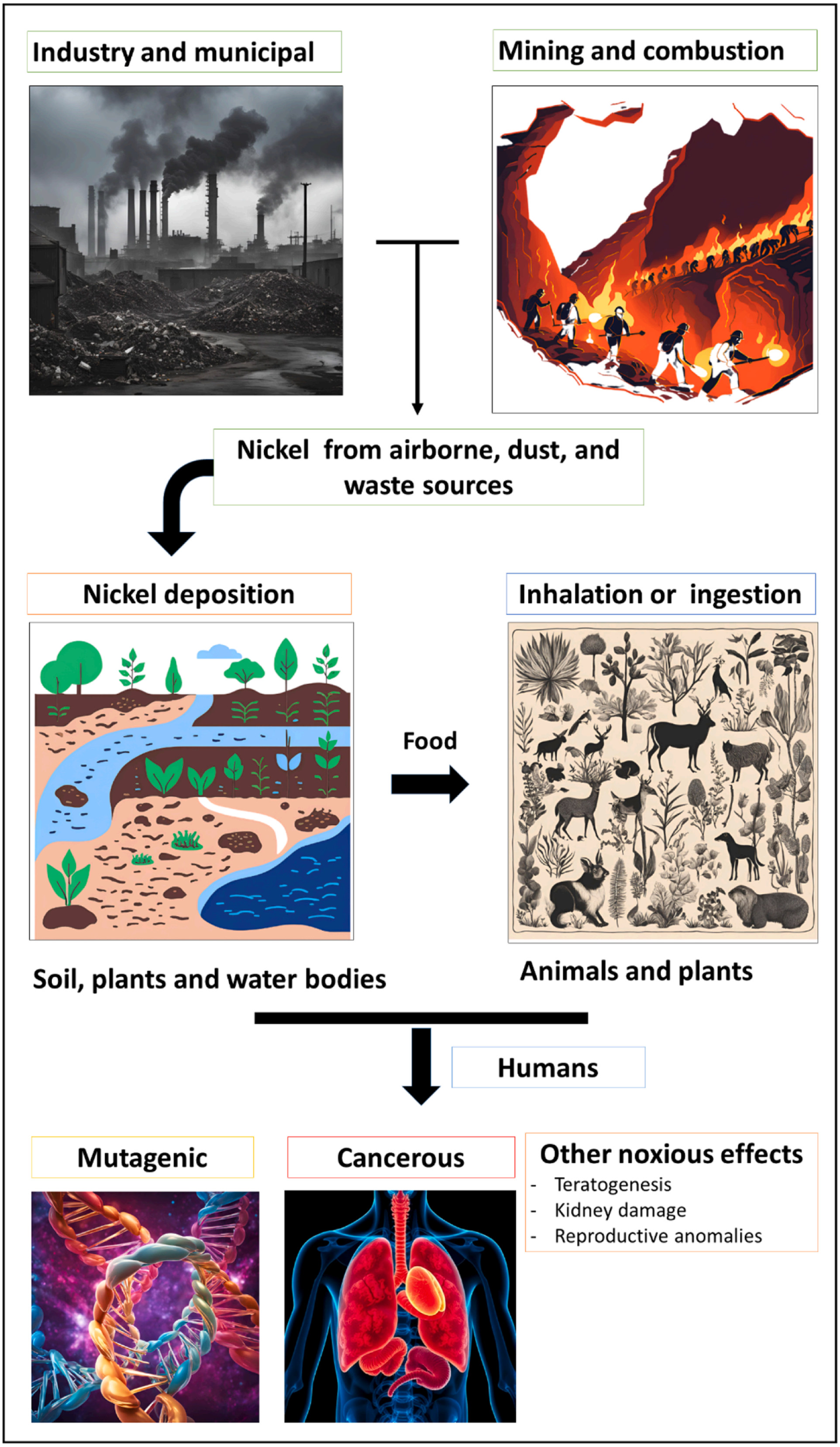


Fig. 1. Nickel sources and the different entry pathways into a biological system.

organisms from different kingdoms, including bacteria, fungi, animals, and plants;, to regulate their cellular growth and metabolic processes (Denkhaus and Salnikow, 2002; Maroney, 1999; Zambelli and Ciurli, 2013). Nickel-dependent enzymes such as glyoxalases, hydrogenases, carbon monoxide dehydrogenases, methyl Co-A reductases, superoxide dismutase, and ureases play crucial roles in the biosynthesis of various metabolites (Macomber and Hausinger, 2011). As an essential micronutrient, nickel has been required by various plant species in the range of 0.01–5 μg^{g-1} (dry weight) to enhance their growth and yield (Gajewska and Skłodowska, 2008; Parida et al., 2003). Within plants, nickel plays a critical role as a cofactor in nickel-based enzyme systems, known as metalloenzymes, such as urease which is responsible for converting urea nitrogen into NH3, which is vital for plant growth. Insufficient nickel levels in plants can result in leaf necrosis due to the accumulation of urea in plant tissues. Studies have demonstrated that barley cannot grow normally without a sufficient supply of nickel (Brown et al., 1987; Polacco et al., 2013). Plants absorb nickel from the soil through a combination of passive and active diffusion processes via the root system. It plays a crucial role in plant growth, seed germination, and fruit development (Aziz et al., 2015). In several leguminous plants, nickel serves as an enzyme catalyst essential for the biological nitrogen fixation processes (Chen et al., 2009; Welch, 1981).

In animals and humans, nickel is involved in the regulation of immune system. Its deficiency can result in reduced growth and reproductive abilities, as well as disruptions of the amino acid and lipid metabolisms and glucose pathways (Denkhaus and Salnikow, 2002). Microorganisms utilize nickel as a cofactor in several microbial enzymes. In microorganisms like *Bacillus pasteurii* and *Streptomyces* species, nickel has been found to regulate various cellular functions, including glycerol-1-phosphate dehydrogenase and quercetinase activity (Macomber and Hausinger, 2011).

Nickel compounds are used in many food and chemical industries and act as a catalyst in different processes i.e. hydrogenation of fats and margarines (Dohnalova et al., 2017). Moreover, it serves as a main component in electrochemical and electroplating industries, electronic instruments, production of Ni-Cd batteries, production of nickel-based alloys like stainless steel utensils, production of jewelry, coinage, and medical prostheses (Garrett, 2000). Nickel is found in natural foods and processed food, including cocoa powder, chocolate, dry fruits, green leafy vegetables, coffee, tea, cashews, kidney beans soybeans, etc. It is also used in many commercial items such as artificial jewelry, watches, eyeglasses, metallic frames, mobile phones, etc (Ricciardi et al., 2014). It serves various purposes in the food industry and functions as a catalyst in the hydrogenation process employed to produce margarine, potentially triggering allergic reactions in some individuals (Sharma, 2013). Lodyga-Chruscinska assessed nickel concentrations in 10 margarine brands available in the Polish market. They discovered that only 3 out of the 10 samples had nickel levels below the acceptable limit of 0.2 mg kg^{-1} (Łodyga-Chruścińska et al., 2012). Opting for a low-nickel diet can help to decrease nickel intake. Three types of nickel-dependent enzymes, such as hydrogenase, carbon monoxide dehydrogenase, and methyl coenzyme play essential roles in various industrial processes, including hydrogenation, desulfurization, and carbonylation (Evans, 2005; Harrop and Mascharak, 2005). Human activities, including solid waste incineration, mining, refining processes, and combustion of coal, residual, and fossil fuels, are the primary sources of atmospheric nickel emissions. These emissions consist of sulfides, oxides, metallic nickel, and silicates. Fossil fuel combustion is the main contributor to the presence of nickel-containing compounds in ambient air. Nickel concentrations in industrial areas range from 120 to 170 ng m^{-3}, while suburban areas have 6–17 ng m^{-3} (Cempel and Nikel, 2006; Denkhaus and Salnikow, 2002; Merian, 1984). Nickel production has been steadily rising due to the impacts of urbanization and industrialization. By 2012, global production had reached an impressive 1.76 million tons (Harasim and Filipek, 2015).

4. Nickel poisoning and its effects on human health

Nickel was categorized as a hazardous trace element and recognized as an acute toxic substance by numerous national and international organizations (Kumar et al., 2021). According to the International Agency for Research on Cancer (IARC), nickel compounds are classified as group 1 carcinogens, posing a significant risk to human health. Additionally, elemental nickel is considered a carcinogen in immuno-compromised individuals and falls under group 2B classification (Tian et al., 2012). Exposure to nickel toxicity can lead to detrimental impacts on multiple organs, including the cardiovascular, respiratory, immune, skin, and kidney systems. Nickel allergies are a significant concern, contributing to conditions like lung fibrosis, dermatitis, and various respiratory, cardiovascular, and chronic kidney disorders (Kasprzak et al., 2003). $Ni(CO)_4$ represents an organic-nickel compound and is considered the most toxic form of nickel. Exposure to this compound can occur through inhalation, skin contact, or ingestion. Its fat-soluble nature enables it to permeate cell membranes via diffusion or calcium ion channels, leading to its accumulation in various body tissues (Duda-Chodak and Blaszczyk, 2008).

Nickel and its compounds are notorious allergens, detectable through atopy patch tests. The prevalence of nickel allergy is higher among females and young patients (under 18 years old) worldwide (da Rosa et al., 2015; Thyssen and Menné, 2010). It has been evident that allergic contact dermatitis (ACD) is induced by nickel as it stimulates T-cell T-cell-mediated response and appears as itchy skin rashes in susceptible patients (Boonstra et al., 2015). It was reported that nickel can stimulate the hypoxia state (oxygen deficiency) by its binding to an oxygen sensor instead of iron which may disrupt cellular growth or suppress apoptosis (Denkhaus and Salnikow, 2002).

5. Nickel Toxicity and Effects in Plants

Over recent years, there has been a growing global concern regarding the escalation of nickel contamination in soil and water. The levels of nickel in these environmental scenarios have progressively surged to levels as high as 26,000 ppm in soil and 0.2 mg L^{-1} in water, significantly surpassing the established threshold limits of 100 ppm for soil and 0.005 ppm for surface water (Chen et al., 2009). The degree of nickel toxicity in plants displays variation from one species to another. For instance, hypersensitive plant species show toxicity effects at levels exceeding > 10 mg kg^{-1} dry weight mass (DWM) of nickel. Slightly tolerant plant species, on the other hand, demonstrate toxicity symptoms at levels surpassing > 50 mg kg^{-1} DWM, while hyperaccumulator plants manifest these effects at levels greater than > 1000 mg kg^{-1} DWM (Belouchrani et al., 2016). Some morphological features associated with nickel toxicity in flowering plants are: lesser root growth, stunted development, chlorosis, necrosis, and reduced leaf area. Additionally, many physiological functionalities are also affected negatively, namely enzymatic activities, photosynthesis, morphogenesis, mineral nutrition and the production of reactive oxygen species (ROS) (Broadhurst and Chaney, 2016; Singh, 2005; Sujkowska-Rybkowska et al., 2022).

High levels of nickel can impair root morphology and function, leading to reduced root elongation, necrosis, and altered root architecture, which collectively diminish the plant's capacity for water and nutrient uptake (Mustafa et al., 2023). Additionally, nickel competes with essential nutrients such as calcium (Ca), zinc (Zn), magnesium (Mg), and iron (Fe) for uptake sites, leading to deficiencies of these nutrients and disrupting ion balance. Nickel also affects membrane permeability and the function of transport proteins like H^+-ATPases, which are crucial for nutrient transport, thereby reducing the uptake of potassium (K), nitrate (NO_3^-), and phosphate (PO_4^{3-}) (Brown et al., 1987; Chen et al., 2009; Deng et al., 2018; Mustafa et al., 2023). Nickel disrupts physiological processes in plants by interacting with functional groups within proteins, leading to alterations in protein conformation and functionality. Plant enzymatic activities have been disrupted by nickel (Fabiano et al., 2015). Moreover, in response to oxidative stress, plants activate their defensive mechanisms, increasing the activity of antioxidant enzymes such as glutathione reductase (GR), peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), and ascorbate oxidase (AO) (Hasanuzzaman et al., 2020). The main cause of reduced cellular metabolism is the suppression of enzyme activities caused by metal ions (Seregin and Kozhevnikova, 2006). Nickel is thought to alter the various gas exchange (transpiration, stomatal openings) and photosynthetic processes. The extent of photosynthesis reduction has been associated with changes in chloroplast structure, disruption of the electron transport chain (ETC), limited CO_2 availability due to closed stomata, impairment in chlorophyll synthesis, and inhibition of key enzymatic processes in the Calvin cycle. These enzymes include Rubisco, 3-phosphoglycerate kinase, fructose-1,6-bisphosphatase, and aldolase, along with NAD- and NADP-dependent phospho-glyceraldehyde dehydrogenases (Seregin and Ivanov, 2001). Numerous studies have highlighted the impact of nickel toxicity, which predominantly leads to the inhibition of plant growth, suppression of root activity, and hindered seed germination. For instance, in the case of pigeon pea, exposure to a 1.5 mM nickel solution significantly hinders the process of seed germination (Rao and Sresty, 2000). Furthermore, shoot growth was influenced by a solution containing 0.2 mM of nickel. For *Nicotiana tabacum*, the roots exhibited a dark brown discoloration following a 7–10 day exposure to a solution containing 0.43 mM of nickel (Boominathan et al., 2004). The accumulated nickel affected plant biomass, leading to decreased leaf area (Ahmad and Ashraf, 2011). Nickel's toxicity reduced plant yield and reproductive capacity, mainly by physiological disruption and competing against the essential nutrients that are usually in limited supply (Ahmad et al., 2007).

6. Remediation Approaches for Nickel

Harnessing effective remediation strategies is essential to protect the environment for future generations (Clemens and Ma, 2016; Glick, 2010). Various biological and physicochemical approaches are employed to remediate and sequester heavy metals and metalloids. However, the intricate technical requirements and associated costs make the process of remediation a formidable task (Ahemad, 2019; Ahemad and Kibret, 2014; Ali et al., 2013; Sheoran et al., 2010). Although physicochemical methods like thermal treatment, landfilling, excavation, electro-reclamation, and leaching can deliver quick remedies, their efficacies are often limited,and incurring higher operational cost. Furthermore, these methods can lead to secondary pollution and have the potential to disrupt both the physicochemical and biological traits of the soil (Ali et al., 2013). Hence, these physicochemical approaches are not recommended for the secure extraction and sequestration of heavy metals (Lambert et al., 2000).

Biological remediation involves employing plants and/or microorganisms to eliminate harmful pollutants from the environment (Doty, 2008; Glick, 2010; Singh et al., 2009). This method is considered the most secure and operationally efficient approach for eliminating problematic metals. This strategy presents an environmentally friendly, economically viable, and naturally supported process with widespread public approval and attention (Doble and Kumar, 2005). Biological remediation technology includes a range of methods such as bioremediation, bioleaching, bioventing, bioreactors, land forming, bio-augmentation, composting, and bio-stimulation. Among these techniques, bioremediation has been widely used as the most efficient and cost-effective approach. It relies on solar energy and maintains the inherent characteristics of the soil (Beškoski et al., 2011; Boopathy, 2000; Vidali, 2001).

Bioremediation stands as an inventive and cost-efficient strategy to eliminate heavy metals and metalloids from soil-water ecosystems through living organisms. This approach can be categorized into two main branches: phytoremediation, which involves plant-based bioremediation, and microbial bioremediation, which centers on the use of microorganisms (Guo et al., 2010). The synergistic utilization of both plants and microbes has significantly amplified the effectiveness of bioremediation (Hadi and Bano, 2010). The interactions observed between hyper-accumulating plants and metal-tolerant microbes have shown remarkable usefulness. A plethora of recent studies have highlighted the genetic capacity of both microbes and plants to gather and detoxify metals from polluted environments (Lyyra et al., 2007; Memon and Schröder, 2009; Pilon-Smits and LeDuc, 2009).

6.1. Phytoremediation - Green Technology

The term "phytoremediation" was initially used in the 1980s to describe the process of using various plant species for remediating contaminated sites. The term originates from the Ancient Greek word "phyto," which means plant, and the Latin word "remedium," which conveys the idea of restoring balance (Willey, 2008). Referred to as a green technology, this method serves as an environmentally friendly solution for the removal, degradation, or decontamination of toxic metals/metalloids, extremely volatile organic or inorganic foreign substances, and a multitude of other carcinogenic pollutants from the ecosystems (Kumar Yadav et al., 2018). Plant species are closely associated with soil microbes such as bacteria, arbuscular mycorrhizal fungi (AMF), protozoa, and algae; the effectiveness of the plant-microbe symbiosis generally vary along with soil properties and agronomic practices. These components collectively contribute to fostering the detoxification or sequestration of toxic pollutants by restoring plant growth under these unfavourable conditions (Vara Prasad and de de de Oliveira Freitas, 2003).

In plants, various mechanisms are involved in the uptake of contaminants and these are based on their distinct characteristics. Plants possess the capability to transform or degrade both organic and inorganic complex pollutants into less bioavailable forms within the rhizosphere, aided by rhizobacteria. This phenomenon is referred to as phytostimulation. Additionally, plants can directly facilitate the breakdown of organic toxic metals through their intrinsic enzymatic processes, which is known as phytodegradation. Certain plant species have potential to accumulate metal complexes within their tissues, eventually releasing these pollutants in volatile form, a process termed phytovolatilization (McCutcheon and Schnoor, 2003). In modern era, microbe-assisted phytoremediation has been widely used in fields because combination of plants and microbes incredibly enhances phytoremediation (Maurya et al., 2023).

6.1.1. Nickel Hyperaccumulating Plants

Certain plant species have the potential to accumulate metals within their shoot and root tissues, measured on a dry weight basis (Maestri et al., 2010; Van der Ent et al., 2013). Hyperaccumulators or metallophyte plants that have potential to uptake as much as 1000 ppm (0.1 %) for metals like nickel, lead, chromium, cobalt, and copper, and 10,000 ppm (1 %) for zinc and manganese, based on the dry weight of their shoots, when cultivated in metalliferous soil (Özyiğit and Doğan, 2014). Nickel is the most accumulated metal in a variety of hyper-accumulator plants. Approximately, over 350 taxa of nickel hyper-accumulators are reported (Van der Ent et al., 2013), while about 25 % of reported nickelophilous plants belong to Brassicaceae family (Prasad, 2005), specifically, genus *Alyssum* has a comprehensive diversity of nickelophilous plants (Rascio and Navari-Izzo, 2011) which can accumulate about 1000–38,000 ppm on a dry leaf matter basis (Reeves et al., 1999). Some well-known nickel hyper-accumulators are highlighted in Table 1. These hyper-accumulator plants offer an effective botanical resource to understand plant adaptative mechanisms to serpentine soils; these interesting genetictraits of certain species can be harnessed for bioremediation.

6.1.2. Nickel uptake Mechanisms in Plants

Similar to other living organisms, plants possess complex homeostasis mechanisms that maintain optimal concentrations of nickel ions within various cellular compartments. These mechanisms regulate the uptake, accumulation, trafficking, and detoxification of metal ions while simultaneously mitigating the adverse impacts stemming from exposure to non-essential metal ions (Clemens, 2001; Li and Zamble, 2009). Basic metal resistance mechanisms are ubiquitous in plants but metal hyper-accumulation is a complex and sporadic phenomenon. It is biggest task for scientists to understand nickel uptake and accumulation mechanisms from soil to translocate in shoot tissues, separation, and distribution in cellular compartments (Everhart et al., 2006). Several transporter proteins take participation in nickel uptake, transportation, and homeostasis mechanisms, including 1) cell membrane transporter proteins 2) vacuole membrane (tonoplast) transporters 3) vacuolar sequestration, and 4) endomembrane transporters (Maestri et al., 2010). Metal transporter proteins include 1) influx transporter protein families which comprise Zinc-Iron Permease (ZIP), Natural Resistance-Association Macrophage Protein (NRAMP), and Yellow-Stripe 1-like (YSL); 2) efflux transporter families such as Heavy Metal ATPase (HMA), Cation Diffusion Facilitator (CDF), Cation exchanger proteins (CAX) and ATP-binding cassette (ABC) transporters (Hall and Williams, 2003).

6.1.2.1. Nickel Uptake through the Roots. Plants can uptake nickel in the Ni^{2+} form by passive and active processes (Tack, 2010). Nickel is also highly reactive with organic acids and other dissolved organic substances that accelerate nickel desorption and dissolution in soils. Its availability in soil is potentially influenced by many factors, including soil redox potential, organic matter content, temperature, and pH (Fageria et al., 2002). Soil pH is a key factor and directly correlates with nickel uptake via roots such as nickel uptake capacity decreases as pH rises from 4.5 to 6.5 (Kabata-Pendias, 2000).

A large population of metal-resistance microorganisms present in the rhizosphere of hyperaccumulators has the potential to enhance the nickel uptake and increase plant biomass by adjusting the soil pH, producing organic substances such as metal-chelating agents, organic acids, and enzymes, protecting the plants against fungus and other microbes (Wenzel et al., 2003; Xiong et al., 2008). Plants also secrete certain chemicals, which are involved in the mobilization of nickel from soil to roots; including organic acids (malonic acid and oxalic acid), reductase enzymes, and metal chelating complexes akin to phytosiderophores (He et al., 2012). It was reported that by introducing *Microbacterium arabinogalactanolyticum* AY50922 to the soil, approximately 2.2–2.6 mg kg^{-1} of nickel was extracted (Abou-Shanab et al., 2003). Another study discovered that *Synechrobacter* sp. SRA1 and *Bacillus cereus* SRA10 have the potential to promote beneficial plant growth-promoting bacteria (PGPB), leading to a significant enhancement in nickel accumulation in the root and shoot tissues of *Brassica juncea* when compared to control plants (Ma et al., 2011). Several studies showed that Plant Growth Promoting Rhizobacteria (PGPR) have potential to enhance the Ni availability to *Alyssum murale* by releasing non-soluble nickel in the soil. These bacteria produced indole-3-acetic acid (IAA), and siderophore compounds, and enhanced the phosphate solubilization which converts non-soluble Ni to a soluble form. Similarly, certain PGPB strains can protect plants from Ni toxicity, and promote root elongation and plant biomass by producing siderophores and 1-amino-cyclopropane-1-carboxylate (ACC) deaminase enzyme, which has the potential to suppress ethylene (plant hormone) production by hydrolysis of ethylene precursor ACC (Abou-Shanab et al., 2003; Idris et al., 2006).

In the roots, cell membrane acts as a barrier for nickel ions movement into cytosol via a variety of channels and transport proteins (Kabała et al., 2008). The hydrogen ion (proton) ATPase (H^{+}-ATPase) is a membrane-bound enzyme involved in the uptake of nutrients via roots, expressed in the xylem, and transport of solutes in the phloem through generating a proton electrochemical gradient (Palmgren, 2001). Transportation of Ni into the xylem occurs by utilizing membrane channels and gradient pumps (Sheoran et al., 2010). The studies revealed that H^{+}-ATPase enzyme activity accelerates or decelerates in roots significantly depending on the availability of metal concentration. For example, when Cucumis sativus seedlings treated with different heavy metals (Cu, Cd, and Ni) in different concentrations induced inhibitory effects on transporting and hydrolysis activities of H^{+}-ATPase in plasma membrane (PM) (Janicka-Russak et al., 2008). Water soluble Ni can penetrate root symplast through the PM of endodermal root cells or it may penetrate to root apoplast via plasmodesmata. Mostly, symplast influx parameters have great importance in the uptake kinetics of trace elements due to the inability of the apoplastic metal ions to cross root casparian band (apoplastic barrier) and their translocation to shoots (Mukhopadhyay and Maiti, 2010; Peer et al., 2006).

6.1.2.2. Root to Shoot Nickel Translocation. In non-hyperaccumulator plants, Ni is absorbed from the soil and subsequently retained into the root cells. Plant employs detoxification mechanisms such as forming chelates in the cytoplasm or sequestering the Ni into vacuoles, as shown in Fig. 2. In paradox, hyperaccumulators possess the ability to absorb nickel from the roots' symplast into the xylem apoplast, and they efficiently transport nickel ions from the xylem to the shoots through transpiration-driven pumps (Maestri et al., 2010; Marschner, 2011). At molecular level, the mechanism and genetics basis of metal translocation into shoots is still unclear. However, in hyperaccumulators, a

Table 1
Nickel uptake and accumulation capacity in some nikelophilous plants.

Plant scientific name	Type of phytoremediation	Uptake capacity (mg kg^{-1})	Accumulation (dry weight)	References
Alyssum argenteum	Phytoextraction	29,400	Leaves	(Mengoni et al., 2003)
Berkheya coddii	Phytoextraction	1700	The upper epidermis of leaves	(Robinson et al., 2003)
Leptoplaxemarginata	Phytoextraction	34,400	Leaves	(Chardot et al., 2005)
Alyssum inflatum	Phytoextraction	3700	Leaves	(Ghaderian et al., 2007)
Alyssum heldreichii	Phytoextraction	1180	Leaves	(Bani et al., 2010)
Pelargonium roseum	Phytoextraction	20,055	Leaves	(Mahdieh et al., 2013)
Alyssoides utriculata L.	Phytoextraction	1065	Leaves and roots	(Roccotiello et al., 2015)
Alyssum serpyllifolium	Phytoextraction	7000	Leaves	(Morais et al., 2015)
Alyssum obovatum	Bioaccumulation	6008	Leaves	(Teptina and Paukov, 2015)
Alyssum tortuosum Willd.	Bioaccumulation	1789	Leaves	(Teptina and Paukov, 2015)
Alyssum murale	Phytoextraction	3600	Stem and leaves	(Broadhurst and Chaney, 2016)
Isatis cappadocica	Phytoextraction	5587	Shoots and leaves	(Çelik et al., 2018)
Hybanthus austrocaledonicus	Phytoextraction	3430–58 500	Leaves	(Paul et al., 2020)
Thlaspi caerulescens	Phytoextraction	5000	Leaves	(Fasani et al., 2023)
Odontarrhena bertolonii	Phytoextraction	3000	Leaves	(Colzi et al., 2023)
Thlaspi triangulare	Rhizofiltration	17000	Roots	(Fasani et al., 2023)

variety of plant metal transporter families, phytochelators/chaperons, and organic acids have been well documented. Such as nickel uptake and transport increased by chelation with citric acid in *Stackhousia tryoni*, *Datura innoxia*, *S. acuminate*, and *Alyssum bertolonii* (Bidwell et al., 2004; Callahan et al., 2008). Organic acids with free amino acids such as nicotinamine and histamine play a key role in metal accumulation because bivalent cations of organic acids and free amino acids form stable ligands which involved in Ni accumulation in plant tissues (Callahan et al., 2008).

Alyssum lesbiacum, characterized as a nickel hyperaccumulator, demonstrates a correlation with elevated tolerance to metals and enhanced translocation of metals into its shoots, which is closely linked to the presence of free histamine amino acids. In *Alyssum montanum* (non-hyperaccumulator), the transportation of histamine-chelated Ni into the xylem was 50 times faster (Krämer et al., 1996). Another chemical called nicotinamide (NA) is associated with iron homeostasis and tolerance to Zn and Ni. Studies have identified a positive correlation between Ni hyperaccumulation in *T. caerulescens* with enhanced nicotinamide synthesis and NA-metal chelation (Vacchina et al., 2003). Following which, an important role was later observed for NA in Ni translocation (Callahan et al., 2008).

6.1.2.3. Distribution/Detoxification/Sequestration of Nickel. Several research studies have revealed a greater accumulation of Ni in the aerial parts of plants compared to their underground components (Bani et al., 2007; Broadhurst et al., 2004). Higher concentration of nickel is accumulated in the leaves compared to the stems within the aerial portions (Deng et al., 2016; Gramlich et al., 2011). Furthermore, the age of the plant could also influence the extent of nickel (Ni) accumulation (Bani et al., 2007; Chaney et al., 2007). Hyperaccumulators are generally much more efficient in detoxification and sequestration (Rascio and Navari-Izzo, 2011). In these plants, heavy metal detoxification occurs via compartmentalization, chelation, and sequestration of the metals by forming ligands, where the metal-ligand complex is transported to vacuoles and cell walls (metabolically inactive sub-cellular compartments). In shoots, the sequestered metal is stored in apoplast or in different types of cells/tissues which include trichomes, mesophyll cells, epidermal cells, and cuticles (Bidwell et al., 2004; Freeman et al., 2004; Robinson et al., 2003). In epidermal cells, metal localization has been considered an important mechanism for Ni accumulation and tolerance (Kachenko et al., 2008). Following the complex formation, Ni is selectively sequestered within the vacuoles of epidermal tissues (Sharma et al., 2016). Furthermore, it has accumulated within the vacuoles of epidermal tissues in stems and leaves, as well as in trichomes (Broadhurst et al., 2004; Everhart et al., 2006). In Ni and Zn/Cd hyperaccumulating plants, cell walls may also play an important role in metal detoxification and it has been reported that about 60–70 % of accumulated Ni is distributed in the apoplast (Kramer et al., 2000).

Metal homeostasis and heavy metals detoxification in plants ultimately depend on the vacuolar sequestration (Martinoia et al., 2007). Vacuoles are supposed to be the principal storage site for metals and phytochelatin (PC)-metal complexes (Salt et al., 1995). When Ni compartmentation is compared between non-accumulating and hyperaccumulating plant species, it has been evident that the primary biochemical detoxification mechanism involves the Ni storage within the vacuoles of leaf cells (Kramer et al., 2000). The compartmentalization of metals in vacuoles is a very effective mechanism for metal dispersal and concentration within cell (Wu et al., 2010). In the tonoplasts, the active transport systems are involved in the sequestration of metal ions inside the vacuole. The process of sequestration is energized directly by ATP hydrolysis (Kramer et al., 2000; Martinoia et al., 2007). Tonoplast antiporters (CDF, CAX, and magnesium exchangers) and efflux transporters are involved in the distribution of metals in the vacuoles (Kobae et al., 2004; Persans et al., 2001). MTP1 tonoplast protein over-expression is linked with tolerance against Co, Cd, and Ni (Persans et al., 2001). Similarly, Ni^{2+}/H^{+}antiport system has been identified in tonoplast of *A. lesbiacum* (Ingle et al., 2008). Proton pumps including V-ATPase and V-PPase are known to facilitate important processes supporting the metal tolerance mechanisms; these molecular pumps produce electrochemical gradient potentials across the tonoplast

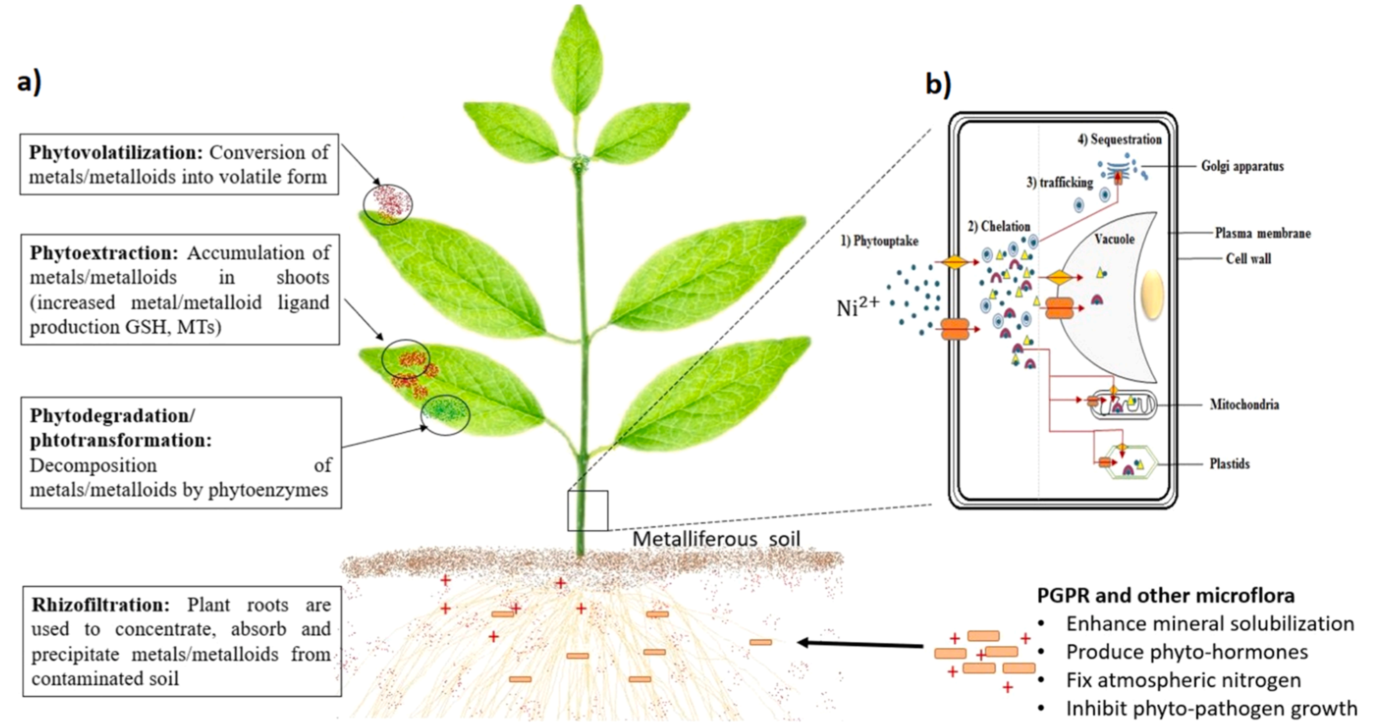


Fig. 2. Phytoremediation techniques and mechanisms. **a)** phytoremediation techniques, **b)** metal homeostasis mechanisms *in planta.* Nickel (Ni) ions enter into the plant cell via transporters (located in the tonoplast) and are chelated with phytochelatins (PCs) and chaperones. These chelated complexes are involved in the trafficking of nickel to specific organelles via metal influx pumps, where the Ni detoxification or accumulation is accomplished via vacuolar sequestration.

and activate secondary transporters which act as H^+-coupled carriers, including metal efflux transporters within plant cells (Kabała and Janicka-Russak, 2011).

6.1.2.4. Role of Transporter Proteins and Phytochelators in Nickel Hyperaccumulators. The binding of metal ions by ligands (metal chelation) affects the accumulation, transportation, and detoxification of heavy metals (Wu et al., 2010). Cellular damage induced by heavy metals has significantly reduced due to the inert nature of chelated metal ions. Metal ions tend to produce chelation with different ligands like amino acids, nitrogen and oxygen donor ligands, peptides, organic acids, metallothioneins (MTs), phytochelators (PCs), and other high molecular weight molecules (proteins, chaperones) (Clemens, 2001). Various types of metallochelators have been identified in plants, including phytochelatin, metallothioneins, amino acids, and organic acids.

Citrate is the major ligand for facilitating Ni entrapment in leaves of *T. goesingense* and *H. floribundus* (Kramer et al., 2000). Similarly, Ni-malate is associated with Ni accumulation in Ni hyperaccumulating *Phyllanthus serpentinus* and *P. douarrei* species (Deng et al., 2018). In *S. acuminata* latex, about 37–99 % of Ni form chelates with citric acid (Schaumlöffel et al., 2003). Another study has suggested that Ni becomes concentrated in the dermal leaf and stem tissues of *A. murale*, and majorly bound with malate and other low molecular weight organic acids (LMWOA) (McNear Jr et al., 2010). In plant sap and vascular tissues, nickel also binds with histidine, malate, and other low molecular weight compounds. Thus, Ni can be transported from roots to shoots (by forming a complex with His) and stored within the foliar dermal tissues (where Ni is complexed with malate and other low molecular weight organic acids or counter-ions)(McNear et al., 2010). The metal tolerance mechanisms have also been associated with the presence of cysteine-rich peptide ligands, specifically metallothioneins (MTs) and phytochelatins (PCs) (Schat et al., 2002). For sequestration, Ni (II) binds with organic sulfur (R-SH) which acts as a functional group of the cysteine residues (Eapen and D'souza, 2005). These MT-metal complexes may be transported into vacuoles for long-term sequestration as they can produce glutathione (GSH) (Eapen and D'souza, 2005). When plants are exposed to heavy metal ions, phytochelatins become activated which further bind with metals and promote metal storage in the vacuole (Rauser, 1995; Yang et al., 2001).

Specific nickel (Ni) transporters have not yet been identified in plants (Rascio and Navari-Izzo, 2011). However, a study has revealed that certain zinc/nickel (Zn/Ni) hyperaccumulating plants exhibit a preference for zinc (Zn) absorption over nickel (Ni). This observation suggested a shared transport system for the entry of zinc and nickel into the roots of these plants (Assunção et al., 2008). Moreover, various transporter proteins, including ZIP/NRAMP, are implicated in facilitating the translocation of metals into the shoots. However, for nickel (Ni) transportation, only the TjNRAMP4 transporter protein has been identified and reported in *Thlaspi japonicum* (Mizuno et al., 2005). Similarly, in *T. caerulescens*, TcYSL3 was also involved in translocation of Ni chelated complex via vascular loading and symplast (Gendre et al., 2007). At protein level, HMAs (heavy metal association domain) are involved in metal ions homeostasis and tolerance (Axelsen and Palmgren, 2001; Sun et al., 2014).

6.2. Microbes assisted remediation of Nickel

Before exploring microbe-assisted phytoremediation, it is crucial to recognize other methods used to enhance phytoremediation efficacy. Researchers have extensively employed various organic and inorganic compounds, including chelating agents, fertilizers, and soil amendments, aiming to augment the capability of plants in metal uptake and remediation (Abbott et al., 2018; Chen et al., 2020; Gul et al., 2020; Sani et al., 2023; Tang et al., 2015; Wei et al., 2024; Wong et al., 2020; Yin et al., 2024). While these additives can indeed enhance metal solubility and availability for plant uptake, they often come with drawbacks such as potential ecological impacts, high costs, and dependency on external inputs. In contrast, microbial assistance presents a compelling alternative. Microbes leverage natural biological processes to not only facilitate metal uptake and promote plant growth but also offer a sustainable and eco-friendly solution. By harnessing the inherent abilities of microorganisms, we can minimize reliance on external inputs and mitigate environmental risks associated with chemical additives. This inherent eco-friendliness and self-sustainability position microbe-assisted phytoremediation as a preferred choice for long-term environmental management and sustainable agriculture practices.

Soil is a complex mixture of minerals, organic substances, and has diverse microbial biomass. Within the soil ecosystem, a variety of microbial genera coexist, contributing to the enhancement of plant growth, refinement of soil structure, and increased crop efficacy through the cycling of nutrients (Abbott et al., 2018; Ahemad, 2019; Ahemad and Kibret, 2014; Marschner, 2011). These microbes also generate various plant growth regulators, provide protection against opportunistic pathogens, and thereby reduce the incidence of different plant diseases. Additionally, microorganisms are actively involved in the remediation of various xenobiotic compounds and heavy metals (Glick, 2010). Moreover, these organisms have evolved different detoxifying mechanisms, including biomineralization, bioaccumulation, biosorption, and biotransformation (Gadd, 2000). Some bacterial strains have abilities to detoxify noxious compounds. For instance, *Xanthomonas maltophyla*, *Escherichia coli,* and *Pseudomonas putida* have been identified to catalyze the precipitation or reduction of highly mobile and relatively less hazardous compounds (Mitch, 2002). Most of the bacterial strains have multiple metal-resistance systems for their survival in extreme environments. A research study has demonstrated that all the rhizobacterial strains exhibit tolerance to numerous metal ions (Abou-Shanab et al., 2003). Similar studies were previously undertaken by other researchers, yielding consistent outcomes (Sabry et al., 1997). Moreover, various anaerobic microorganisms possess the capacity to independently detoxify several metal ions from the environment through their reduction to a lower redox state (Gadd, 2004).

Microorganisms are also involved in metal immobilization in different ways such as the accumulation of metal ions in their biomass or cell walls through intracellular sequestration or adsorption or precipitation (Fein et al., 2001; Leyval and Joner, 2001). Reportedly, when *Bacillus subtilis* and *Brassica juncea* were co-inoculated, it was noted that *Bacillus subtilis* offered protection to *Brassica juncea* against Ni toxicity. This safeguarding effect was attributed to the significant Ni accumulation capability of *Bacillus subtilis* (Zaidi et al., 2006). Ni resistance mechanisms in microorganisms were documented earlier, of which certain mechanisms could be exploited for the remediation of sites contaminated with selected hazardous metals. The screening of Ni-resistant microbes with the ability to immobilize Ni from polluted sites could have a substantial effect on environmental management (Puglisi et al., 2012). Furthermore, bacterial inoculants possessing metal immobilization capabilities along with plant growth-promoting (PGP) characteristics have introduced additional eco-friendly approaches for sustainable agriculture (Denton, 2007; Rajkumar and Freitas, 2008).

At genetic level, the *anik* locus is well characterized and recognized in *E. coli*, which transcribes 5 proteins, including NikA, B, C, D, and E, that have been found closed resemblance with periplasmic binding protein-dependent transport systems of gram-negative and positive species. The Nik operon has ATP-dependent ABC cassette proteins (Higgins, 2001). Sequence homology and phylogeny analysis identified a close relationship of Nik proteins with oligopeptide transporters (Dassa and Bouige, 2001). NikR is a unique class of nickel-binding regulatory proteins that control the Nik operon and are characterized as a nickel sensor. The Nik locus genes are suppressed under nickel availability. The NikR protein is encoded in the presence of nickel and transcribes DNA-binding proteins that inhibit the expression of Nik genes. Regulation of nikR expression also involves two promoters. The first promoter is positioned upstream of the nikA gene, which serves as a Ni-binding site and governs the expression of genes that regulate microbial respiration and transition from aerobic to anaerobic phase. The second promotor is present at 51 base pairs upstream of the start site of nikR and partially auto-regulates the nikR expression. The expression of Nik locus is strictly regulated by global regulatory protein FNR (fumarate nitrate regulatory protein) under an anaerobic environment (Eitinger and Mandrand-Berthelot, 2000). Tetrameric NikR protein has four high affinity binding sites for nickel with additional lower affinity potassium binding sites. The NikR protein serves several regulatory functions in different microorganisms. For example, two transporters NmtR and KmtR belonged to the ArsR-SmtB metal-sensor transcriptional repressor family, and have been reported to regulate nickel and cobalt ions in *Mycobacterium tuberculosis* (Campbell et al., 2007; Cavet et al., 2002). However, certain bacterial species possess transporters specific to both nickel (Ni) and cobalt (Co). Apart from the nikABCDE system, additional nickel transporter proteins have also been identified in *Escherichia coli* (Navarro et al., 1993), these transport proteins belong to the NiCoT family that are conserved in eubacteria, archaea, and fungi, and some ABC transporters (Mulrooney and Hausinger, 2003; Rodionov et al., 2006). Interestingly, interruption of nickel uptake activity fails to completely block nickel accumulation and nickel-dependent enzyme activity. This indicates the presence of redundant nickel influx systems (Li and Zamble, 2009). The availability of complete genome sequences and advancements in omics techniques may facilitate the search for novel players in nickel-related processes in these microbes. Different types of bacteria have been discussed in context of their nickel homeostasis properties and potentials.

Microbe-assisted phytoremediation is a desirable, eco-friendly, and cost-effective approach to remediate heavy metal polluted soil-water ecosystems using plants and microbes. In soil, there is a huge variety of microbes, beneficial for plant growth and biomass including bacteria, fungi, algae, protozoa, and cyanobacteria. According to various soil microbiota, microbe-assisted phytoremediation is further subdivided into bacterial-assisted phytoremediation cyanoremediation, mycorrhizal-assisted remediation, and rhizoremediation.

6.2.1. *Mechanisms involved in the microbe-assisted phytoremediation of Nickel*

Microbe-assisted phytoremediation of nickel involves a complex interplay of biochemical and physiological mechanisms that enhance the bioavailability, uptake, and detoxification of nickel (Ni) in plants. These processes are facilitated by specific microbial activities in the rhizosphere and within plant tissues, ensuring effective remediation of nickel-contaminated environments (Ma et al., 2016; Mani and Kumar, 2014).

One of the key mechanisms is the microbial solubilization and mobilization of nickel in the rhizosphere. Certain bacteria, such as *Pseudomonas fluorescens* and *Bacillus subtilis*, secrete organic acids like citric acid, oxalic acid, and malic acid that chelate nickel ions, increasing their solubility and bioavailability for plant uptake (Becerra-Castro et al., 2011). For instance, in experiments involving *Brassica juncea*, the inoculation with *Bacillus subtilis* significantly enhanced nickel uptake due to increased solubilization in the rhizosphere (Zaidi et al., 2006). Similarly, siderophore-producing microbes, such as *Microbacterium liquefaciens*, mobilize nickel by altering soil chemistry and reducing nickel binding to organic matter or mineral surfaces (Abou-Shanab et al., 2003).

Microbes produce enzymes, such as phytases and reductases, which release nickel bound to soil particles and organic matter (Daunoras et al., 2024). Additionally, extracellular polymeric substances (EPS) produced by microbes stabilize nickel ions, preventing their leaching and maintaining their availability in the root zone (Li et al., 2024). Microbial metabolites, such as siderophores and chelators, also form stable complexes with nickel, facilitating its transport into plant root systems. In a study involving *Alyssum murale*, inoculation with *Microbacterium arabinogalactanolyticum* increased nickel uptake from 8500 mg kg^{-1} to 11,500 mg kg^{-1}, demonstrating the role of microbial chelation in enhancing phytoextraction (Abou-Shanab et al., 2003).

Plant growth-promoting microbes (PGPMs) like *Pseudomonas putida* and *Azospirillum brasilense* enhance root growth and development by producing phytohormones such as auxins, cytokinins, and gibberellins (Ahemad and Kibret, 2014; Ansari et al., 2023; Rothballer et al., 2003; Wong et al., 2020). These hormones stimulate root elongation and branching, thereby increasing the surface area available for metal uptake. For example, *Pseudomonas sp.* significantly enhanced root biomass and nickel uptake in *Alyssum murale*, a known hyperaccumulator plant (Ma et al., 2011). Furthermore, microbes producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase alleviate ethylene stress in plants exposed to nickel toxicity, promoting healthier root systems (Gupta and Pandey, 2019).

Microbes contribute to the detoxification of nickel within plant tissues through processes such as compartmentalization and biotransformation (Li et al., 2024; Mustafa et al., 2023). For example, nickel ions are sequestered in vacuoles by forming complexes with phytochelatins (PCs) or metallothioneins (MTs), reducing their toxicity to plant cellular processes (Faizan et al., 2024). Certain microbes, such as *Psychrobacter sp.* and *Bacillus cereus*, have demonstrated the ability to convert toxic nickel forms into less harmful compounds, such as nickel sulfides, through biomineralization processes (Ma et al., 2009). In *Brassica juncea*, *Bacillus subtilis* SJ-101 not only facilitated nickel accumulation in shoots and roots but also protected the plants from nickel toxicity by promoting better biomass production and stress resilience (Zaidi et al., 2006).

Microbial activities significantly influence the physicochemical properties of soil, such as pH, redox potential, and organic matter composition, all of which directly affect nickel mobility and bioavailability. Microbes that produce organic acids, including citric acid, oxalic acid, and lactic acid, can lower the soil pH, thereby enhancing nickel solubility (Wei et al., 2024). This increased solubility allows for more efficient uptake of nickel by plant roots. For instance, studies have shown that inoculation with *Pseudomonas putida* can result in significant reductions in soil pH, facilitating the mobilization of nickel ions from less bioavailable forms (Becerra-Castro et al., 2011). Additionally, certain microbes influence the soil's redox potential by releasing reductive metabolites or altering oxygen availability (Rinklebe and Shaheen, 2017). This shift in redox conditions can convert nickel into forms that are either more soluble for plant uptake or less mobile, depending on environmental needs. For example, microbes such as *Geobacter* species can reduce nickel ions under anaerobic conditions, leading to the precipitation of nickel sulfides, which are less bioavailable and less toxic (Sitte et al., 2013). Microbes also promote nickel stabilization by facilitating its adsorption onto soil particles or through the formation of insoluble compounds. Some species produce extracellular polymeric substances (EPS), which create a sticky matrix that binds nickel ions to soil particles, preventing leaching into groundwater. Similarly, precipitation of nickel as hydroxides, phosphates, or sulfides by microbial metabolic activities significantly reduces environmental risks associated with nickel contamination (Gao et al., 2023). Furthermore, microbial contributions to soil organic matter decomposition enhance the availability of chelating agents, such as humic substances, which can bind nickel and modulate its mobility (Li et al., 2022). These interactions not only stabilize nickel in the soil matrix but also create a more favorable environment for plant-microbe interactions. For instance, it was reported that *Bacillus subtilis* released metabolites that facilitate both nickel adsorption and bioavailability; providing a balance between stabilization and uptake for phytoremediation (Zaidi et al., 2006).

Microbe-assisted phytoremediation of nickel involves a complex interplay of various mechanisms that enhance the efficiency of remediation processes. Chlorophyll fluorescence is a powerful tool used to assess the health and efficiency of the photosynthetic apparatus in plants

(Ma et al., 2021a; Ma et al., 2021b; Qin et al., 2023). Key chlorophyll fluorescence attributes include Fv/Fm (maximum quantum efficiency of PSII), ΦPSII (effective quantum yield of PSII), qP (photochemical quenching), qN (non-photochemical quenching), NPQ (non--photochemical quenching), Fo (minimal fluorescence), and Fm (maximum fluorescence) (Nabi et al., 2020). Beneficial microbes can mitigate nickel-induced stress, maintaining higher Fv/Fm values by protecting the photosynthetic machinery and ensuring better energy conversion efficiency in PSII. Microbial inoculants can enhance the effective quantum yield of PSII (ΦPSII) by promoting better nickel uptake and detoxification, ensuring more efficient use of absorbed light for photochemistry. By improving root health and nutrient uptake, microbes can maintain higher qP values under nickel stress, indicating more open PSII reaction centers available for photochemistry (Elbagory et al., 2022). Additionally, microbes can help plants better manage excess light energy, reducing photodamage through regulated non-photochemical quenching mechanisms, reflected in stable qN and NPQ values. Inoculated plants often exhibit lower Fo values under stress conditions, indicating less damage to the PSII reaction centers and better overall health of the photosynthetic apparatus. Moreover, microbes can help in maintaining higher Fm levels by protecting PSII from nickel toxicity, ensuring efficient energy capture and transfer processes (Marchetto et al., 2024). Nickel hyperaccumulating plants treated with nickel-resistant *Psychrobacter sp.* exhibited improved chlorophyll content, protein synthesis, and biomass accumulation under nickel-contaminated conditions (Ma et al., 2010).

Microbes achieve these beneficial effects through various mechanisms, such as enhancing nutrient availability, producing growth-promoting substances, and modulating stress-responsive pathways. These interactions not only improve plant growth and nickel uptake but also safeguard the photosynthetic competence of plants, as evidenced by stable and improved chlorophyll fluorescence attributes.

Overall, the synergistic interactions between microbes and plants play a crucial role in enhancing the effectiveness and sustainability of nickel phytoremediation processes. Understanding these mechanisms is essential for the development of effective microbial inoculants and the design of optimized phytoremediation strategies for nickel-contaminated environments.

Table 2
Examples of PGPB-plant interaction in nickel phytoremediation.

PGPB(s)	Test Plant(s)	Change in Ni Concentration Due to Inoculation	Effects on Plant(s)	References
Microbacterium arabinogalactanolyticum *Sphingomonas macrogoltabidu* *Microbacterium liquefaciens*	*Alyssum murale*	~8500 mg kg^{-1} → ~11,500 mg kg^{-1}	Significantly increased Ni uptake in shoots	(Abou-Shanab et al., 2003)
Bacillus subtilis SJ−101	*Brassica juncea*	415 mg kg^{-1} (stem) → 736 mg kg^{-1} (stem) 290 mg kg^{-1} (roots) → 460 mg kg^{-1} (roots) 237 mg kg^{-1} (leaves) → 272 mg kg^{-1} (leaves)	Facilitated Ni accumulation; protected plants from Ni toxicity	(Zaidi et al., 2006)
Pseudomonas sp. 29 C, Bacillus megaterium 4 C	*Brassica juncea*	~140 mg kg^{-1} (roots) → ~175 mg kg^{-1} (roots) ~32 mg kg^{-1} (shoots) → ~38 mg kg^{-1} (shoots)	Enhanced shoots and root system, decreased Ni accumulation in plants	(Rajkumar et al., 2009)
Psychrobacter sp. SRA2 Psychrobacter sp. SRA1, *Bacillus cereus SRA10*	*Brassica juncea*	350 mg kg^{-1} → 520 mg kg^{-1} (SRA1) 350 mg kg^{-1} → 580 mg kg^{-1} (SRA10)	Enhanced biomass and Ni accumulation in plant tissues	(Ma et al., 2009)
Pseudomonas sp.	*Cicer arietinum*	~0.25 mg^{g-1} → ~0.39 mg^{g-1}	Increased fresh and dry weight at 2 mM Ni concentration; protected plants against Ni toxicity	(Tank and Saraf, 2009)
Paenibacillus macerans NBRFT5, Bacillus endophyticus NBRFT4, B. pumilus NBRFT9	*Brassica juncea*	300 µg/plant → 950 µg/plant (combination of bacteria)	Facilitated Ni uptake	(Tiwari et al., 2012)
Pseudomonas sp. A3R3	*Alyssum serpyllifolium, Brassica juncea*	~85 mg kg^{-1} → ~115 mg kg^{-1}	In *B. juncea*, significantly enhanced biomass; In *A. serpyllifolium*, increased Ni content under Ni stress	(Ma et al., 2011)
Psychrobacter sp. SRS8	*Ricinus communis,* *Helianthus annuus*	~325 mg kg^{-1} → ~500 mg kg^{-1} Approx. 250 mg kg^{-1} → Approx. 400 mg kg^{-1}	Enhanced biomass, Ni accumulation, chlorophyll, and protein content	(Ma et al., 2010)
Bacillus megaterium SR28C	*Brassica juncea*	75 mg kg^{-1} (roots) → 90 mg kg^{-1} (SR12) 300 mg kg^{-1} (shoots) → 400 mg kg^{-1} (SR12)	Increased Ni accumulation by releasing Ni from non-soluble phases in the soil	(Rajkumar et al., 2013)
Bornmuellera tymphaea *Bornmuellera tymphaea*	*Noccaea tymphaea* *Alyssum murale*	320 mg kg^{-1} (roots) → 520 mg kg^{-1} (roots) 220 mg kg^{-1} (shoots) → 460 mg kg^{-1} (shoots)	39.9–79.6 % increase in Ni uptake after inoculation with PGPR	(A. Durand et al., 2016)
Klebsiella pneumoniae	*Juncus effusus*	69.5–11.5 mg kg^{-1} (Ni in root)	Promoted Ni transformation and exchangeable Ni content in the soil.	(Gao et al., 2022)
Morganella morganii Anthyllis vulneraria	*Arabidopsis thaliana*	0.01 mg kg^{-1} to 25 mg kg^{-1} in shoots	Improved nutrient availability and antioxidative enzyme activities	(Naqqash et al., 2024; Sujkowska-Rybkowska et al., 2022)
Pseudomonas fluorescens 20 *Pseudomonas fluorescens 21* *Pseudomonas putida 23*	*Triticum aestivum*	254 mg kg^{-1} (shoots) → 395 mg kg^{-1} (shoots)	Improved resistance to Ni toxicity, plant biomass and eliminated Ni phytotoxicity at full maturity.	(Shabayev and Ostroumov, 2023)
Agrococcus terreus	*Zea maize*	0.125 mg kg^{-1} to less than 0.01 mg kg^{-1}	Increased the plant growth, nutrient uptake, and defense system. Decreased Ni uptake	(Shahzad et al., 2023)

6.2.2. Bacterial Assisted Phytoremediation

Among various bioremediation approaches, bacterial-assisted phytoremediation has garnered significant public interest (Kumar et al., 2019). This method involves the utilization of beneficial bacteria that not only aid in remediation, but also promote plant growth and development. These bacteria are referred to as plant growth-promoting bacteria (PGPB). A few bacterial-assisted phytoremediation trials are mentioned in Table 2.

In the presence of elevated levels of heavy metals, certain plant species are able to adapt biological to the unfavourable growth environment and continue to grow (Chaudhry et al., 2005; M. Li et al., 2024; Y. Li et al., 2024; Li and Zamble, 2009). Moreover, the remediation of contaminated soils is further hindered by their nutrient-deficient nature. Soil microbes are believed to positively influence plant health through mutualistic interactions. Microbes are highly susceptible to the effects of pollution, and contaminated soils often experience a depletion in both the diversity and abundance of microbial populations (Shi et al., 2002). Such bacteria are part of the soil's free-living microbiota, and they can be found in various ecological niches, including the rhizosphere, rhizoplane, histoplane, and phyloplane. PGPB is involved in nitrogen fixation, phosphorous, and iron solubilization, also produces plant growth hormones including auxins or IAA, cytokinins, gibberellins, and ethylene, protects plants from phytopathogens (Bashan et al., 2014). PGPBs are further classified into two categories based on their colonization area: Plant Growth Promoting Rhizobacteria (PGPR) and Plant Growth Promoting Endophytes (PGPE). In the following section, these two PGPBs are discussed in detail.

6.2.3. Plant Growth-Promoting Rhizobacteria

Microbial residents are integral and naturally interactive components of the soil's biota. When bacteria interact with plants in diverse ecological environments like the rhizosphere, they trigger a boost in plant growth by directly impacting plant metabolism and suppressing prevalent plant-harming pathogens found in the soil. Rhizobacteria colonization is of two types: 1) bacterial colonization within roots takes place in clusters along root tissues and/or the rhizoplane. The rhizoplane is the root surface where soil particles tightly adhere. Root tissues, on the other hand, are inhabited by specific microorganisms referred to as endophytes (Backer et al., 2018; Vacheron et al., 2013). 2) rhizosphere colonization refers to PGPR colonization in adjacent soil (Santoyo et al., 2021). The rhizosphere can contain up to 10^{11} bacterial CFU per gram of root (Egamberdieva et al., 2008) and over 30,000 prokaryotic species (Mendes et al., 2011). The diversity of rhizobacteria is vast, encompassing thousands of species. This intricate plant-associated PGPR community plays a vital role in maintaining plant growth and health (Berendsen et al., 2012). These PGPR encompass a wide range of genera, including *Arthrobacter*, *Kluyvera*, *Vibrio*, *Anabaena*, *Azotobacter*, *Staphylococcus*, *Bacillus*, *Serratia*, *Pseudomonas*, *Rhizobium*, *Enterobacter*, *Achromobacter*, *Azospirillum*, *Burkholderia*, *Flavobacterium*, *Phyllobacterium*, *Streptomyces*, *Azoarcos*, *Frankia*, *Clostridium*, *Microcoleus*, *Hydrogenophaga*, and *Acetobacter* (Bashan et al., 2008; Bashan and Holguin, 1998; Garbeva et al., 2001; Rothballer et al., 2003). Plant Growth Promoting Rhizobacteria (PGPR) is characterized by three inherent attributes including the organisms' capacity to establish root colonization, their ability to survive, multiply, and compete within microenvironments linked to the root surface, and their capability to enhance plant growth (Espinosa-Urgel, 2004; Gamalero et al., 2004).

A complex and dynamic microenvironment exists in the rhizosphere that promotes the growth of microorganism communities which ultimately possess the capacity to detoxify hazardous substances and establish a symbiotic relationship with roots (Alford et al., 2010). Rhizobacteria has been involved in metal mobilization for easy metal uptake by hyperaccumulator plants (Lebeau et al., 2008). On the other hand, the rhizosphere zone of hyperaccumulator plants also supports a variety of metal-resistant bacterial genera (Aboudrar et al., 2007). Moreover, they play an important role in regulating the metal bioavailability of metallophytes (Whiting et al., 2001). Such as, nickel-resistant rhizosphere bacteria have been isolated from the shoots of *Alyssum murale* which is involved in the significant uptake of nickel into the shoots (Becerra-Castro et al., 2009). Biotic or abiotic stress through a minute change in the physicochemical and biological properties of rhizosphere may induce a negative impact on plant-microbe symbiosis. Plant growth-promoting rhizobacteria have received attention in the profitability of phytoremediation process; because they enhance metal tolerance and adequate biomass in plants (Aafi et al., 2012; De Maria et al., 2011; Ma and Wang, 2010). Phytoremediation and bio-augmentation have been used to describe rhizoremediation, in conjunction with PGPR (Kuiper et al., 2004).

PGPRs play a crucial role in nutrient cycling and plant growth regulation. They are involved in various activities, such as producing siderophores, fixing atmospheric nitrogen, generating phytohormones like gibberellins, cytokinins, and auxins, and facilitating the solubilization of minerals like phosphorus (Ahemad and Kibret, 2014; Yong et al., 2014). These actions enhance nutrient availability for plant growth and development. PGPRs also up-regulate ACC-deaminase, which reduces ethylene levels that are generally inhibitory to growth. Additionally, they contribute to biocontrol by depleting iron from the rhizosphere, producing chitinase enzymes to break down fungal cell walls, and competing for resources by binding with plant roots (Glick et al., 2007). Numerous reports have indicated that certain PGPR species exhibit notable resilience to elevated amounts of heavy metals and remain active in metalliferous soils (AIu et al., 1999). These naturally occurring rhizobacteria have the potential to support phytoremediation efforts via the up-regulation of metalliferous soil fertility, plant growth regulation by efficient uptake of nutrients and control of pathogenicity, and transformation of certain organics into biodegradation products (Kamnev et al., 1999).

Brassica juncea has been treated with *Azotobacter chroococcum*, *Bacillus megaterium*, and *Bacillus mucilaginosus* strains to increase phytoremediation potential of *Brassica juncea* grown on Pb–Zn mine tailings. It has been observed that these bacterial strains increased the plant growth and biomass, consequently enhancing plants' metal uptake capacity (Wu et al., 2006). Similarly, growth of *Brassica juncea* has been increased by the inoculation of *Bacillus subtilis* under Ni stress, which ultimately enhanced the production of phytohormone indole acetic acid (IAA) and solubilized the inorganic phosphates (Zaidi et al., 2006). The root-associated PGPB also has ACC-deaminase activity that provides a massive root system in metalliferous soils (Arshad et al., 2007). Elevated levels of ethylene, induced by metal toxicity and various stress factors, significantly inhibit root growth and differentiation. Bacterial ACC-deaminase plays an important role in mitigating this effect by reducing ACC levels through the conversion of its ethylene precursor ACC into alpha-keto butyric acid and ammonia (Glick, 2005). PGPR with ACC-deaminase activity leads to enhanced metal tolerance in Ni-tolerant *Thlaspi goesingense* (Idris et al., 2004). An investigative study has revealed that *Kluyvera ascorbata* has developed resistance to various heavy metals and has been observed to shield plants from nickel toxicity, without affecting the nickel uptake by seedlings (Dixit et al., 2015). The bacterium's ACC-deaminase activity might be linked to both the augmentation of plant growth and the escalation of Ni stress (Gupta and Pandey, 2019). Efficient Ni phytoextraction has been observed in the field experiments when a combination of hyperaccumulator plants *N. tymphaea* and *B. tymphaea* were treated with Ni resistant PGPR strain, which was isolated from the rhizosphere of these plants (Durand et al., 2016; Visioli et al., 2015).

6.2.4. Plant Growth Promoting Endophytes

Within the rhizosphere, several rhizobacteria and endophytic partnerships in bacteria-plant interactions participate in the breakdown of harmful substances. Endophytic bacteria are defined as beneficial plant growth-promoting microorganisms that reside within the internal tissues of plants without causing any harm to their host (Ryan et al., 2008).

The root serves as the main point of entry for endophytes. Numerous microscopic investigations validate this colonization pathway (Mengistu, 2020). Following their entry, endophytes may either remain localized within particular plant tissues, such as the root cortex or vascular tissues or establish themselves within the host's inner tissues through the transport of xylem/phloem sap or within the apoplast (Weyens et al., 2010). Endophytes have been reported in various herbaceous crop plants (Xia et al., 2022) different grass species (Dalton et al., 2004; Pašakinskienė et al., 2024; Zinniel et al., 2002), and woody tree species (Araújo et al., 2024; Cankar et al., 2005; Pandey et al., 2005). Generally, the most frequently encountered genera of cultivable endophytic species belong to *Burkholderiaceae, Enterobacteriaceae,* and *Pseudomonaceae* (Hossain et al., 2023). Plant-endophyte relationships are built upon the sysmbiotic, usually advantageous to both partners, interactions. In this dynamic relationship, plants provide habitat and nutrients to the endophytes, while endophytes reciprocate by generating metabolites that can improve plant growth through direct or indirect means (Tan and Zou, 2001). PGPEs act as biocontrol agents that safeguard plants from pathogens through multifaceted mechanisms. These mechanisms include resource competition for space and nutrients, the production of hydrolases, antibiosis, the breakdown of toxins produced by pathogens, and the synthesis of plant growth regulators such as auxins, cytokinins, and gibberellins. Additionally, PGPEs stimulate ACC-deaminase activity in response to increased ethylene stress (Glick, 2005; Weyens et al., 2009).

The phytoremediation of specific organic contaminants, such as trichloroethene (TCE), hinges on crucial factors, namely, transpiration rate and concentrations. In the process of removing TCE from soils, plants use a phytovolatilization mechanism (Ma and Burken, 2003). Phytoremediation involves the use of plants to establish ideal conditions for the microbial breakdown of pollutants and to facilitate the absorption of pollutants by the plants (Boominathan et al., 2004; Tamaoki et al., 2008). Hence, plants play a dual role in phytoremediation, providing optimal conditions for root-colonizing bacteria and offering a straightforward method for extracting pollutants (Suresh and Ravishankar, 2004). In last several decades, metal-resistant PGPEs have been frequently used in phytoremediation of metalliferous soils (Doty et al., 2003; Mastretta et al., 2006). Although an excess amount of heavy metals such as Ni is notorious for plant growth. Metal-resistant plant growth-promoting endophytic bacteria (PGPE) have been isolated from the root and shoot interiors of various metallophytes (Idris et al., 2004). This shows that PGPEs can tolerate high metal concentrations and assist in the translocation of metal ions within the plant. Furthermore, they have been reported to enhance plant growth through the production of siderophores, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, indole-3-acetic acid (IAA), as well as the solubilization of phosphate (P), iron (Fe) (Rajkumar et al., 2009), biosurfactants and organic acids (Ma et al., 2016). While numerous studies have investigated the endophytic bacteria present in various metallophytes, only a limited number of experimental trials have been conducted to examine the role of Ni accumulation in plants with PGPE inoculation (Barzanti et al., 2007). Microbe-assisted phytoremediation can be enhanced through the genetic modification of plants and bacterial strains, a concept known as geno-remediation.

6.2.5. Advanced Mechanisms of Microbial Action

Recent studies have identified new mechanisms through which microbes help alleviate nickel phytotoxicity. Beyond traditional methods such as the production of siderophores and phytohormones, microbes have been found to induce systemic tolerance in plants. For instance, species like *Pseudomonas* and *Bacillus* can activate plant defense pathways via the production of signaling molecules like jasmonic acid and salicylic acid (Shi et al., 2024). These signaling molecules trigger antioxidant responses in plants, leading to the upregulation of stress-responsive genes, and enhancing the plant's ability to detoxify nickel through both enzymatic and non-enzymatic pathways (Naqqash et al., 2024). Additionally, certain microbial communities (*Sporosarcina pasteurii* and *Bacillus megaterium*) have been discovered to engage in "chemo-attraction" of nickel ions, whereby microbial cells trap and compartmentalize the nickel within their biofilms or intracellular components (Gheethi et al., 2017; Phour et al., 2020; Shi et al., 2024). This biofilm-mediated immobilization offers a dual benefit: microbial protection against nickel toxicity and enhanced plant tolerance (Yousuf and Singh, 2024).

Microbial Synergy and Co-inoculation Strategies

Recent advancements have highlighted the importance of microbial consortia—combinations of bacteria and fungi—that act synergistically to enhance nickel tolerance in plants. Co-inoculation of beneficial microbes has been shown to provide superior protection against nickel stress compared to single inoculants. For example, co-inoculation with *Nitrosomonas, Pseudomonas, Penicillium, Bacillus, Xanthobacter, Flavobacterium,* and *Mycobacterium* can improve root growth, enhance metal sequestration, and reduce nickel uptake in plants (Sharma et al., 2023; Wu et al., 2024). The combined action of bacteria and fungi leads to more effective bioaccumulation and detoxification mechanisms, promoting healthier plant development in contaminated environments. Bioleaching with bio-surfactants (sugar esters) produced by *Burkholderia sp*. was conducted (Yang et al., 2016). The results demonstrated leaching efficiencies of 44.0 % for Zn, 52.2 % for Mn, and 37.7 % for Cd. Additionally, the presence of the surfactant enhanced carbon source consumption by *Aspergillus niger*, leading to improved nickel leaching (Dong et al., 2023).

Munoz et al. (Muñoz et al., 2006) explored the use of a microalgae-bacteria consortium for the remediation of Ni(II) and other heavy metals in wastewater, showing that metals were initially adsorbed onto cell surfaces, followed by a slower metabolically driven absorption. Another study reported that this consortium removed up to 62 % of nickel from industrial wastewater (Safonova et al., 2004). Microbial consortia can produce a range of beneficial metabolites, such as organic acids, which alter the rhizosphere pH and reduce the solubility of nickel, thus limiting its uptake by plants (Gadd, 2010). The role of mycorrhizal fungi in forming symbiotic relationships with plant roots has been particularly emphasized, as these fungi increase the surface area for nutrient absorption while reducing metal translocation to the shoots (Sharma et al., 2024). Some microbes not only detoxify nickel but may also help control microbial populations that could interfere with plant growth during phytoremediation (Parseghian et al., 2024; Rajabi et al., 2023). Additionally, the microbial synthesis of metal-organic nanostructures, such as bio-surfactants, nanoparticles, and metal-organic frameworks, may play a crucial role in enhancing the bioavailability of nickel, thereby improving its uptake in plants and contributing to more efficient nickel solubilization and sequestration (Moradi Alvand et al., 2019; Rajabi et al., 2017)

6.3. Gene-Targetedeted Bioremediation (Geno-Remediation)

The concept of geno-remediation originated from advanced research in phytoremediation, involving the stimulation of genes through safe biotechnological tools (Rafeeq et al., 2023). The potential of phytoremediation can be further enhanced by expressing selective metal-tolerant genes in transgenic plants and bacteria (Doty, 2008). The metal tolerance and accumulation capacity in plants could be increased by inducing genes that are involved in antioxidant enzymes, biosynthesis of glutathione (GSH), metallothioneins (MTs), and phytochelatins (PCs) (Mani and Kumar, 2014). Genetically, it was evident that the nutrient transporter proteins showed specificity towards Co(II) and Ni (II) can be induced in various bacterial strains (Deng et al., 2013; Zhang et al., 2007). Currently, it is possible to isolate metal defense genes from hyperaccumulators and introduce them into non-hyperaccumulators. Numerous bacterial, yeast, or fungal metal tolerance genes have been incorporated into plants to enhance phytoremediation potential. For instance, the SAT (Serine Acetyl Transferase) gene was isolated from *T. goesingense* and expressed in *Arabidopsis*. The results showed that Ni tolerance increased by five times in shoots and 1.5 times in roots of *Arabidopsis* when grown under 100 mM Ni stress (Freeman et al., 2004). The bacterial ACC deaminase gene has also been introduced into plants to decrease ethylene production under stress conditions, ultimately leading to an increase in plant biomass (Stearns et al., 2005).

The rcnA system is a well-studied *E. coli* efflux pump for Ni(II) and Co (II) ions (Rodrigue et al., 2005). It is possible to disable genes that encode these efflux pumps, thereby trapping the imported metals inside the cytoplasm and preventing their exit through the cell membranes. Following these principles, an *E. coli* strain that accumulates cobalt has been engineered (Raghu et al., 2008). However, this strain had a significant drawback: bacteria could not be easily recovered from the decontaminated effluent. To overcome this challenge, a previously described bacterium capable of accumulating Ni and Co was engineered by incorporating a metal-inducible curli overproduction system (Raghu et al., 2008). The enhanced adhesive capacity of the engineered strain to inert surfaces facilitates its immobilization onto a solid support and subsequent removal from the decontaminated effluents. As a result, this strain could potentially serve as a promising candidate for utilization in an industrial-scale biofilter (Duprey et al., 2014). The findings from a series of experiments showed that endophytic bacteria can help to clean-up pollution. These bacteria can degrade harmful substances and resist or trap metals via degradation pathways and metal resistance/-sequestration systems. They can make phytoremediation work better for different types of pollution, like TCE (trichloroethylene) (Weyens et al., 2015).

7. Challenges and Limitations

Phytoremediation and microbial methods offer promising solutions for environmental cleanup, but various environmental and biological factors often limit their effectiveness. One major challenge is the variability in environmental conditions, such as soil type, pH, temperature, and moisture content, which can significantly affect the growth and activity of plants and microorganisms involved in remediation. For instance, some plant species may be more tolerant to certain contaminants or environmental stressors than others, limiting the generalizability of these methods across different ecosystems. Additionally, the availability of nutrients and the presence of other pollutants can influence the ability of plants and microbes to effectively remove or stabilize contaminants like heavy metals, including nickel.

Another limitation lies in the slow rate of remediation and the long-term sustainability of these methods. Phytoremediation often requires extended periods to achieve substantial detoxification, which may not be feasible for sites with high contamination levels or urgent remediation needs. Similarly, microbial methods, while effective in reducing bioavailable nickel, may not be as efficient under extreme environmental conditions or at high contaminant concentrations. The complexity of microbial communities also poses challenges, as not all microbes have the same capacity for nickel uptake or transformation, making it difficult to predict outcomes. Moreover, the persistence of beneficial microbes in the field is a concern, as changes in environmental conditions can lead to the decline or loss of these populations, hindering the long-term effectiveness of microbial-assisted remediation strategies.

8. Conclusions and Future Perspectives

Nickel plays a crucial role in regulating key metabolic processes. However, when present in excess, its toxicity poses significant risks to both plant systems and human health. As Ni contamination in soils becomes more prevalent due to anthropogenic activities, effective remediation strategies are urgently required. This review has highlighted the negative effects of nickel toxicity on plant growth and metabolism, emphasizing the potential of harnessing microbial-assisted phytoremediation in mitigating these emerging environmental pollution challenges.

Microbes play a pivotal role in nickel (Ni) remediation, particularly through their interactions with plants in phytoremediation processes. Plant growth-promoting bacteria (PGPB), such as *Microbacterium*, *Pseudomonas*, and *Bacillus* species, enhance the bioavailability of Ni and increase its uptake by plants. For instance, inoculation with *Microbacterium* strains led to a significant increase in Ni concentration in *Alyssum murale* from 8500 mg kg^{-1} to 11500 mg kg^{-1}, highlighting their potential to increase Ni accumulation in shoots (Table 2). Similarly, *Bacillus subtilis* promoted Ni uptake in *Brassica juncea*, increasing its concentration in roots and stems, while also protecting the species from Ni toxicity (Table 2). This dual action of enhancing Ni uptake and providing biological bufferring against toxicity is a common feature of these microbes. Additionally, *Pseudomonas* strains were able to improve plant biomass accumulation while reducing Ni phytotoxicity (Table 2). By facilitating metal solubilization and improving the adjacent soil properties, these microbes support the effectiveness of the phytoremediation efforts, contributing to better and plausibly sustainable Ni decontamination strategies.

Looking ahead, advancements in omics technologies—such as genomics, transcriptomics, proteomics, and metabolomics—are opening new avenues for gaining deeper insights into understanding the microbial-facilitated nickel stress alleviation. These technologies have enabled the identification of some key genes, regulatory networks, and metabolic pathways in both plants and microbes during exposure to high nickel levels. For example, transcriptomic studies have revealed plant genes related to metal chelation, antioxidative defense, and nutrient uptake, all activated by microbial interactions. Proteomic and metabolomic approaches have further elucidated how microbial consortia modulate plant metabolic profiles, leading to the production of critical metabolites like proline, glutathione, and ascorbate, which detoxify reactive oxygen species (ROS) generated under nickel stress. Moving forward, integrating these omics platforms will be essential in identifying novel plant-microbe interactions and improving the effectiveness and sustainability of phytoremediation.

In addition to omics technologies, gene editing tools such as CRISPR-Cas9 hold significant promise in advancing the understanding of microbial-assisted phytoremediation. Gene editing can be employed to enhance microbial resilience to high nickel concentrations or to engineer plants with enhanced metal-uptake capabilities. Targeted modifications in microbial genomes could also optimize the production of biosurfactants, siderophores, and organic acids, which facilitate nickel mobilization and uptake. Furthermore, systems biology approaches will provide a more comprehensive understanding of the complex interactions within plant-microbe-soil systems under nickel stress. By integrating multi-omics data, systems biology can help construct predictive models to fine-tune phytoremediation strategies for diverse environmental conditions. Emerging biotechnological applications, such as synthetic biology and nano-biotechnology, offer additional tools to enhance microbial-assisted remediation. Synthetic biology can be used to design custom microbial consortia tailored for specific soil types or contamination levels, while nano-biotechnology could deliver nanoscale amendments (nanobiochar, biogas digestates; nano-materials impregnated with suitable microbial consortia) that may increase nickel bioavailability to engineered microbes, accelerating the remediation process (Li et al., 2024; Sani et al., 2023, 2024; Visioli et al., 2015; Wu et al., 2024; Yang et al., 2016; Yin et al., 2024; Yousuf and Singh, 2024).

Finally, field-scale trials and the integration of these technologies into sustainable agricultural practices are critical for translating lab-scale successes into real-world solutions. Future research must also address the socio-economic and regulatory aspects of implementing microbial-assisted phytoremediation. Assessing cost-effectiveness, public acceptance, and potential risks will be essential for the widespread adoption of these remediation strategies. By leveraging upon cuttingedge technologies and fostering cross-disciplinary collaborations, we can better understand the scientific basis of phytoremediation of nickel-contaminated environments, ultimately contributing to better liveability for humans and all other organisms.

Funding

Government College University Faisalabad, Pakistan

CRediT authorship contribution statement

Abeed Amany H. A.: Writing – review & editing, Methodology, Funding acquisition, Formal analysis. **Shaghaleh Hiba:** Writing – review & editing, Software, Methodology, Conceptualization. **Hamoud Yousef Alhaj:** Writing – review & editing, Software, Resources, Data curation. **Waseem Muhammad:** Writing – review & editing, Software, Resources, Data curation. **Azeem Farrukh:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Hussain Sabir:** Writing – review & editing, Visualization, Validation. **Ahmad Bilal:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Mao Xinyu:** Writing – original draft, Data curation, Conceptualization. **Yong Jean Wan Hong:** Writing – review & editing, Supervision, Funding acquisition. **Rizwan Muhammad:** Writing – review & editing, Validation, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declared that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledged the financial support from the Government College University Faisalabad.

Data Availability

Data will be made available on request.

References

Aafi, N.El, Brhada, F., Dary, M., Maltouf, A.F., Pajuelo, E., 2012. Rhizostabilization of metals in soils using *Lupinus luteus* inoculated with the metal resistant rhizobacterium *Serratia* sp. MSMC541. Int. J. Phytoremediat. 14, 261–274.

Abbott, L.K., Macdonald, L.M., Wong, M.T.F., Webb, M.J., Jenkins, S.N., Farrell, M., 2018. Potential roles of biological amendments for profitable grain production – A review. Agric. Ecosyst. Environ. 256, 34–50. https://doi.org/10.1016/j.agee.2017.12.021.

Aboudrar, W., Schwartz, C., Benizri, E., Morel, J.L., Boularbah, A., 2007. Soil microbial diversity as affected by the rhizosphere of the hyperaccumulator *Thlaspi caerulescens* under natural conditions. Int. J. Phytoremediat. 9, 41–52.

Abou-Shanab, R.I., Delorme, T.A., Angle, J.S., Chaney, R.L., Ghanem, K., Moawad, H., Ghozlan, H.A., 2003. Phenotypic characterization of microbes in the rhizosphere of *Alyssum murale*. Int. J. Phytoremediat. 5, 367–379. https://doi.org/10.1080/16226510390268766.

Abou-Shanab, R.A., Angle, J.S., Delorme, T.A., Chaney, R.L., Van Berkum, P., Moawad, H., Ghanem, K., Ghozlan, H.A., 2003. Rhizobacterial effects on nickel extraction from soil and uptake by *Alyssum murale*. N. Phytol. 158, 219–224.

Adil, N., Ashraf, K., Munir, M., Mohiuddin, M., Abbasi, A., Riaz, U., Aslam, A., Marey, S. A., Hatamleh, A.A., Zaman, Q. uz, 2023. Pesticides, Heavy metals and plasticizers: contamination and risk assessment of drinking-water quality. Sustainability 15, 13263. https://doi.org/10.3390/su151713263.

Ahemad, M., 2019. Remediation of metalliferous soils through the heavy metal resistant plant growth promoting bacteria: paradigms and prospects. Arab. J. Chem. 12, 1365–1377.

Ahemad, M., Kibret, M., 2014. Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. J. King Saud. Univ. 26, 1–20.

Ahmad, M.S., Ashraf, M., 2011. Essential roles and hazardous effects of nickel in plants. Rev. Env. Contam. Toxicol. 214, 125–167. https://doi.org/10.1007/978-1-4614-0668-6_6.

Ahmad, M.S.A., Hussain, M., Saddiq, R., Alvi, A.K., 2007. Mungbean: a nickel indicator, accumulator or excluder? Bull. Environ. Contam. Toxicol. 78, 319–324.

AIu, I., Gavriushkin, A.V., Siunova, T.V., Khasanova, L.A., Khasanova, Z.M., 1999. Resistance of certain strains of *Pseudomonas* bacteria to toxic effect of heavy metal ions. Mikrobiologiia 68, 366–374.

Alamgir, A., Ali, Q., Fatima, N., Khan, M., Nawaz, M.F., Tariq, S., Rizwan, M., Yong, J.W. H., 2024. Geospatial quality assessment of locally available ice for heavy metals and metalloids and their potential risks for human health in Karachi, Pakistan. Heliyon 10, e28252. https://doi.org/10.1016/j.heliyon.2024.e28252.

Alford, É .R., Pilon-Smits, E.A.H., Paschke, M.W., 2010. Metallophytes—a view from the rhizosphere. Plant Soil 337, 33–50.

Ali, H., Khan, E., Sajad, M.A., 2013. Phytoremediation of heavy metals–concepts and applications. Chemosphere 91, 869–881. https://doi.org/10.1016/j.chemosphere.2013.01.075.

Ansari, M., Devi, B.M., Sarkar, A., Chattopadhyay, A., Satnami, L., Balu, P., Choudhary, M., Shahid, M.A., Jailani, A.A.K., 2023. Microbial exudates as biostimulants: role in plant growth promotion and stress mitigation. J. Xenobiotics 13, 572–603. https://doi.org/10.3390/jox13040037.

Araújo, K.S., Alves, J.L., Pereira, O.L., de Queiroz, M.V., 2024. Five new species of endophytic *Penicillium* from rubber trees in the Brazilian Amazon. Braz. J. Microbiol. https://doi.org/10.1007/s42770-024-01478-9.

Arshad, M., Saleem, M., Hussain, S., 2007. Perspectives of bacterial ACC deaminase in phytoremediation. TRENDS Biotechnol. 25, 356–362.

Assunção, A.G.L., Bleeker, P., ten Bookum, W.M., Vooijs, R., Schat, H., 2008. Intraspecific variation of metal preference patterns for hyperaccumulation in *Thlaspi caerulescens*: evidence from binary metal exposures. Plant Soil 303, 289–299.

Axelsen, K.B., Palmgren, M.G., 2001. Inventory of the superfamily of P-type ion pumps in *Arabidopsis*. Plant Physiol. 126, 696–706.

Aziz, H., Sabir, M., Ahmad, H.R., Aziz, T., Zia-ur-Rehman, M., Hakeem, K.R., Ozturk, M., 2015. Alleviating effect of calcium on nickel toxicity in rice. CLEAN – Soil, Air, Water 43, 901–909. https://doi.org/10.1002/clen.201400085.

Backer, R., Rokem, J.S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., Smith, D.L., 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Front. Plant Sci. 9, 402666.

Bani, A., Echevarria, G., Sulçe, S., Morel, J.L., Mullai, A., 2007. *In-situ* phytoextraction of Ni by a native population of *Alyssum murale* on an ultramafic site (Albania). Plant Soil 293, 79–89.

Bani, A., Pavlova, D., Echevarria, G., Mullaj, A., Reeves, R.D., Morel, J.L., Sulçe, S., 2010. Nickel hyperaccumulation by the species of *Alyssum* and *Thlaspi* (Brassicaceae) from the ultramafic soils of the Balkans. Bot. Serbica 34, 3–14.

Barzanti, R., Ozino, F., Bazzicalupo, M., Gabbrielli, R., Galardi, F., Gonnelli, C., Mengoni, A., 2007. Isolation and characterization of endophytic bacteria from the nickel hyperaccumulator plant *Alyssum bertolonii*. Microb. Ecol. 53, 306–316. https://doi.org/10.1007/s00248-006-9164-3.

Bashan, Y., Holguin, G., 1998. Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. Soil Biol. Biochem. 30, 1225–1228. https://doi.org/10.1016/S0038-0717(97)00187-9.

Bashan, Y., Puente, M.E., de-Bashan, L.E., Hernandez, J.-P., 2008. Environmental uses of plant growth-promoting bacteria. Plant-Microbe Inter. 661, 69–93.

Bashan, Y., De-Bashan, L.E., Prabhu, S.R., Hernandez, J.-P., 2014. Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). Plant Soil 378, 1–33. https://doi.org/10.1007/s11104-013-1956-x.

Bauddh, K., Singh, K., Singh, B., Singh, R.P., 2015. *Ricinus communis*: A robust plant for bio-energy and phytoremediation of toxic metals from contaminated soil. Ecol. Eng. 84, 640–652.

Becerra-Castro, C., Monterroso, C., García-Lestón, M., Prieto-Fernández, A., Acea, M.J., Kidd, P.S., 2009. Rhizosphere microbial densities and trace metal tolerance of the nickel hyperaccumulator *Alyssum serpyllifolium* subsp. *lusitanicum*. Int. J. Phytoremediat. 11, 525–541. https://doi.org/10.1080/15226510902717549.

Becerra-Castro, C., Prieto-Fernández, A., Álvarez-Lopez, V., Monterroso, C., Cabello-Conejo, M.I., Acea, M.J., Kidd, P.S., 2011. Nickel solubilizing capacity and characterization of rhizobacteria isolated from hyperaccumulating and non-hyperaccumulating subspecies of *Alyssum serpyllifolium*. Int. J. Phytoremediat. 13, 229–244. https://doi.org/10.1080/15226514.2011.568545.

Begum, W., Rai, S., Banerjee, S., Bhattacharjee, S., Mondal, M.H., Bhattarai, A., Saha, B., 2022. A comprehensive review on the sources, essentiality and toxicological profile of nickel. RSC Adv. 12, 9139–9153.

Belouchrani, A.S., Mameri, N., Abdi, N., Grib, H., Lounici, H., Drouiche, N., 2016. Phytoremediation of soil contaminated with Zn using canola (*Brassica napus* L). Ecol. Eng. 95, 43–49.

Berendsen, R.L., Pieterse, C.M.J., Bakker, P.A.H.M., 2012. The rhizosphere microbiome and plant health. Trends Plant Sci. 17, 478–486.

Beškoski, V.P., Gojgić-Cvijović, G., Milić, J., Ilić, M., Miletić, S., Šolević, T., Vrvić, M.M., 2011. *Ex situ* bioremediation of a soil contaminated by mazut (heavy residual fuel oil)–A field experiment. Chemosphere 83, 34–40.

Bidwell, S.D., Crawford, S.A., Woodrow, I.E., Sommer-Knudsen, J., Marshall, A.T., 2004. Sub-cellular localization of Ni in the hyperaccumulator, *Hybanthus floribundus* (Lindley) F. Muell. Plant. Cell Environ. 27, 705–716.

Bishop, P.L., 2002. Handbook of Air Pollution Prevention and Control. Elsevier. https://doi.org/10.1016/B978-0-7506-7499-7.X5000-7.

Boominathan, R., Saha-Chaudhury, N.M., Sahajwalla, V., Doran, P.M., 2004. Production of nickel bio-ore from hyperaccumulator plant biomass: applications in phytomining. Biotechnol. Bioeng. 86, 243–250.

Boonstra, M.B., Christoffers, W.A., Coenraads, P.-J., Schuttelaar, M.-L.A., 2015. Patch test results of hand eczema patients: relation to clinical types. J. Eur. Acad. Dermatol. Venereol. 29, 940–947.

Boopathy, R., 2000. Factors limiting bioremediation technologies. Bioresour. Technol. 74, 63–67.

Broadhurst, C.L., Chaney, R.L., 2016. Growth and metal accumulation of an *Alyssum murale* nickel hyperaccumulator ecotype co-cropped with *Alyssum montanum* and perennial ryegrass in serpentine soil. Front. Plant Sci. 7, 183062.

Broadhurst, C.L., Chaney, R.L., Angle, J.S., Erbe, E.F., Maugel, T.K., 2004. Nickel localization and response to increasing Ni soil levels in leaves of the Ni hyperaccumulator *Alyssum murale*. Plant Soil 265, 225–242.

Brown, P.H., Welch, R.M., Cary, E.E., 1987. Nickel: A micronutrient essential for higher plants. Plant Physiol. 85, 801–803.

Callahan, D.L., Roessner, U., Dumontet, V., Perrier, N., Wedd, A.G., Richard, A.J., Baker, A.J.M., Kolev, S.D., 2008. LC–MS and GC–MS metabolite profiling of nickel (II) complexes in the latex of the nickel-hyperaccumulating tree *Sebertia acuminata* and identification of methylated aldaric acid as a new nickel (II) ligand. Phytochemistry 69, 240–251.

Campbell, D.R., Chapman, K.E., Waldron, K.J., Tottey, S., Kendall, S., Cavallaro, G., Andreini, C., Hinds, J., Stoker, N.G., Robinson, N.J., 2007. Mycobacterial cells have dual nickel-cobalt sensors: sequence relationships and metal sites of metal-responsive repressors are not congruent. J. Biol. Chem. 282, 32298–32310.

Cankar, K., Kraigher, H., Ravnikar, M., Rupnik, M., 2005. Bacterial endophytes from seeds of Norway spruce (*Picea abies* L. Karst). FEMS Microbiol. Lett. 244, 341–345.

Cavet, J.S., Meng, W., Pennella, M.A., Appelhoff, R.J., Giedroc, D.P., Robinson, N.J., 2002. A nickel-cobalt-sensing ArsR-SmtB family repressor: contributions of cytosol and effector binding sites to metal selectivity. J. Biol. Chem. 277, 38441–38448.

Çelik, J., Aksoy, A., Leblebici, Z., 2018. Metal hyperaccumulating Brassicaceae from the ultramafic area of Yahyalı in Kayseri province, Turkey. Ecol. Res. 33, 705–713. https://doi.org/10.1007/s11284-018-1606-0.

Cempel, M., Nikel, G., 2006. Nickel: a review of its sources and environmental toxicology. Pol. J. Environ. Stud. 15.

Chaney, R.L., Angle, J.S., Broadhurst, C.L., Peters, C.A., Tappero, R.V., Sparks, D.L., 2007. Improved understanding of hyperaccumulation yields commercial phytoextraction and phytomining technologies. J. Environ. Qual. 36, 1429–1443.

Chardot, V., Massoura, S.T., Echevarria, G., Reeves, R.D., Morel, J.-L., 2005. Phytoextraction potential of the nickel hyperaccumulators *Leptoplax emarginata* and *Bornmuellera tymphaea*. Int. J. Phytoremediat. 7, 323–335.

Chaudhry, Q., Blom-Zandstra, M., Gupta, S.K., Joner, E., 2005. Utilising the synergy between plants and rhizosphere microorganisms to enhance breakdown of organic pollutants in the environment (15 pp). Environ. Sci. Pollut. Res. 12, 34–48.

Chen, C., Huang, D., Liu, J., 2009. Functions and toxicity of nickel in plants: recent advances and future prospects. CLEAN - Soil, Air, Water 37, 304–313. https://doi.org/10.1002/clen.200800199.

Chen, X., Kumari, D., Cao, C.J., Plaza, G., Achal, V., 2020. A review on remediation technologies for nickel-contaminated soil. Hum. Ecol. Risk Assess. Int. J. 26, 571–585. https://doi.org/10.1080/10807039.2018.1539639.

Clemens, S., 2001. Molecular mechanisms of plant metal tolerance and homeostasis. Planta 212, 475–486.

Clemens, S., Ma, J.F., 2016. Toxic heavy metal and metalloid accumulation in crop plants and foods. Annu Rev Plant Biology 67, 489–512. https://doi.org/10.1146/annurev-arplant-043015-112301.

Colzi, I., Gonnelli, C., Bettarini, I., Selvi, F., 2023. Polyploidy affects responses to nickel in Ni-hyperaccumulating plants: evidence from the model species *Odontarrhena bertolonii* (Brassicaceae). Environ. Exp. Bot. 213, 105403. https://doi.org/10.1016/j.envexpbot.2023.105403.

Dalton, D.A., Kramer, S., Azios, N., Fusaro, S., Cahill, E., Kennedy, C., 2004. Endophytic nitrogen fixation in dune grasses (*Ammophila arenaria* and *Elymus mollis*) from Oregon. FEMS Microbiol. Ecol. 49, 469–479.

Dassa, E., Bouige, P., 2001. The ABC of ABCs: a phylogenetic and functional classification of ABC systems in living organisms. Res. Microbiol. 152, 211–229.

Daunoras, J., Kačergius, A., Gudiukaitė, R., 2024. Role of soil microbiota enzymes in soil health and activity changes depending on climate change and the type of soil ecosystem. Biol. (Basel) 13, 85. https://doi.org/10.3390/biology13020085.

de Bang, Husted, S., Laursen, K.H., Persson, D.P., Schjoerring, J.K., 2021. Themolecular–physiological functions of mineral macronutrients and theirconsequences for deficiency symptoms in plants. New Phytol 229, 2446–2469. https://doi.org/10.1111/nph.17074.

De Maria, S., Rivelli, A.R., Kuffner, M., Sessitsch, A., Wenzel, W.W., Gorfer, M., Strauss, J., Puschenreiter, M., 2011. Interactions between accumulation of trace elements and macronutrients in *Salix caprea* after inoculation with rhizosphere microorganisms. Chemosphere 84, 1256–1261.

Deng, T.-H.-B., Tang, Y.-T., van der Ent, A., Sterckeman, T., Echevarria, G., Morel, J.-L., Qiu, R.-L., 2016. Nickel translocation via the phloem in the hyperaccumulator *Noccaea caerulescens* (Brassicaceae). Plant Soil 404, 35–45.

Deng, T.-H.-B., van der Ent, A., Tang, Y.-T., Sterckeman, T., Echevarria, G., Morel, J.-L., Qiu, R.-L., 2018. Nickel hyperaccumulation mechanisms: a review on the current state of knowledge. Plant Soil 423, 1–11.

Deng, X., He, J., He, N., 2013. Comparative study on Ni(2+)-affinity transport of nickel/cobalt permeases (NiCoTs) and the potential of recombinant *Escherichia coli* for Ni($^{2+}$) bioaccumulation. Bioresour. Technol. 130, 69–74. https://doi.org/10.1016/j.biortech.2012.11.133.

Denkhaus, E., Salnikow, K., 2002. Nickel essentiality, toxicity, and carcinogenicity. Crit. Rev. Oncol. Hematol. 42, 35–56.

Denton, B., 2007. Advances in phytoremediation of heavy metals using plant growth promoting bacteria and fungi. MMG 445 Basic Biotechnol. 3, 1–5.

Dixit, R., Wasiullah, Malaviya, D., Pandiyan, K., Singh, U.B., Sahu, A., Shukla, R., Singh, B.P., Rai, J.P., Sharma, P.K., Lade, H., Paul, D., 2015. Bioremediation of heavy metals from soil and aquatic environment: An overview of principles and criteria of fundamental processes. Sustain 7, 2189–2212. https://doi.org/10.3390/su7022189.

Doble, M., Kumar, A., 2005. Biotreatment of Industrial Effluents. Elsevier.

Dohnalova, L., Bucek, P., Vobornik, P., Dohnal, V., 2017. Determination of nickel in hydrogenated fats and selected chocolate bars in Czech Republic. Food Chem. 217, 456–460.

Dong, Y., Zan, J., Lin, H., 2023. Bioleaching of heavy metals from metal tailings utilizing bacteria and fungi: Mechanisms, strengthen measures, and development prospect. J. Environ. Manag. 344, 118511. https://doi.org/10.1016/j.jenvman.2023.118511.

Doty, S.L., 2008. Enhancing phytoremediation through the use of transgenics and endophytes. N. Phytol. 179, 318–333. https://doi.org/10.1111/j.1469-8137.2008.02446.x.

Doty, S.L., Shang, T.Q., Wilson, A.M., Moore, A.L., Newman, L.A., Strand, S.E., Gordon, M.P., 2003. Metabolism of the soil and groundwater contaminants, ethylene dibromide and trichloroethylene, by the tropical leguminous tree, *Leuceana leucocephala*. Water Res 37, 441–449.

Duda-Chodak, A., Blaszczyk, U., 2008. The impact of nickel on human health. J. Elem. 13, 685–693.

Duprey, A., Chansavang, V., Frémion, F., Gonthier, C., Louis, Y., Lejeune, P., Springer, F., Desjardin, V., Rodrigue, A., Dorel, C., 2014. "NiCo Buster": engineering *E. coli* for fast and efficient capture of cobalt and nickel. J. Biol. Eng. 8, 1–11.

Durand, A., Piutti, S., Rue, M., Morel, J.L., Echevarria, G., Benizri, E., 2016. Improving nickel phytoextraction by co-cropping hyperaccumulator plants inoculated by plant growth promoting rhizobacteria. Plant Soil 399, 179–192. https://doi.org/10.1007/s11104-015-2691-2.

Eapen, S., D'souza, S.F., 2005. Prospects of genetic engineering of plants for phytoremediation of toxic metals. Biotechnol. Adv. 23, 97–114.

Egamberdieva, D., Kamilova, F., Validov, S., Gafurova, L., Kucharova, Z., Lugtenberg, B., 2008. High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ. Microbiol. 10, 1–9.

Eitinger, T., Mandrand-Berthelot, M.A., 2000. Nickel transport systems in microorganisms. Arch. Microbiol. 173, 1–9. https://doi.org/10.1007/s002030050001.

Ejaz, U., Khan, S.M., Khalid, N., Ahmad, Z., Jehangir, S., Fatima Rizvi, Z., Lho, L.H., Han, H., Raposo, A., 2023. Detoxifying the heavy metals: a multipronged study of tolerance strategies against heavy metals toxicity in plants. Front. Plant Sci. 14. https://doi.org/10.3389/fpls.2023.1154571.

Elbagory, M., El-Nahrawy, S., Omara, A.E.-D., 2022. Synergistic Interaction between Symbiotic N2 fixing bacteria and bacillus strains to improve growth, physiological parameters, antioxidant enzymes and Ni Accumulation in Faba Bean Plants (Vicia faba) under nickel stress. Plants 11, 1812. https://doi.org/10.3390/plants11141812.

Espinosa-Urgel, M., 2004. Plant-associated *Pseudomonas* populations: molecular biology, DNA dynamics, and gene transfer. Plasmid 52, 139–150.

Evans, D.J., 2005. Chemistry relating to the nickel enzymes CODH and ACS. Coord. Chem. Rev. 249, 1582–1595.

Everhart, J.L., McNear Jr, D., Peltier, E., Van der Lelie, D., Chaney, R.L., Sparks, D.L., 2006. Assessing nickel bioavailability in smelter-contaminated soils. Sci. Total Environ. 367, 732–744.

Fabiano, C.C., Tezotto, T., Favarin, J.L., Polacco, J.C., Mazzafera, P., 2015. Essentiality of nickel in plants: a role in plant stresses. Front. Plant Sci. 6, 754.

Fageria, N.K., Baligar, V.C., Clark, R.B., 2002. Micronutrients in crop production. Adv. Agron. 77, 185–268.

Faizan, M., Alam, P., Hussain, A., Karabulut, F., Tonny, S.H., Cheng, S.H., Yusuf, M., Adil, M.F., Sehar, S., Alomrani, S.O., Albalawi, T., Hayat, S., 2024. Phytochelatins: Key regulator against heavy metal toxicity in plants. Plant Stress 11, 100355. https://doi.org/10.1016/j.stress.2024.100355.

Fasani, E., Zamboni, A., Sorio, D., Furini, A., DalCorso, G., 2023. Metal interactions in the Ni hyperaccumulating population of *Noccaea caerulescens* Monte Prinzera. Biol. (Basel) 12, 1537. https://doi.org/10.3390/biology12121537.

Fayiga, A.O., Saha, U.K., 2016. Soil pollution at outdoor shooting ranges: Health effects, bioavailability and best management practices. Environ. Pollut. 216, 135–145.

Fein, J.B., Martin, A.M., Wightman, P.G., 2001. Metal adsorption onto bacterial surfaces: development of a predictive approach. Geochim. Cosmochim. Acta 65, 4267–4273.

Freeman, J.L., Persans, M.W., Nieman, K., Albrecht, C., Peer, W., Pickering, I.J., Salt, D. E., 2004. Increased glutathione biosynthesis plays a role in nickel tolerance in Thlaspi nickel hyperaccumulators. Plant Cell 16, 2176–2191.

Friberg, L., Nordberg, G.F., Vouk, V.B., 1979. Handbook on the Toxicology of Metals, 335. Elsevier/North-Holland Biomedical Press, Jan van Galenstraat, 1061 AZ.

Gadd, G.M., 2000. Bioremedial potential of microbial mechanisms of metal mobilization and immobilization. Curr. Opin. Biotechnol. 11, 271–279.

Gadd, G.M., 2004. Microbial influence on metal mobility and application for bioremediation. Geoderma 122, 109–119.

Gadd, G.M., 2010. Metals, minerals and microbes: geomicrobiology and bioremediation. Microbiology 156, 609–643. https://doi.org/10.1099/mic.0.037143-0.

Gajewska, E., Skłodowska, M., 2008. Differential biochemical responses of wheat shoots and roots to nickel stress: antioxidative reactions and proline accumulation. Plant Growth Regul. 54, 179–188. https://doi.org/10.1007/s10725-007-9240-9.

Gamalero, E., Lingua, G., Giusy Caprì, F., Fusconi, A., Berta, G., Lemanceau, P., 2004. Colonization pattern of primary tomato roots by Pseudomonas fluorescens A6RI characterized by dilution plating, flow cytometry, fluorescence, confocal and scanning electron microscopy. FEMS Microbiol. Ecol. 48, 79–87.

Gangwar, S., Singh, V.P., Srivastava, P.K., Maurya, J.N., 2011. Modification of chromium (VI) phytotoxicity by exogenous gibberellic acid application in Pisum sativum (L.) seedlings. Acta Physiol. Plant. 33, 1385–1397.

Gao, M., Gao, B., Zhang, X., Fan, J., Liu, X., Wang, C., 2022. Effects of Plant Growth–Promoting Rhizobacteria (PGPR) on the Phytoremediation of Pyrene-Nickel-Contaminated Soil by Juncus effusus. Water, Air, Soil Pollut. 233, 458. https://doi.org/10.1007/s11270-022-05933-x.

Gao, W., He, W., Zhang, J., Chen, Y., Zhang, Z., Yang, Y., He, Z., 2023. Effects of biochar-based materials on nickel adsorption and bioavailability in soil. Sci. Rep. 13, 5880. https://doi.org/10.1038/s41598-023-32502-x.

Garbeva, P., Van Overbeek, L.S., Van Vuurde, J.W.L., Van Elsas, J.D., 2001. Analysis of endophytic bacterial communities of potato by plating and denaturing gradient gel electrophoresis (DGGE) of 16S rDNA based PCR fragments. Microb. Ecol. 41, 369–383.

Garrett, R.G., 2000. Natural sources of metals to the environment. Hum. Ecol. risk Assess. 6, 945–963.

Gendre, D., Czernic, P., Conéjéro, G., Pianelli, K., Briat, J., Lebrun, M., Mari, S., 2007. TcYSL3, a member of the YSL gene family from the hyper-accumulator *Thlaspi caerulescens*, encodes a nicotianamine-Ni/Fe transporter. Plant J. 49, 1–15.

Ghaderian, S.M., Mohtadi, A., Rahiminejad, R., Reeves, R.D., Baker, A.J.M., 2007. Hyperaccumulation of nickel by two *Alyssum* species from the serpentine soils of Iran. Plant Soil 293, 91–97.

Gheethi, A., Efaq, A., Mohamed, R., Abdel-Monem, M., Abdullah, A.H., Amir Hashim, M., 2017. Bio-removal of nickel ions by *Sporosarcina pasteurii* and *Bacillus megaterium*, a comparative study. IOP Conf. Ser. Mater. Sci. Eng. 226, 012044. https://doi.org/10.1088/1757-899X/226/1/012044.

Glick, B.R., 2005. Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol. Lett. 251, 1–7.

Glick, B.R., 2010. Using soil bacteria to facilitate phytoremediation. Biotechnol. Adv. 28, 367–374.

Glick, B.R., Cheng, Z., Czarny, J., Duan, J., 2007. Promotion of plant growth by ACC deaminase-producing soil bacteria. N. Perspect. Approaches Plant Growth-Promot. Rhizobacteria Res. 329–339.

Gramlich, A., Moradi, A.B., Robinson, B.H., Kaestner, A., Schulin, R., 2011. Dimethylglyoxime (DMG) staining for semi-quantitative mapping of Ni in plant tissue. Environ. Exp. Bot. 71, 232–240.

Gul, I., Manzoor, M., Kallerhoff, J., Arshad, M., 2020. Enhanced phytoremediation of lead by soil applied organic and inorganic amendments: Pb phytoavailability, accumulation and metal recovery. Chemosphere 258, 127405. https://doi.org/10.1016/j.chemosphere.2020.127405.

Guo, H., Luo, S., Chen, L., Xiao, X., Xi, Q., Wei, W., Zeng, G., Liu, C., Wan, Y., Chen, J., 2010. Bioremediation of heavy metals by growing hyperaccumulaor endophytic bacterium *Bacillus* sp. L14. Bioresour. Technol. 101, 8599–8605.

Gupta, S., Pandey, S., 2019. ACC deaminase producing bacteria with multifarious plant growth promoting traits alleviates salinity stress in French bean (*Phaseolus vulgaris*) plants. Front. Microbiol. 10, 442191.

Hadi, F., Bano, A., 2010. Effect of diazotrophs (*Rhizobium* and *Azatebactor*) on growth of maize (*Zea mays* L.) and accumulation of lead (Pb) in different plant parts. Pak. J. Bot. 42, 4363–4370.

Hall, J. áL., Williams, L.E., 2003. Transition metal transporters in plants. J. Exp. Bot. 54, 2601–2613.

Harasim, P., Filipek, T., 2015. Nickel in the environment. J. Elem. 20.

Harrop, T.C., Mascharak, P.K., 2005. Structural and spectroscopic models of the A-cluster of acetyl coenzyme a synthase/carbon monoxide dehydrogenase: nature's Monsanto acetic acid catalyst. Coord. Chem. Rev. 249, 3007–3024.

Hasanuzzaman, M., Bhuyan, M.H.M.B., Zulfiqar, F., Raza, A., Mohsin, S.M., Mahmud, J., Al, Fujita, M., Fotopoulos, V., 2020. Reactive oxygen species and antioxidant defense in plants under abiotic stress: revisiting the crucial role of a universal defense regulator. Antioxidants 9, 681. https://doi.org/10.3390/antiox9080681.

He, S., He, Z., Yang, X., Baligar, V.C., 2012. Mechanisms of nickel uptake and hyperaccumulation by plants and implications for soil remediation. Adv. Agron. 117, 117–189.

Higgins, C.F., 2001. ABC transporters: physiology, structure and mechanism–an overview. Res. Microbiol. 152, 205–210.

Hossain, M.S., Frith, C., Bhattacharyya, S.S., DeLaune, P.B., Gentry, T.J., 2023. Isolation and characterization of bacterial endophytes from small nodules of field-grown peanut. Microorganisms 11, 1941. https://doi.org/10.3390/microorganisms11081941.

Idris, R., Trifonova, R., Puschenreiter, M., Wenzel, W.W., Sessitsch, A., 2004. Bacterial communities associated with flowering plants of the Ni hyperaccumulator *Thlaspi goesingense*. Appl. Environ. Microbiol. 70, 2667–2677.

Idris, R., Kuffner, M., Bodrossy, L., Puschenreiter, M., Monchy, S., Wenzel, W.W., Sessitsch, A., 2006. Characterization of Ni-tolerant methylobacteria associated with the hyperaccumulating plant *Thlaspi goesingense* and description of *Methylobacterium goesingense* sp. nov. Syst. Appl. Microbiol. 29, 634–644.

Ingle, R.A., Fricker, M.D., Smith, J.A.C., 2008. Evidence for nickel/proton antiport activity at the tonoplast of the hyperaccumulator plant *Alyssum lesbiacum*. Plant Biol. 10, 746–753.

Janicka-Russak, M., Kabała, K., Burzyński, M., Kłobus, G., 2008. Response of plasma membrane H+ -ATPase to heavy metal stress in *Cucumis sativus* roots. J. Exp. Bot. 59, 3721–3728.

Kabała, K., Janicka-Russak, M., 2011. Differential regulation of vacuolar H+ -ATPase and H+ -PPase in *Cucumis sativus* roots by zinc and nickel. Plant Sci. 180, 531–539.

Kabała, K., Janicka-Russak, M., Burzyński, M., Kłobus, G., 2008. Comparison of heavy metal effect on the proton pumps of plasma membrane and tonoplast in cucumber root cells. J. Plant Physiol. 165, 278–288.

Kabata-Pendias, A., 2000. Trace Elements in Soils and Plants. CRC press.

Kachenko, A.G., Singh, B., Bhatia, N.P., Siegele, R., 2008. Quantitative elemental localisation in leaves and stems of nickel hyperaccumulating shrub *Hybanthusfloribundus* subsp. *floribundus* using micro-PIXE spectroscopy. Nucl. Instrum. Methods Phys. Res. Sect. B Beam Interact. Mater. At. 266, 667–676.

Kamnev, A.A., Antonyuk, L.P., Ignatov, V.V., 1999. Biodegradation of organic pollution involving soil iron (III) solubilized by bacterial siderophores as an electron acceptor: possibilities and perspectives, in. Novel Approaches for Bioremediation of Organic Pollution. Springer, pp. 205–217.

Kasprzak, K.S., Sunderman Jr, F.W., Salnikow, K., 2003. Nickel carcinogenesis. Mutat. Res. Mol. Mech. Mutagen. 533, 67–97.

Khaliq, M.A., Alsudays, I.M., Alhaithloul, H.A.S., Rizwan, M., Yong, J.W.H., Rahman, S. U., Sagir, M., Bashir, S., Ali, H., Zuo, H., 2024. Biochar impacts on carbon dioxide, methane emission, and cadmium accumulation in rice from Cd-contaminated soils: a meta-analysis. Ecotoxicology and Environmental Safety 274, 116204. https://doi.org/10.1016/j.ecoenv.2024.116204.

Kierczak, J., Pietranik, A., Pędziwiatr, A., 2021. Ultramafic geoecosystems as a natural source of Ni, Cr, and Co to the environment: A review. Sci. Total Environ. 755, 142620.

Kobae, Y., Uemura, T., Sato, M.H., Ohnishi, M., Mimura, T., Nakagawa, T., Maeshima, M., 2004. Zinc transporter of *Arabidopsis thaliana* AtMTP1 is localized to vacuolar membranes and implicated in zinc homeostasis. Plant Cell Physiol. 45, 1749–1758.

Kramer, U., Pickering, I.J., Prince, R.C., Raskin, I., Salt, D.E., 2000. Subcellular localization and speciation of nickel in hyperaccumulator and non-accumulator *Thlaspi* species. Plant Physiol. 122, 1343–1354.

Krämer, U., Cotter-Howells, J.D., Charnock, J.M., Baker, A.J.M., Smith, J.A.C., 1996. Free histidine as a metal chelator in plants that accumulate nickel. Nature 379, 635–638.

Kuiper, I., Lagendijk, E.L., Bloemberg, G.V., Lugtenberg, B.J.J., 2004. Rhizoremediation: a beneficial plant-microbe interaction. Mol. Plant-Microbe Interact. 17, 6–15.

Kumar, A., Jigyasu, D.K., Kumar, A., Subrahmanyam, G., Mondal, R., Shabnam, A.A., Cabral-Pinto, M.M.S., Malyan, S.K., Chaturvedi, A.K., Gupta, D.K., Fagodiya, R.K., Khan, S.A., Bhatia, A., 2021. Nickel in terrestrial biota: comprehensive review on contamination, toxicity, tolerance and its remediation approaches. Chemosphere 275, 129996. https://doi.org/10.1016/j.chemosphere.2021.129996.

Kumar, S., Prasad, S., Yadav, K.K., Shrivastava, M., Gupta, N., Nagar, S., Bach, Q.-V., Kamyab, H., Khan, S.A., Yadav, S., Malav, L.C., 2019. Hazardous heavy metals contamination of vegetables and food chain: Role of sustainable remediation approaches - A review. Environ. Res. 179, 108792. https://doi.org/10.1016/j.envres.2019.108792.

Kumar Yadav, K., Gupta, N., Kumar, A., Reece, L.M., Singh, N., Rezania, S., Ahmad Khan, S., 2018. Mechanistic understanding and holistic approach of phytoremediation: a review on application and future prospects. Ecol. Eng. 120, 274–298. https://doi.org/10.1016/j.ecoleng.2018.05.039.

Lambert, M., Leven, B.A., Green, R.M., 2000. New methods of cleaning up heavy metal in soils and water. Environ. Sci. Technol. briefs Citiz. 7, 133–163.

Lebeau, T., Braud, A., Jézéquel, K., 2008. Performance of bioaugmentation-assisted phytoextraction applied to metal contaminated soils: a review. Environ. Pollut. 153, 497–522.

Leyval, C., Joner, E.J., 2001. Bioavailability of heavy metals in the mycorrhizosphere. Trace Elem. Rhizosph. 165–185.

Li, M., Heng, Q., Wang, Z., Jiang, Y., Wang, X., He, X., Yong, J.W.H., Dawoud, T.M., Rahman, S.U., Fan, J., Zhang, Y., 2024. Phytoremediation efficiency of poplar hybrid varieties with diverse genetic backgrounds in soil contaminated by multiple toxic metals (Cd, Hg, Pb, and As). Ecotoxicology and Environmental Safety 283, 116843. https://doi.org/10.1016/j.ecoenv.2024.116843.

Li, H., Wang, T., Du, H., Guo, P., Wang, S., Ma, M., 2024. Research progress in the joint remediation of plants–microbes–soil for heavy metal-contaminated soil in mining areas: a review. Sustainability 16, 8464. https://doi.org/10.3390/su16198464.

Li, Q., Wang, Y., Li, Y., Li, L., Tang, M., Hu, W., Chen, L., Ai, S., 2022. Speciation of heavy metals in soils and their immobilization at micro-scale interfaces among diverse soil components. Sci. Total Environ. 825, 153862. https://doi.org/10.1016/j.scitotenv.2022.153862.

Li, Y., Zamble, D.B., 2009. Nickel homeostasis and nickel regulation: an overview. Chem. Rev. 109, 4617–4643. https://doi.org/10.1021/cr900010n.

Li, Y., Cheng, L., Yang, B., Zhao, Y., Ding, Y., Zhou, C., Wu, Y., Dong, R., Liu, Y., Xu, A., 2024. Remediation of Cd-As-Ni co-contaminated soil by extracellular polymeric substances from *Bacillus subtilis*: dynamic improvements of soil properties and ecotoxicity. Sci. Total Environ. 955, 177009. https://doi.org/10.1016/j.scitotenv.2024.177009.

Liu, L., Zhang, Q., Hu, L., Tang, J., Xu, L., Yang, X., Yong, J.W.H., Chen, X., 2012. Legumes can increase cadmium contamination in neighboring crops. Plos One 7, e42944. https://doi.org/10.1371/journal.pone.0042944.

Łodyga-Chruścińska, E., Sykuła-Zając, A., Olejnik, D., 2012. Determination of nickel in Polish brands of margarines. Food Addit. Contam. Part B 5, 251–254.

Lyyra, S., Meagher, R.B., Kim, T., Heaton, A., Montello, P., Balish, R.S., Merkle, S.A., 2007. Coupling two mercury resistance genes in Eastern cottonwood enhances the processing of organomercury. Plant Biotechnol. J. 5, 254–262.

Ma, X., Burken, J.G., 2003. TCE diffusion to the atmosphere in phytoremediation applications. Environ. Sci. Technol. 37, 2534–2539.

Ma, X., Wang, C., 2010. Fullerene nanoparticles affect the fate and uptake of trichloroethylene in phytoremediation systems. Environ. Eng. Sci. 27, 989–992.

Ma, Y., Rajkumar, M., Freitas, H., 2009. Improvement of plant growth and nickel uptake by nickel resistant-plant-growth promoting bacteria. J. Hazard. Mater. 166, 1154–1161. https://doi.org/10.1016/j.jhazmat.2008.12.018.

Ma, Y., Rajkumar, M., Vicente, J.A.F., Freitas, H., 2010. Inoculation of Ni-resistant plant growth promoting bacterium *Psychrobacter* sp. strain SRS8 for the improvement of nickel phytoextraction by energy crops. Int. J. Phytoremediat. 13, 126–139. https://doi.org/10.1080/15226511003671403.

Ma, Y., Rajkumar, M., Vicente, J.A.F., Freitas, H., 2011. Inoculation of Ni-resistant plant growth promoting bacterium *Psychrobacter* sp. strain SRS8 for the improvement of nickel phytoextraction by energy crops. Int. J. Phytoremediat. 13, 126–139.

Ma, M., Liu, Y., Bai, C., Yang, Y., Sun, Z., Liu, X., Zhang, S., Han, X., Yong, J.W.H., 2021a. The physiological functionality of PGR5/PGRL1-dependent cyclic electron transport in sustaining photosynthesis. Frontiers in Plant Science 12, 702196. https://doi.org/10.3389/fpls.2021.702196.

Ma, M., Liu, Y., Bai, C., Yong, J.W.H., 2021b. The significance of chloroplast NAD(P)H dehydrogenase complex and its dependent cyclic electron transport in photosynthesis. Frontiers in Plant Science 12, 661863. https://doi.org/10.3389/fpls.2021.661863.

Ma, Y., Oliveira, R.S., Freitas, H., Zhang, C., 2016. Biochemical and molecular mechanisms of plant-microbe-metal interactions: relevance for phytoremediation. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00918.

Macomber, L., Hausinger, R.P., 2011. Mechanisms of nickel toxicity in microorganisms. Metallomics 3, 1153–1162.

Maestri, E., Marmiroli, M., Visioli, G., Marmiroli, N., 2010. Metal tolerance and hyperaccumulation: costs and trade-offs between traits and environment. Environ. Exp. Bot. 68, 1–13.

Mahdieh, M., Yazdani, M., Mahdieh, S., 2013. The high potential of *Pelargonium roseum* plant for phytoremediation of heavy metals. Environ. Monit. Assess. 185, 7877–7881. https://doi.org/10.1007/s10661-013-3141-3.

Mani, D., Kumar, C., 2014. Biotechnological advances in bioremediation of heavy metals contaminated ecosystems: an overview with special reference to phytoremediation. Int. J. Environ. Sci. Technol. 11, 843–872.

Marchetto, F., Santaeufemia, S., Lebiedzińska-Arciszewska, M., Śliwińska, M.A., Pich, M., Kurek, E., Naziębło, A., Strawski, M., Solymosi, D., Szklarczyk, M., Bulska, E., Szymański, J., Wierzbicka, M., Allahverdiyeva, Y., Więckowski, M.R., Kargul, J., 2024. Dynamic adaptation of the extremophilic red microalga *Cyanidioschyzon merolae* to high nickel stress. Plant Physiol. Biochem. 207, 108365. https://doi.org/10.1016/j.plaphy.2024.108365.

Maroney, M.J., 1999. Structure/function relationships in nickel metallobiochemistry. Curr. Opin. Chem. Biol. 3, 188–199.

Marschner, H., 2011. Marschner's Mineral Nutrition of Higher Plants. Academic press.

Martinoia, E., Maeshima, M., Neuhaus, H.E., 2007. Vacuolar transporters and their essential role in plant metabolism. J. Exp. Bot. 58, 83–102.

Mastretta, C., Barac, T., Vangronsveld, J., Newman, L., Taghavi, S., Lelie, D. van der, 2006. Endophytic bacteria and their potential application to improve the phytoremediation of contaminated environments. Biotechnol. Genet. Eng. Rev. 23, 175–188.

Maurya, A., Sharma, D., Partap, M., Kumar, R., Bhargava, B., 2023. Microbially-assisted phytoremediation toward air pollutants: current trends and future directions. Environ. Technol. Innov. 31, 103140. https://doi.org/10.1016/j.eti.2023.103140.

Maurya, P.K., Malik, D.S., Yadav, K.K., Kumar, A., Kumar, S., Kamyab, H., 2019. Bioaccumulation and potential sources of heavy metal contamination in fish species in River Ganga basin: Possible human health risks evaluation. Toxicol. Rep. 6, 472–481. https://doi.org/10.1016/j.toxrep.2019.05.012.

McCutcheon, S.C., Schnoor, J.L., 2003. Overview of phytotransformation and control of wastes. Phytoremediat. Transform. Control Contam. 1–58.

McNear Jr., D.H., Chaney, R.L., Sparks, D.L., 2010. The hyperaccumulator *Alyssum murale* uses complexation with nitrogen and oxygen donor ligands for Ni transport and storage. Phytochemistry 71, 188–200.

Memon, A.R., Schröder, P., 2009. Implications of metal accumulation mechanisms to phytoremediation. Environ. Sci. Pollut. Res. 16, 162–175.

Mendes, R., Kruijt, M., De Bruijn, I., Dekkers, E., Van Der Voort, M., Schneider, J.H.M., Piceno, Y.M., DeSantis, T.Z., Andersen, G.L., Bakker, P.A.H.M., 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Sci. (80-.) 332, 1097–1100.

Mengistu, A.A., 2020. Endophytes: colonization, behaviour, and their role in defense mechanism. Int. J. Microbiol. 2020, 1–8. https://doi.org/10.1155/2020/6927219.

Mengoni, A., Baker, A.J.M., Bazzicalupo, M., Reeves, R.D., Adigüzel, N., Chianni, E., Galardi, F., Gabbrielli, R., Gonnelli, C., 2003. Evolutionary dynamics of nickel hyperaccumulation in Alyssum revealed by its nrDNA analysis. N. Phytol. 159, 691–699. https://doi.org/10.1046/j.1469-8137.2003.00837.x.

Merian, E., 1984. Introduction on environmental chemistry and global cycles of chromium, nickel, cobalt beryllium, arsenic, cadmium and selenium, and their derivatives.

Mitch, M.L., 2002. Phytoextraction of toxic metals: a review of biological mechanism. J. Environ. Qual. 31, 109–120.

Mizuno, T., Usui, K., Horie, K., Nosaka, S., Mizuno, N., Obata, H., 2005. Cloning of three ZIP/Nramp transporter genes from a Ni hyperaccumulator plant Thlaspi japonicum and their Ni2+ -transport abilities. Plant Physiol. Biochem. 43, 793–801.

Moradi Alvand, Z., Rajabi, H.R., Mirzaei, A., Masoumiasl, A., Sadatfaraji, H., 2019. Rapid and green synthesis of cadmium telluride quantum dots with low toxicity based on a plant-mediated approach after microwave and ultrasonic assisted extraction: Synthesis, characterization, biological potentials and comparison study. Mater. Sci. Eng. C. 98, 535–544. https://doi.org/10.1016/j.msec.2019.01.010.

Morais, I., Campos, J.S., Favas, P.J.C., Pratas, J., Pita, F., Prasad, M.N.V., 2015. Nickel accumulation by Alyssum serpyllifolium subsp. lusitanicum (Brassicaceae) from serpentine soils of Bragança and Morais (Portugal) ultramafic massifs: plant–soil relationships and prospects for phytomining. Aust. J. Bot. 63, 17. https://doi.org/10.1071/BT14245.

Mukhopadhyay, S., Maiti, S.K., 2010. Phytoremediation of metal mine waste. Appl. Ecol. Environ. Res. 8, 207–222.

Mulrooney, S.B., Hausinger, R.P., 2003. Nickel uptake and utilization by microorganisms. FEMS Microbiol. Rev. 27, 239–261.

Muñoz, R., Alvarez, M.T., Muñoz, A., Terrazas, E., Guieysse, B., Mattiasson, B., 2006. Sequential removal of heavy metals ions and organic pollutants using an algal-bacterial consortium. Chemosphere 63, 903–911. https://doi.org/10.1016/j.chemosphere.2005.09.062.

Musiani, F., Zambelli, B., Bazzani, M., Mazzei, L., Ciurli, S., 2015. Nickel-responsive transcriptional regulators. Metallomics 7, 1305–1318.

Mustafa, A., Zulfiqar, U., Mumtaz, M.Z., Radziemska, M., Haider, F.U., Holatko, J., Hammershmiedt, T., Naveed, M., Ali, H., Kintl, A., Saeed, Q., Kucerik, J., Brtnicky, M., 2023. Nickel (Ni) phytotoxicity and detoxification mechanisms: a review. Chemosphere 328, 138574. https://doi.org/10.1016/j.chemosphere.2023.138574.

Nabi, A., Naeem, M., Aftab, T., Khan, M.M.A., 2020. Alterations in photosynthetic pigments, antioxidant machinery, essential oil constituents and growth of menthol mint (*Mentha arvensis* L.) upon nickel exposure. Braz. J. Bot. 43, 721–731. https://doi.org/10.1007/s40415-020-00649-w.

Naqqash, T., Aziz, A., Baber, M., Shahid, M., Sajid, M., Emanuele, R., Gaafar, A.-R.Z., Hodhod, M.S., Haider, G., 2024. Metal-tolerant *Morganella morganii* isolates can potentially mediate nickel stress tolerance in *Arabidopsis* by upregulating antioxidative enzyme activities. Plant Signal. Behav. 19. https://doi.org/10.1080/15592324.2024.2318513.

Navarro, C., Wu, L.F., Mandrand-Berthelot, M.A., 1993. The *nik* operon of *Escherichia coli* encodes a periplasmic binding-protein-dependent transport system for nickel. Mol. Microbiol. 9, 1181–1191. https://doi.org/10.1111/j.1365-2958.1993.tb01247.x.

Özyiğit, İ.İ., Doğan, İ., 2014. Plant-microbe interactions in phytoremediation. Soil Remediat. plants Prospect. challenges.

Palmgren, M.G., 2001. Plant plasma membrane H+ -ATPases: powerhouses for nutrient uptake. Annu. Rev. Plant Biol. 52, 817–845.

Pandey, P., Kang, S.C., Maheshwari, D.K., 2005. Isolation of endophytic plant growth promoting *Burkholderia* sp. MSSP from root nodules of *Mimosa pudica*. Curr. Sci. 177, 180.

Parida, B.K., Chhibba, I.M., Nayyar, V.K., 2003. Influence of nickel-contaminated soils on fenugreek (*Trigonella corniculata* L.) growth and mineral composition. Sci. Hortic. (Amst.). 98, 113–119.

Parseghian, L., Esmaeili, H., Rafati, H., Rajabi, H.R., Alvand, Z.M., 2024. Rapid synthesis of magnetic Fe3O4/Ag nanocomposite based on a plant-mediated approach and its biological activity. Environ. Sci. Pollut. Res. 31, 65559–65573. https://doi.org/10.1007/s11356-024-35614-7.

Pašakinskienė, I., Stakelienė, V., Matijošiūtė, S., Martūnas, J., 2024. Diversity of endophytic fungi and bacteria inhabiting the roots of the woodland grass, *Festuca gigantea* (Poaceae). Diversity 16, 453. https://doi.org/10.3390/d16080453.

Paul, A.L.D., Gei, V., Isnard, S., Fogliani, B., Echevarria, G., Erskine, P.D., Jaffré, T., Munzinger, J., van der Ent, A., 2020. Nickel hyperaccumulation in New Caledonian *Hybanthus* (Violaceae) and occurrence of nickel-rich phloem in *Hybanthus austrocaledonicus*. Ann. Bot. 126, 905–914. https://doi.org/10.1093/aob/mcaa112.

Peer, W.A., Baxter, I.R., Richards, E.L., Freeman, J.L., Murphy, A.S., 2006. Phytoremediation and hyperaccumulator plants. Mol. Biol. Met. Homeost. Detoxif. Microbes Man 299–340.

Persans, M.W., Nieman, K., Salt, D.E., 2001. Functional activity and role of cation-efflux family members in Ni hyperaccumulation in thlaspi goesingense. Proc. Natl. Acad. Sci. 98, 9995–10000.

Phour, M., Sehrawat, A., Sindhu, S.S., Glick, B.R., 2020. Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. Microbiol. Res. 241, 126589. https://doi.org/10.1016/j.micres.2020.126589.

Pilon-Smits, E.A.H., LeDuc, D.L., 2009. Phytoremediation of selenium using transgenic plants. Curr. Opin. Biotechnol. 20, 207–212.

Polacco, J.C., Mazzafera, P., Tezotto, T., 2013. Opinion–nickel and urease in plants: still many knowledge gaps. Plant Sci. 199, 79–90.

Prasad, M.N.V., 2005. Nickelophilous plants and their significance in phytotechnologies. Braz. J. Plant Physiol. 17, 113–128.

Puglisi, E., Hamon, R., Vasileiadis, S., Coppolecchia, D., Trevisan, M., 2012. Adaptation of soil microorganisms to trace element contamination: a review of mechanisms, methodologies, and consequences for risk assessment and remediation. Crit. Rev. Environ. Sci. Technol. 42, 2435–2470.

Qin, G.W., Niu, Z.D., Yu, J.D., Li, Z.H., Ma, J.Y., Xiang, P., 2021. Soil heavy metal pollution and food safety in China: Effects, sources and removing technology. Chemosphere 267, 129205. https://doi.org/10.1016/j.chemosphere.2020.129205.

Qin, C., Shen, J., Ahanger, M.A., 2023. Corrigendum: Supplementation of nitric oxide and spermidine alleviates the nickel stress induced damage to growth, chlorophyll metabolism and photosynthesis by up-regulating ascorbate-glutathione and glyoxalase cycle functioning in tomato. Front. Plant Sci. 14. https://doi.org/10.3389/fpls.2023.1239602.

Rafeeq, H., Afsheen, N., Rafique, S., Arshad, A., Intisar, M., Hussain, A., Bilal, M., Iqbal, H.M.N., 2023. Genetically engineered microorganisms for environmental remediation. Chemosphere 310, 136751. https://doi.org/10.1016/j.chemosphere.2022.136751.

Raghu, G., Balaji, V., Venkateswaran, G., Rodrigue, A., Maruthi Mohan, P., 2008. Bioremediation of trace cobalt from simulated spent decontamination solutions of nuclear power reactors using E. coli expressing NiCoT genes. Appl. Microbiol. Biotechnol. 81, 571–578. https://doi.org/10.1007/s00253-008-1741-6.

Rajabi, H.R., Naghiha, R., Kheirizadeh, M., Sadatfaraji, H., Mirzaei, A., Alvand, Z.M., 2017. Microwave assisted extraction as an efficient approach for biosynthesis of zinc oxide nanoparticles: Synthesis, characterization, and biological properties. Mater. Sci. Eng. C. 78, 1109–1118. https://doi.org/10.1016/j.msec.2017.03.090.

Rajabi, H.R., Alvand, Z.M., Mirzaei, A., 2023. Sonochemical-assisted synthesis of copper oxide nanoparticles with the plant-mediated approach and comparative evaluation of some biological activities. Environ. Sci. Pollut. Res. 30, 120236–120249. https://doi.org/10.1007/s11356-023-30684-5.

Rajkumar, M., Freitas, H., 2008. Effects of inoculation of plant-growth promoting bacteria on Ni uptake by Indian mustard. Bioresour. Technol. 99, 3491–3498. https://doi.org/10.1016/j.biortech.2007.07.046.

Rajkumar, M., Ae, N., Freitas, H., 2009. Endophytic bacteria and their potential to enhance heavy metal phytoextraction. Chemosphere 77, 153–160. https://doi.org/10.1016/j.chemosphere.2009.06.047.

Rajkumar, M., Ma, Y., Freitas, H., 2013. Improvement of Ni phytostabilization by inoculation of Ni resistant Bacillus megaterium SR28C. J. Environ. Manage. 128, 973–980. https://doi.org/10.1016/j.jenvman.2013.07.001.

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

Rascio, N., Navari-Izzo, F., 2011. Heavy metal hyperaccumulating plants: how and why do they do it? And what makes them so interesting? Plant Sci. 180, 169–181.

Rashid, A., Schutte, B.J., Ulery, A., Deyholos, M.K., Sanogo, S., Lehnhoff, E.A., Beck, L., 2023. Heavy metal contamination in agricultural soil: environmental pollutants affecting crop Health. Agronomy 13, 1521. https://doi.org/10.3390/agronomy13061521.

Rauser, W.E., 1995. Phytochelatins and related peptides. structure, biosynthesis, and function. Plant Physiol. 109, 1141.

Reeves, R.D., Baker, A.J.M., Borhidi, A., Berazain, R., 1996. Nickel-accumulating plants from the ancient serpentine soils of Cuba. N. Phytol. 133, 217–224.

Reeves, R.D., Baker, A.J.M., Borhidi, A., Berazain, R., 1999. Nickel hyperaccumulation in the serpentine flora of Cuba. Ann. Bot. 83, 29–38.

Ricciardi, L., Arena, A., Arena, E., Zambito, M., Ingrassia, A., Valenti, G., Loschiavo, G., D'Angelo, A., Saitta, S., 2014. Systemic nickel allergy syndrome: epidemiological data from four Italian allergy units. Int. J. Immunopathol. Pharmacol. 27, 131–136.

Rinklebe, J., Shaheen, S.M., 2017. Redox chemistry of nickel in soils and sediments: a review. Chemosphere 179, 265–278. https://doi.org/10.1016/j.chemosphere.2017.02.153.

Robinson, B.H., Lombi, E., Zhao, F.J., McGrath, S.P., 2003. Uptake and distribution of nickel and other metals in the hyperaccumulator Berkheya coddii. N. Phytol. 158, 279–285.

Roccotiello, E., Serrano, H.C., Mariotti, M.G., Branquinho, C., 2015. Nickel phytoremediation potential of the mediterranean *Alyssoides utriculata* (L.) Medik. Chemosphere 119, 1372–1378. https://doi.org/10.1016/j.chemosphere.2014.02.031.

Rodionov, D.A., Hebbeln, P., Gelfand, M.S., Eitinger, T., 2006. Comparative and functional genomic analysis of prokaryotic nickel and cobalt uptake transporters: evidence for a novel group of ATP-binding cassette transporters. J. Bacteriol. 188, 317–327. https://doi.org/10.1128/JB.188.1.317-327.2006.

Rodrigue, A., Effantin, G., Mandrand-Berthelot, M.-A., 2005. Identification of rcnA (yohM), a nickel and cobalt resistance gene in Escherichia coli. J. Bacteriol. 187, 2912–2916. https://doi.org/10.1128/JB.187.8.2912-2916.2005.

da Rosa, J.C., Malajian, D., Shemer, A., Rozenblit, M., Dhingra, N., Czarnowicki, T., Khattri, S., Ungar, B., Finney, R., Xu, H., 2015. Patients with atopic dermatitis have attenuated and distinct contact hypersensitivity responses to common allergens in skin. J. Allergy Clin. Immunol. 135, 712–720.

Rothballer, M., Schmid, M., Hartmann, A., 2003. *In situ* localization and PGPR-effect of *Azospirillum brasilense* strains colonizing roots of different wheat varieties. Symbiosis 34, 261–279.

Ryan, R.P., Germaine, K., Franks, A., Ryan, D.J., Dowling, D.N., 2008. Bacterial endophytes: recent developments and applications. FEMS Microbiol. Lett. 278, 1–9.

Sabry, S.A., Ghozlan, H.A., Abou-Zeid, D., 1997. Metal tolerance and antibiotic resistance patterns of a bacterial population isolated from sea water. J. Appl. Microbiol. 82, 245–252.

Safonova, E., Kvitko, K.V., Iankevitch, M.I., Surgko, L.F., Afti, I.A., Reisser, W., 2004. Biotreatment of industrial wastewater by selected algal-bacterial consortia. Eng. Life Sci. 4, 347–353. https://doi.org/10.1002/elsc.200420039.

Salt, D.E., Prince, R.C., Pickering, I.J., Raskin, I., 1995. Mechanisms of cadmium mobility and accumulation in Indian mustard. Plant Physiol. 109, 1427–1433.

Sani, M.N.H., Amin, M., Bergstrand, K.J., Caspersen, S., Prade, T., Yong, J.W.H., 2024. Harnessing biostimulants from biogas digestates for high-value resource recovery: a review. Environmental Chemistry Letters 22. https://doi.org/10.1007/s10311-024-01801-8.

Sani, M.N.H., Amin, M., Siddique, A.B., Nasif, S.O., Ghaley, B.B., Ge, L., Wang, F., Yong, J.W.H., 2023. Waste-derived nanobiochar: a new avenue towards sustainable agriculture, environment, and circular bioeconomy. Science of the Total Environment 905, 166881. https://doi.org/10.1016/j.scitotenv.2023.166881.

Santoyo, G., Urtis-Flores, C.A., Loeza-Lara, P.D., Orozco-Mosqueda, M. del C., Glick, B.R., 2021. Rhizosphere colonization determinants by plant growth-promoting rhizobacteria (PGPR). Biol. (Basel) 10, 475.

Schat, H., Llugany, M., Vooijs, R., Hartley-Whitaker, J., Bleeker, P.M., 2002. The role of phytochelatins in constitutive and adaptive heavy metal tolerances in hyperaccumulator and non-hyperaccumulator metallophytes. J. Exp. Bot. 53, 2381–2392.

Schaumlöffel, D., Ouerdane, L., Bouyssiere, B., Łobiński, R., 2003. Speciation analysis of nickel in the latex of a hyperaccumulating tree Sebertia acuminata by HPLC and CZE with ICP MS and electrospray MS-MS detection. J. Anal. At. Spectrom. 18, 120–127.

Schrenk, D., Bignami, M., Bodin, L., Chipman, J.K., del Mazo, J., Grasl-Kraupp, B., Hogstrand, C., Hoogenboom, L. (Ron), Leblanc, J., Nebbia, C.S., Ntzani, E., Petersen, A., Sand, S., Schwerdtle, T., Vleminckx, C., Wallace, H., Guérin, T., Massanyi, P., Van Loveren, H., Baert, K., Gergelova, P., Nielsen, E., 2020. Update of the risk assessment of nickel in food and drinking water. EFSA J. 18. https://doi.org/10.2903/j.efsa.2020.6268.

Seregin, I.V., Ivanov, V.B., 2001. Physiological aspects of cadmium and lead toxic effects on higher plants. Russ. J. Plant Physiol. 48, 523–544.

Seregin, Iv, Kozhevnikova, A.D., 2006. Physiological role of nickel and its toxic effects on higher plants. Russ. J. Plant Physiol. 53, 257–277.

Shabayev, V.P., Ostroumov, V.E., 2023. Soil-agrochemical aspects of remediation of nickel-contaminated soil using growth-promoting rhizosphere bacteria. Eurasia Soil Sci. 56, 198–209. https://doi.org/10.1134/S1064229322601731.

Shaghaleh, H., Azhar, M., Zia-ur-Rehman, M., Hamoud, Y.A., Hamad, A.A.A., Usman, M., Rizwan, M., Yong, J.W.H., Alharby, H.F., Al-Ghamdi, A.J., Alharbi, B.M., 2024. Effects of agro based organic amendments on growth and cadmium uptake in wheat and rice crops irrigated with raw city effluents: Three years field study. Environmental Pollution 344, 123365. https://doi.org/10.1016/j.envpol.2024.123365.

Shahzad, A., Siddique, A., Ferdous, S., Amin, M.A., Qin, M., Aslam, U., Naeem, M., Bashir, T., Shakoor, A., 2023. Heavy metals mitigation and growth promoting effect of endophytic *Agrococcus terreus* (MW 979614) in maize plants under zinc and nickel contaminated soil. Front. Microbiol. 14. https://doi.org/10.3389/fmicb.2023.1255921.

Sharma, A., 2013. Low nickel diet in dermatology. Indian J. Dermatol. 58, 240. https://doi.org/10.4103/0019-5154.110846.

Sharma, N., Yadav, G., Varma, A., Koul, M., Mishra, A., 2024. Heavy metal remediation from rhizospheric soil by using microbial consortium, in: Microbiology-2.0 Update for a Sustainable Future. Springer Nature Singapore, Singapore, pp. 57–76. https://doi.org/10.1007/978-981-99-9617-9_4.

Sharma, S., Sharma, M., Kumar, R., Akhtar, M.S., Umar, A., Alkhanjaf, A.A.M., Baskoutas, S., 2023. Recent advances and mechanisms of microbial bioremediation of nickel from wastewater. Environ. Sci. Pollut. Res. 31, 40224–40244. https://doi.org/10.1007/s11356-023-30556-y.

Sharma, S.S., Dietz, K., Mimura, T., 2016. Vacuolar compartmentalization as indispensable component of heavy metal detoxification in plants. Plant. Cell Environ. 39, 1112–1126. https://doi.org/10.1111/pce.12706.

Sheoran, V., Sheoran, A.S., Poonia, P., 2010. Role of hyperaccumulators in phytoextraction of metals from contaminated mining sites: a review. Crit. Rev. Environ. Sci. Technol. 41, 168–214.

Shi, A., Liu, J., Zou, S., Rensing, C., Zhao, Y., Zhang, L., Xing, S., Yang, W., 2024. Enhancement of cadmium uptake in *Sedum alfredii* through interactions between salicylic acid/jasmonic acid and rhizosphere microbial communities. Sci. Total Environ. 947, 174585. https://doi.org/10.1016/j.scitotenv.2024.174585.

Shi, W., Becker, J., Bischoff, M., Turco, R.F., Konopka, A.E., 2002. Association of microbial community composition and activity with lead, chromium, and hydrocarbon contamination. Appl. Environ. Microbiol. 68, 3859–3866.

Sigel, A., Sigel, H., Sigel, R.K.O., 2007. Nickel and Its Surprising Impact in Nature, 2. John Wiley & Sons.

Singh, A., Kuhad, R.C., Ward, O.P., 2009. Biological remediation of soil: an overview of global market and available technologies. Adv. Appl. bioremediation 1–19.

Singh, V.P., 2005. Metal Toxicity and Tolerance In Plants And Animals. Sarup & sons.

Sitte, J., Pollok, K., Langenhorst, F., Küsel, K., 2013. Nanocrystalline nickel and cobalt sulfides formed by a heavy metal-tolerant, sulfate-reducing enrichment culture. Geomicrobiol. J. 30, 36–47. https://doi.org/10.1080/01490451.2011.653082.

Song, J., Finnegan, P.M., Liu, W., Xiang, L., Yong, J.W.H., Xu, J., Zhang, Q., Wen, Y., Qin, K., Guo, J., Li, T., Zhao, C., Zhang, Y., 2019. Mechanisms underlying enhanced Cd translocation and tolerance in roots of *Populus euramericana* in response to nitrogen fertilization. Plant Science 287, 110206. https://doi.org/10.1016/j.plantsci.2019.110206.

Stearns, J.C., Shah, S., Greenberg, B.M., Dixon, D.G., Glick, B.R., 2005. Tolerance of transgenic canola expressing 1-aminocyclopropane-1-carboxylic acid deaminase to growth inhibition by nickel. Plant Physiol. Biochem. 43, 701–708.

Sujkowska-Rybkowska, M., Rusaczonek, A., Kasowska, D., Gediga, K., Banasiewicz, J., Stępkowski, T., Bernacki, M.J., 2022. Potential of rhizobia nodulating *Anthyllis vulneraria* L. from ultramafic soil as plant growth promoting bacteria alleviating nickel stress in *Arabidopsis thaliana* L. Int. J. Mol. Sci. 23, 11538. https://doi.org/10.3390/ijms231911538.

Sun, X.-H., Yu, G., Li, J.-T., Jia, P., Zhang, J.-C., Jia, C.-G., Zhang, Y.-H., Pan, H.-Y., 2014. A heavy metal-associated protein (AcHMA1) from the halophyte, *Atriplex canescens* (Pursh) Nutt., confers tolerance to iron and other abiotic stresses when expressed in *Saccharomyces cerevisiae*. Int. J. Mol. Sci. 15, 14891–14906.

Suresh, B., Ravishankar, G.A., 2004. Phytoremediation—a novel and promising approach for environmental clean-up. Crit. Rev. Biotechnol. 24, 97–124.

Tack, F.M.G., 2010. Trace elements: general soil chemistry, principles and processes. Trace Elem. Soils 9–37.

Tamaoki, M., Freeman, J.L., Pilon-Smits, E.A.H., 2008. Cooperative ethylene and jasmonic acid signaling regulates selenite resistance in *Arabidopsis*. Plant Physiol. 146, 1219–1230.

Tan, S.N., Yong, J.W.H., Ng, Y.F., 2010. Arsenic exposure from drinking water and mortality in Bangladesh. Lancet 376, 1641–1642. https://doi.org/10.1016/S0140-6736(10)62090-9.

Tan, R.X., Zou, W.X., 2001. Endophytes: a rich source of functional metabolites. Nat. Prod. Rep. 18, 448–459.

Tang, X., Li, X., Liu, X., Hashmi, M.Z., Xu, J., Brookes, P.C., 2015. Effects of inorganic and organic amendments on the uptake of lead and trace elements by *Brassica chinensis* grown in an acidic red soil. Chemosphere 119, 177–183. https://doi.org/10.1016/j.chemosphere.2014.05.081.

Tank, N., Saraf, M., 2009. Enhancement of plant growth and decontamination of nickel-spiked soil using PGPR. J. Basic Microbiol. 49, 195–204.

Teptina, A.Y., Paukov, A.G., 2015. Nickel accumulation by species of *Alyssum* and *Noccaea* (Brassicaceae) from ultramafic soils in the Urals, Russia. Aust. J. Bot. 63, 78. https://doi.org/10.1071/BT14265.

Thyssen, J.P., Menné, T., 2010. Metal allergy–a review on exposures, penetration, genetics, prevalence, and clinical implications. Chem. Res. Toxicol. 23, 309–318.

Tian, H.Z., Lu, L., Cheng, K., Hao, J.M., Zhao, D., Wang, Y., Jia, W.X., Qiu, P.P., 2012. Anthropogenic atmospheric nickel emissions and its distribution characteristics in China. Sci. Total Environ. 417, 148–157.

Tiwari, S., Singh, S.N., Garg, S.K., 2012. Stimulated phytoextraction of metals from fly ash by microbial interventions. Environ. Technol. 33, 2405–2413.

Tow, T.S.W., Eng, Z.X., Wong, S.P., Ge, L., Tan, S.N., Yong, J.W.H., 2019. *Axonopus compressus* (Sw.) Beauv.: A potential biomonitor for molybdenum in soil pollution. International Journal of Phytoremediation 20, 1363–1368. https://doi.org/10.1080/15226514.2016.1207599.

Vacchina, V., Mari, S., Czernic, P., Marquès, L., Pianelli, K., Schaumlöffel, D., Lebrun, M., Łobiński, R., 2003. Speciation of nickel in a hyperaccumulating plant by high-performance liquid chromatography– inductively coupled plasma mass spectrometry and electrospray MS/MS assisted by cloning using yeast complementation. Anal. Chem. 75, 2740–2745.

Vacheron, J., Desbrosses, G., Bouffaud, M.-L., Touraine, B., Moënne-Loccoz, Y., Muller, D., Legendre, L., Wisniewski-Dyé, F., Prigent-Combaret, C., 2013. Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci. 4. https://doi.org/10.3389/fpls.2013.00356.

Van der Ent, A., Baker, A.J.M., Reeves, R.D., Pollard, A.J., Schat, H., 2013. Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant Soil 362, 319–334.

Vara Prasad, M.N., de Oliveira Freitas, H.M., 2003. Metal hyperaccumulation in plants: biodiversity prospecting for phytoremediation technology. Electron. J. Biotechnol. 6, 285–321.

Vidali, M., 2001. Bioremediation. an overview. Pure Appl. Chem. 73, 1163–1172.

Visioli, G., Vamerali, T., Mattarozzi, M., Dramis, L., Sanangelantoni, A.M., 2015. Combined endophytic inoculants enhance nickel phytoextraction from serpentine soil in the hyperaccumulator *Noccaea caerulescens*. Front. Plant Sci. 6, 156553.

Wang, F., Gao, J., Yong, J.W.H., Wang, Q, Ma, J., He, X., 2020. Higher atmospheric CO_2 levels favor C_3 plants over C_4 plants in utilizing ammonium as a nitrogen source. Frontiers in Plant Science 11, e537443. https://doi.org/10.3389/fpls.2020.537443.

Wei, X., Xie, B., Wan, C., Song, R., Zhong, W., Xin, S., Song, K., 2024. Enhancing soil health and plant growth through microbial fertilizers: mechanisms, benefits, and sustainable agricultural practices. Agronomy 14, 609. https://doi.org/10.3390/agronomy14030609.

Welch, R.M., 1981. The biological significance of nickel. J. Plant Nutr. 3, 345–356.

Wen, M., Ma, Z., Gingerich, D.B., Zhao, X., Zhao, D., 2022. Heavy metals in agricultural soil in China: A systematic review and meta-analysis. Eco-Environ. Heal 1, 219–228. https://doi.org/10.1016/j.eehl.2022.10.004.

Wenzel, W.W., Bunkowski, M., Puschenreiter, M., Horak, O., 2003. Rhizosphere characteristics of indigenously growing nickel hyperaccumulator and excluder plants on serpentine soil. Environ. Pollut. 123, 131–138.

Weyens, N., van der Lelie, D., Taghavi, S., Vangronsveld, J., 2009. Phytoremediation: plant–endophyte partnerships take the challenge. Curr. Opin. Biotechnol. 20, 248–254.

Weyens, N., Croes, S., Dupae, J., Newman, L., van der Lelie, D., Carleer, R., Vangronsveld, J., 2010. Endophytic bacteria improve phytoremediation of Ni and TCE co-contamination. Environ. Pollut. 158, 2422–2427. https://doi.org/10.1016/j.envpol.2010.04.004.

Weyens, N., Beckers, B., Schellingen, K., Ceulemans, R., van der Lelie, D., Newman, L., Taghavi, S., Carleer, R., Vangronsveld, J., 2015. The potential of the ni-resistant TCE-degrading *Pseudomonas putida* W619-TCE to reduce phytotoxicity and improve phytoremediation efficiency of poplar cuttings on a Ni-TCE co-contamination. Int. J. Phytoremediat. 17, 40–48. https://doi.org/10.1080/15226514.2013.828016.

Whiting, S.N., de Souza, M.P., Terry, N., 2001. Rhizosphere bacteria mobilize Zn for hyperaccumulation by *Thlaspi caerulescens*. Environ. Sci. Technol. 35, 3144–3150.

Willey, N., 2008. Phytoremediation: Methods And Reviews. Springer Science & Business Media.

Wu, G., Kang, H., Zhang, X., Shao, H., Chu, L., Ruan, C., 2010. A critical review on the bio-removal of hazardous heavy metals from contaminated soils: issues, progress, eco-environmental concerns and opportunities. J. Hazard. Mater. 174, 1–8.

Wu, H., Eckhardt, C.M., Baccarelli, A.A., 2023. Molecular mechanisms of environmental exposures and human disease. Nat. Rev. Genet. 24, 332–344. https://doi.org/10.1038/s41576-022-00569-3.

Wong, W.S., Zhong, H.T., Cross, A.T., Yong, J.W.H., 2020. Plant biostimulants in vermicomposts: characteristics and plausible mechanisms. In: Geelen, D., Xu, L. (Eds.) (Eds.), The Chemical Biology of Plant Biostimulants. Wiley, pp. 155–180. https://doi.org/10.1002/9781119357254.ch6.

Wu, S.C., Cheung, K.C., Luo, Y.M., Wong, M.H., 2006. Effects of inoculation of plant growth-promoting rhizobacteria on metal uptake by *Brassica juncea*. Environ. Pollut. 140, 124–135.

Wu, Z., Li, F., Wang, F., Jin, R., Li, Y., Li, S., Zhou, Z., Jia, P., Li, J., 2024. A synthetic bacterial consortium improved the phytoremediation efficiency of ryegrass on polymetallic contaminated soil. Ecotoxicol. Environ. Saf. 282, 116691. https://doi.org/10.1016/j.ecoenv.2024.116691.

Xia, Y., Liu, J., Chen, C., Mo, X., Tan, Q., He, Y., Wang, Z., Yin, J., Zhou, G., 2022. The multifunctions and future prospects of endophytes and their metabolites in plant disease management. Microorganisms 10, 1072. https://doi.org/10.3390/microorganisms10051072.

Xiong, J., He, Z., Liu, D., Mahmood, Q., Yang, X., 2008. The role of bacteria in the heavy metals removal and growth of *Sedum alfredii* Hance in an aqueous medium. Chemosphere 70, 489–494.

Yang, X.E., Yang, M.J., Shen, Z.Y., Bacon, J.R., Paterson, E., Wilson, J.M., 2001. Some mechanisms of zinc and cadmium detoxification in a zinc and cadmium hyper-accumulating plant species (*Thlaspi*). Plant Nutr. Food Secur. Sustain. agro-Ecosyst. Basic Appl. Res. 444–445. https://doi.org/10.1007/0-306-47624-X_214.

Yang, Z., Zhang, Z., Chai, L., Wang, Y., Liu, Y., Xiao, R., 2016. Bioleaching remediation of heavy metal-contaminated soils using *Burkholderia* sp. Z-90. J. Hazard. Mater. 301, 145–152. https://doi.org/10.1016/j.jhazmat.2015.08.047.

Yin, F., Li, J., Wang, Y., Yang, Z., 2024. Biodegradable chelating agents for enhancing phytoremediation: mechanisms, market feasibility, and future studies. Ecotoxicol. Environ. Saf. 272, 116113. https://doi.org/10.1016/j.ecoenv.2024.116113.

Yong, J.W.H., Letham, D.S., Wong, S.C., Farquhar, G.D., 2014. *Rhizobium*-induced elevation in xylem cytokinin delivery in pigeonpea induces changes in shoot development and leaf physiology. Funct Plant Biol 41, 1323–1335. https://doi.org/10.1071/FP14066.

Yong, J.W.H., Tan, S.N., Ng, Y.F., Low, K.K.K., Peh, S.F., Chua, J.C., Lim, A.A.B., 2010. Arsenic hyperaccumulation by *Pteris vittata* and *Pityrogramma calomelanos*: A comparative study of uptake efficiency in arsenic treated soils and waters. Water Science and Technology 61, 3041–3049. https://doi.org/10.2166/wst.2010.223.

Yousuf, S., Singh, R., 2024. Biofilm-mediated heavy metals bioremediation. In: Microbial Applications for Environmental Sustainability. Springer Nature Singapore, Singapore, pp. 201–215. https://doi.org/10.1007/978-981-97-0676-1_12.

Zaidi, S., Usmani, S., Singh, B.R., Musarrat, J., 2006. Significance of *Bacillus subtilis* strain SJ-101 as a bioinoculant for concurrent plant growth promotion and nickel accumulation in *Brassica juncea*. Chemosphere 64, 991–997. https://doi.org/10.1016/j.chemosphere.2005.12.057.

Zambelli, B., Ciurli, S., 2013. Nickel and human health. Interrelat. Essent. Met. ions Hum. Dis. 321–357.

Zhang, Y.-M., Yin, H., Ye, J.-S., Peng, H., Zhang, N., Qin, H.-M., Yang, F., He, B.-Y., 2007. Cloning and expression of the nickel/cobalt transferase gene in *E. coli* BL21 and bioaccumulation of nickel ion by genetically engineered strain (in Chinese). Huan jing ke xue (Environmental Science) 28, 918–923.

Zinniel, D.K., Lambrecht, P., Harris, N.B., Feng, Z., Kuczmarski, D., Higley, P., Ishimaru, C.A., Arunakumari, A., Barletta, R.G., Vidaver, A.K., 2002. Isolation and characterization of endophytic colonizing bacteria from agronomic crops and prairie plants. Appl. Environ. Microbiol. 68, 2198–2208.