





MINIREVIEW

Plant nutrition challenges for a sustainable agriculture of the future

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Abstract

This article offers a comprehensive review of sustainable plant nutrition concepts, examining a multitude of cutting-edge techniques that are revolutionizing the modern area. The review copes with the crucial role of biostimulants as products that stimulate plant nutrition processes, including their potential for biofertilization, followed by an exploration of the significance of micronutrients in plant health and growth. We then delve into strategies for enhancing plants' tolerance to mineral nutrient contaminants and the promising realm of biofortification to increase the essential nutrients necessary for human health. Furthermore, this work also provides a concise overview of the burgeoning field of nanotechnologies in fertilization, while the integration of circular economy principles underscores the importance of sustainable resource management. Then, with examined the interrelation between micronutrients. We conclude with the future challenges and opportunities that lie ahead in the pursuit of more sustainable and resilient plant systems.

1 | INTRODUCTION

The future of plant nutrition is at the forefront of agricultural research, as global challenges such as climate change, soil degradation, and population growth intensify the need for more efficient and sustainable farming practices (Prasad & Shivay 2020). Traditional fertilization methods are becoming less effective, often leading to environmental harm through nutrient runoff, soil depletion, and contamination. Current research is trying to address the multifaceted challenges of plant nutrition, from identifying nutrient-dense germplasm and optimizing crop nutrient content under changing climate conditions to understanding the socio-economic factors influencing consumer acceptance and market integration. The objective is to integrate plant nutrition more closely into the global food production system, thereby ensuring its effective contribution to the reduction of

malnutrition and the improvement of public health on a large scale (Schjørring & Cakmak, 2014).

In response, scientists are exploring innovative approaches to plant nutrition beyond conventional techniques, focusing on enhancing nutrient use efficiency, improving plant tolerance to contaminants, and ensuring food security in a rapidly changing world (Figure 1). Emerging technologies such as biostimulants, biofortification, and nanofertilizers, with special attention to micronutrients, hold great promise in reshaping the way nutrients are delivered to plants, promoting healthier crops and minimizing environmental impact. As we look toward the future, the integration of these advancements, along with a deeper understanding of plant physiology and soil health, we should be able to create more resilient, productive, and sustainable plants. Therefore, in this review, we provide a comprehensive overview of the latest advancements in plant nutrition, with a focus on innovative approaches that enhance nutrient use efficiency, improve plant health, and contribute to sustainable plant production with a

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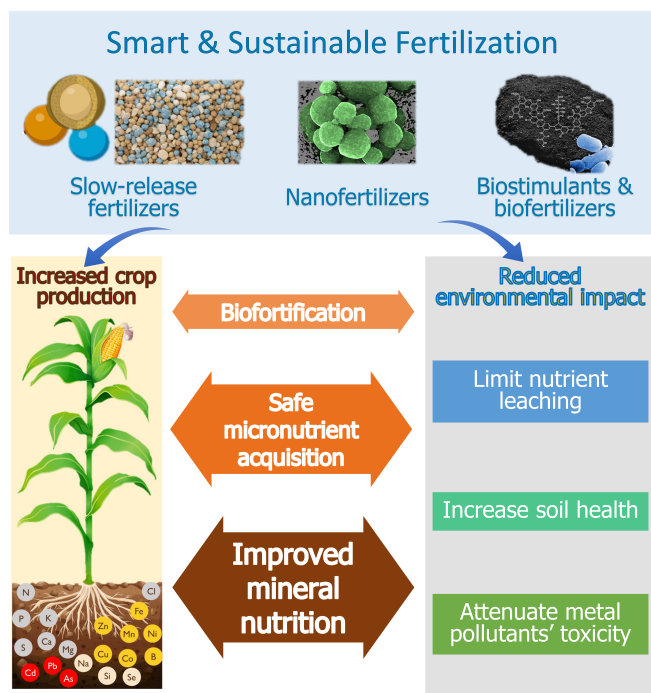


FIGURE 1 The application of fertilizers has resulted in a discernible and persistent enhancement in crop yields over time. Nevertheless, it is now imperative to mitigate the environmental consequences of excessive fertilization and to propose innovative alternatives for sustainable plant nutrition. This will require the development of novel approaches to plant nutrition that foster more sustainable and environmentally friendly forms of agriculture. In accordance with the “One Health” concept, research is advancing new plant nutrition technologies that employ all available organic, inorganic, and biological nutrient sources with high efficiency, tailored to the specific characteristics of agroecosystems. This will provide innovative fertilizer formulas essential for reducing nutrient leaching into ecosystems while simultaneously enabling the inclusion of essential deficient nutrients through biofortification strategies, including the safe input of micronutrients. Moreover, this approach will restrict the discharge of potential metal and metalloids pollutants into agroecosystems, which may present health hazards.

special focus on micronutrients. This review seeks to explore cutting-edge technologies such as biostimulants, nanofertilizers, and biofortification and their potential to address challenges posed by soil degradation, climate change, and the need for increased plant production. The review aims to highlight the opportunities and future directions for improving plant nutrition.

2 | THE POWER OF THE MICRONUTRIENTS

The micronutrients essential for plants are six transition metals, including iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni), molybdenum (Mo), one metalloid, boron (B), and one halogen, chloride (Cl). Despite the low requirements ($< 1000 \mu\text{g g}^{-1}$ plant dry weight, except for Cl with often higher levels), these nutrients are as vital as

macronutrients for normal plant growth and development but they have been paid less attention. Each has unique chemical properties, such as ligand preferences, redox potentials, and coordination geometries, whose exploitation allows diverse yet highly specific chemistry. Micronutrients expand the range of biochemical transformations catalyzed in a cell (Merchant, 2010) and contribute to the structure and the electrical balance (only Cl). Thus, micronutrients participate in multiple essential plant cellular processes such as electron transport, oxygen metabolism, DNA replication, regulation of gene expression, protein trafficking, lipid metabolism and reactive oxygen species detoxification (Cakmak et al., 2023). The main physiological functions of micronutrients have been recently linked to the resulting deficiency symptoms in plants (Lilay et al., 2024). Micronutrients can also become toxic to plants, interfering with the uptake and function of other nutrients and damaging cells through uncontrolled reactions. As both deficiencies and excesses of micronutrients can disrupt many cellular processes, plants must carefully regulate intracellular micronutrient levels within a remarkably narrow range of physiological concentrations. Unbalanced micronutrient nutrition of crops reduces the yield and quality. Micronutrients are generally in adequate amounts in soils; however, their availability to plants is often below plant requirements for optimal growth and development; different edaphic (e.g., pH, organic matter and interactions with other elements) and biological factors (e.g., soil microbiome) impact in their bioavailability (Alloway, 2008). As the base of the food chain, plants are sources of these essential elements for animals and humans. Therefore, plant access to adequate concentrations of micronutrients alongside macronutrients and beneficial elements (e.g., silicon and sodium) is crucial for meeting the continuous global demand for nutritious food and agricultural raw materials (Assunção et al., 2022).

A rapid depletion of phytoavailable micronutrients in agricultural soils is recognized as a key factor limiting crop yields (Alloway, 2008). In the last decades, impressive increases in yield and human availability of foods were achieved with the adoption of intensive farming techniques, including mineral-based macronutrient fertilization, intensive irrigation, pesticides, and high-yielding varieties of crops. As a result, the plant demand for micronutrients in cultivated soils remarkably increased. In parallel, long-term continuous cropping became a regular practice and abandonment of crop fertilization with micronutrient-rich livestock manures occurred, increasing the rates of micronutrient depletion from the soil even further. Nowadays, micronutrient deficiencies are common nutritional worldwide alterations of crops that must be prevented or treated to sustain yield rates and food nutritional quality (Assunção et al., 2022).

In the last sixty years, there has been a continued fall in the nutritional quality of plant-based food, mainly due to the introduction of varieties with a higher yield, growth rate, and pest and disease resistance but poorer micronutrient levels (Bhardwaj et al., 2024). This fact has contributed to malnutrition and ‘hidden hunger’; thus, micronutrient deficiencies now affect $\sim 30\%$ of the human population (Li et al., 2024). Iron and Zn deficiencies are the most widespread and lead to severe outcomes such as neuropsychologic impairment and perinatal complications. Micronutrient undernutrition may further threaten future health

generations and well-being since recent research has shown that elevated atmospheric CO₂ concentrations can decrease Fe and Zn levels of staple crops (Zhu et al., 2018). Therefore, biofortification needs to be a standard agronomical practice.

2.1 | New form of plant micronutrient enhancement

Micronutrients are crucial in sustaining crop quality and yield and suppressing plant diseases and abiotic stressors (Dhaliwal et al., 2022). These co-benefits enhance the sustainability and resiliency of agricultural production systems. Also, micronutrients interaction with the microbiome is critical to agroecosystem health (Noman et al., 2022). Therefore, effective ways to increase the content of available micronutrients in crops are needed. Micronutrient fertilization and biostimulant application ameliorate micronutrient deficiency and, as a result, improve crop yield levels and nutritional quality. These improvements have also been found when using decreased amounts of macronutrient fertilizers, which may contribute to reducing macronutrient losses to the environment (Dimkpa and Bindraban, 2016). Micronutrients are applied directly to soil or plant foliage using specific fertilizer formulations as nanofertilizants; they are also administered in hydroponic systems and via seed coating and priming (Alloway, 2008; Mikula et al., 2020). Foliar treatments with micronutrients are markedly variable in effectiveness (Fernández and Brown, 2013), whereas soil-applied inorganic micronutrients show low effectiveness as they become easily fixed to soil particles (Alloway, 2008). Less conventional formulations used as micronutrient fertilizers are highly soluble chelates, particularly the synthetic aminopolycarboxylates derived from ethylenediamine tetraacetic acid (EDTA). Despite the high effectiveness of these molecules in providing micronutrients to plants, in the last decade, the search for alternatives has been the focus of intensive research as they behave as persistent substances. Novel ligands such as ethylenediamine-N,N'-disuccinic acid (S,S-EDDS), imidodisuccinic acid (IDHA) and 2-((1,2-dicarboxylethyl)amino)pentanedioic acid (IGSA), and natural complexing agents such as gluconate and lignosulfonate and protein derivatives, are some of the more biodegradable chelators successfully tested for micronutrient fertilization (López-Rayó et al., 2015; Brusko et al., 2023). New trends in micronutrient fertilization include the use of controlled released micronutrient fertilizers, including low-solubility fertilizers, coated fertilizers, bio-based and nano fertilizers (Mikula et al., 2020), as well as micronutrient-embedded NPK fertilizers (Bana et al., 2022).

Other agriculture practices allowing the control of micronutrient deficiencies and sustaining crop yield and nutritive value of key crop products are intercropping and genotypic exploitation. Cereal/legume intercropping, an ancient practice, has shown the potential to improve micronutrient nutrition, mainly Fe and Zn, by increasing their solubility and bioavailability in alkaline and calcareous soils through rhizosphere acidification and root exudation of specialized metabolites (Ebbisa, 2022). Also, investigation with other micronutrients, as B, has proposed the existence of a wide range of B ligands necessary for regulating B levels in plants (Bolaños et al., 2023). Furthermore, breeding and selecting some

micronutrient-efficient genotypes is an eco-friendly approach to overcome micronutrient deficiencies as specific genotypes may mine soil micronutrients through adaptative strategies such as the expansion of root systems, the inducible expression of highly efficient micronutrient transporters, and, importantly, the root-released of exudates able to dissolve poorly soluble minerals (White et al., 2013; Assunção et al., 2022).

3 | COUNTERACTING HEAVY METAL TOXICITY IN CROPS

In addition to this above-mentioned group of essential metallic micronutrients, there is a group of ions that are commonly known as heavy metals (HMs) (Kabata-Pendias 2000) that should be borne in mind because they can be harmful to most living organisms. These are also present in the Earth's crust and the upper arable soil horizon. Such chemicals can also be absorbed by plants and are considered some of the most dangerous in the field of ecotoxicology. This group includes elements such as cadmium (Cd), lead (Pb), chromium (Cr), and mercury (Hg) (Dalcorsó et al., 2014).

The group of essential micronutrients, such as Fe, Cu, Zn or Mn, can readily result in poisoning when their concentration reaches supra-optimal values. In contrast, non-essential HMs may evoke toxicity at much lower concentrations (Muszyńska & Labudda, 2019). Furthermore, there are a multitude of interactions between mineral nutrients when a specific micronutrient is present at insufficient or supra-optimal levels. These interactions affect the overall plant metabolism and development, including the onset of toxic responses through the induction of oxidative stress and the activation of phytohormone signaling (Lešková et al., 2022). Consequently, metallic elements present in plants can be considered a double-edged sword, with a narrow range of outcomes that can vary from beneficial to harmful (Muszyńska & Labudda, 2019).

Since the advent of the Industrial Revolution, the demand for metal ores has increased exponentially, resulting in the release of toxic HMs into the environment at concentrations well above original levels. This has led to widespread soil pollution (Vangronsveld et al., 1995). Furthermore, agricultural practices frequently contribute to soil metal contamination. The achievement of optimal crop yields hinges on the provision of fertilizers and sufficient water, which may contain trace amounts of metals. Over time, this can lead to the accumulation of HMs in the soil (Chary et al., 2008) and Spain is a clear example. In this way, there are numerous documented cases of soil contamination with HMs, predominantly associated with mining activities in the Iberian pyrite belt (Fernández-Caliani et al., 2009). This includes the mining spill disaster that occurred in the Guadiamar river basin in 1998 (Santos et al., 2020). Conversely, numerous agricultural practices designed to enhance crop yields, including the extensive utilization of phosphate fertilizers, the incorporation of sewage sludge compost amendments, the application of Cu-sulphate pesticides, and irrigation with reclaimed wastewater, can also contribute to the increased bioavailability of HMs in soils (Martínez-Cortijo & Ruiz-Canales, 2018). Consequently, the accumulation of HMs above safe levels in croplands has been linked to adverse effects on plant growth and survival (Srivastava et al., 2017).

The management of HMs in agriculture is critical to ensure soil health, crop safety and environmental sustainability. Utilization of some strategies such as phytoremediation, addition of appropriate soil amendments (i.e., organic matter), inoculation of microorganisms and use of nanotechnologies can help to mitigate the effects of HMs in agricultural systems. In this sense, knowledge of the mechanisms of HMs uptake and detoxification, as well as the mode of action, can provide valuable tools to optimize the planned remediation techniques to counteract HMs poisoning.

3.1 | Heavy metal uptake

The use of plants as a means of sustainable HMs pollution clean-up has been proposed, taking advantage of the natural ability of plants to absorb and accumulate HMs (Vangronsveld et al., 1995). Given the prevalence of HMs pollution in agricultural lands, significant research has been conducted to elucidate the physiological responses of plants to metal toxicity. The capacity of a plant to tolerate HMs is contingent upon the extent to which the plant is able to accumulate and tolerate these metals, as well as its adaptability to the specific edaphic and environmental conditions present in the polluted croplands in which it is growing. (DalCorso et al., 2019). In order to utilize plants as tools for the remediation of soil contaminated with HMs, it is essential to select plants with sufficient biomass and the capacity to uptake these contaminants from the substrate. It is important to note that comprehensive studies must be carried out to evaluate the specific capacities of each plant species to be used in phytoremediation. This was demonstrated in a study that examined the ability of different Brassicaceae species to grow in metal-polluted soils (Gisbert et al., 2006). A number of different grasses and brushes were observed to exhibit either hyperaccumulator (i.e., a strong root-to-shoot metal translocator) or phytostabilization (i.e., a shoot metal excluder) behaviors. Both of these behaviors have been reported to enable plants to accumulate Pb, Hg, and Cd from soils (Fernández et al., 2017). Similarly, studies of natural flora *in situ* near a metal recycling facility indicated a correlation between plant metal bioaccumulation and extractable metal and metalloid soil concentrations. *Drittrichia viscosa* was identified as a potentially useful natural plant for phytoremediation of soils polluted with complex mixtures of HMs (Mykolenko et al., 2018). It is worth noting that certain agricultural techniques may enhance the resilience of plants to HMs by stimulating growth and conditioning the microbial environment in the rhizosphere (Lacalle et al., 2023).

To comprehend the capacity of disparate plant species to accumulate assorted classes of metals and metalloids and to identify those more resilient, a significant endeavor has been undertaken to characterize the types of transporters involved in metal uptake, translocation, and compartmentation within plants (Jogawat et al., 2021). A genome-wide analysis of *Medicago truncatula* accessions enabled the identification of metal transporters involved in Cd and Hg tolerance, including P-type ABC tonoplast transporters and P_{1B}-type Heavy Metal ATPases (HMAs) (Paape et al., 2022). Similarly, several populations of *Noccaea* hyperaccumulator species collected from the Eastern

Pyrenees exhibited elevated expression of Zn/Cd-transporter genes, including HMA3, HMA4, and MTP1. This could contribute to their capacity to accumulate Cd, facilitating the compartmentation of this toxic metal within cells (Martos et al., 2016). With regard to the metalloid arsenic, due to the chemical similarities between its most oxidized status [i.e., As(V)] and the phosphate anion, arsenate [As(V)] is able to enter plant cells through the phosphate transporter PHT1;1 (Catarcha et al., 2007). However, under rhizosphere-reducing redox conditions, arsenite [As(III)] is the prevalent form of As that can be taken up by plants and enter plant cells via channels of the Nodulin 26-like Intrinsic Protein (NIP) family (Yamaji & Ma, 2021). Conversely, plant tolerance to HMs can be influenced by the accumulation and transport of macronutrients. This is exemplified by potassium transport *Arabidopsis* mutants (*Atkup8-2*), which exhibited a resistant phenotype to a mixture of HMs (Sanz-Fernández et al., 2021). Similarly, Hg exposure was less detrimental in *Medicago* plants subjected to augmented nitrate nutritional status (Carrasco-Gil et al., 2023). It is noteworthy that an *Arabidopsis* mutant with a defect in a nitrate transporter (*NRT1.1*) exhibited a reduction in nitrate and Cd accumulation, suggesting that nitrate metabolism regulation may influence Cd uptake or compartmentation within plant cells (Lu et al., 2024). Nevertheless, the mechanisms by which macronutrients interact with heavy metals remain unclear. It is plausible that adequate nutritional status and/or optimal water (osmotic) balance, in conjunction with metabolic adjustments, may contribute to enhanced tolerance to metal stress, potentially through the involvement of aquaporins (Neri et al., 2024).

3.2 | Heavy metal transportation, compartmentation and complexation

It is crucial to acknowledge that the HMs tolerance traits are not solely shaped by the local transportation and compartmentation processes within cells. Long-distance transport of the HMs to the aerial plant parts and storage organs also has a substantial impact on this phenomenon. HM chemical speciation by binding with different organic ligands represents a vital process that facilitates high mobility (Álvarez-Fernández et al., 2014). The speciation of metals within plant cells is of paramount importance in determining the tolerance of plants to heavy metals. The binding of HMs to different metabolites and macromolecules can result in the formation of less toxic organo-metallic compounds (see Zhao et al., 2022 for review). For example, several organic acids, including citric and malic acids, have been demonstrated to bind metals such as Zn and Cd. This phenomenon was observed in the leaves of the *Brassica oleracea* plant subjected to Zn stress (Barrameda-Medina et al., 2014b). In addition to metabolites, a number of macromolecules and cell components contribute to metal retention, thereby attenuating their toxicity. With regard to this matter, a genome-wide analysis of *Arabidopsis thaliana* accessions cultivated in Pb-contaminated soil revealed that a cell wall extensin and a protein involved in Golgi vesicle trafficking may contribute to Pb tolerance by reinforcing cell wall stiffness and metal cellular compartmentation, respectively (Busoms et al., 2021).

It is noteworthy that biothiols represent a fundamental group of ligands that assist in mitigating the toxicity of HMs in plants and unicellular phototrophs. These organisms produce non-ribosomal thiol-rich peptides, including glutathione (GSH) and phytochelatins (PCs) (Hernández et al., 2015). The cellular redox status is a crucial factor influencing the tolerance of HMs, with the metabolism of GSH and PCs playing a pivotal role. This was recently demonstrated in a screening of *Medicago* accessions treated with Cd (García de la Torre et al., 2021). This work corroborated previously observed phenotypes in *Arabidopsis* mutants with altered levels of endogenous GSH, as previously reported by Sobrino-Plata et al. (2014). Limited levels of GSH impede the cellular redox balance and the ability to synthesize PCs. GSH serves as the precursor to PCs through the action of phytochelatin synthase (PCS), a constitutive enzyme that is capable of producing a range of PCs through the sequential addition of successive g-GluCys units, resulting in the formation of (g-GluCys)_nGly (n = 1–5) and alternative thiol-rich peptides, which vary considerably across different plant species (Loscos et al. 2006), particularly in legumes (Vázquez et al., 2009). It is noteworthy that arsenic, a metalloid, has been demonstrated to possess a pronounced capacity to stimulate the synthesis of PCs. The chemical form of these compounds within cells, namely arsenate and arsenite anions, exhibit a striking divergence in chemical properties when compared to accumulated Cd²⁺ (Sobrino-Plata et al., 2013; Uraguchi et al., 2017). Furthermore, the formation of metal-PCs complexes is not only relevant for the amelioration of HMs toxicity, but also for the mobilization of HMs to the aerial parts of the plant. This has been demonstrated in the xylem sap of *Arabidopsis* exposed to Hg (Sobrino-Plata et al., 2021).

3.3 | Redox balance and biothiols

It should be noted that not all HMs induce the synthesis of PCs in a uniform manner. For example, the tolerance of *Lactuca sativa* and *Brassica oleracea* plants to the essential metal Zn was found to depend largely on the cellular level of GSH (Barrameda-Medina et al., 2014a). In addition to its function as a precursor to PCs, GSH plays a crucial role as an antioxidant, maintaining cellular redox homeostasis (see Hernández et al., 2015 for review). This provides an explanation for the evident depletion of GSH in *Erica andevalensis* plants treated with Cd despite the absence of independent measurements of PCs (Márquez-García et al., 2012). Indeed, one of the most widely recognized symptoms of heavy metals is the induction of oxidative stress and the generation of reactive oxygen species (ROS) (Rodríguez-Serrano et al., 2009). This is particularly evident in the case of supra-optimal accumulation of redox-active HMs such as Cu and Fe, which can eventually generate ROS through Fenton reactions. These include superoxide (O₂^{•-}), hydrogen peroxide (H₂O₂) and hydroxyl radicals (•OH) (Rodrigo-Moreno et al., 2013). Non-essential HMs typically induce ROS production by modulating the redox antioxidant machinery of plant cells, reducing the levels of reduced glutathione (GSH) as previously discussed, and by influencing the activity of antioxidant enzymes such as ascorbate peroxidases (APX), superoxide dismutases

(SOD), catalases (CAT), or glutathione reductases (GR). These enzymes are subject to varying degrees of impairment by toxic metals or metalloids (Palma et al., 2013). One significant area of uncertainty pertains to the regulatory processes of the enzymatic antioxidant machinery. ROS and reactive nitrogen species, including radical species such as nitric oxide (NO[•]) and nitric dioxide (NO₂[•]), have been shown to play a pivotal role in post-translational modification of limiting redox enzymes in a multitude of oxidative stress defense pathways, in addition to the modification of transcriptional factors that regulate transcriptional responses (Del Río, 2015). Conversely, it has been postulated that ROS and RNS may facilitate modifications to the function of metal ion channels and transporters through the redox alteration of critical cysteine and thyroxine residues, which can ultimately contribute to metal homeostasis in plant cells (Sandalio et al., 2023). It can be reasonably deduced that a significant factor influencing the tolerance of HMs is the redox balance within plant cells. Therefore, strategies such as micronutrient supplementation to help maintain redox balance or the use of biostimulants to enhance antioxidant capacity may contribute to improved crop health and resilience in the face of the increasingly prevalent environmental issue of metal/metalloid pollution of agro-systems.

4 | BIOSTIMULANTS FOR A SUSTAINABLE FERTILIZATION

The massive and prolonged use of fertilizers has made it possible to increase agricultural production but has caused the contamination of agricultural soils and also negatively affected human health and the environment (Gnanaprakasam & Vanisree, 2022). Agriculture must address the increase in food demand and face the challenge of preserving ecosystems and addressing global climate change, problems that raise the urgent need to modify the current production systems (Sachdev et al., 2021). This process must be achieved with greater resource use efficiency and environmental respect (Cristofano et al., 2021) while also ensuring the development of the agricultural sector (Rudnicki et al., 2023). Del Buono (2021) pointed out how biostimulants can allow for the reduction of fertilizers and contribute to the development of a green circular economy. Agriculture requires the development of strategies that allow for the reduction of agrochemicals while ensuring and improving production and mineral nutrition.

The European Union regulation (2019/1009) defines a biostimulant as “a product that stimulates plant nutrition processes regardless of the nutrient content of the product with the sole objective of improving one or more of the following plant or plant rhizosphere characteristics: (a) efficient use of nutrients; (b) tolerance to abiotic stress; (c) quality traits; (d) availability of nutrients confined to the soil or rhizosphere”, and indicates that these products are by nature more similar to fertilizer products than to most categories of phytosanitary products. This definition includes humic substances, hydrolysates of animal and plant proteins, seaweed extracts, chitosan and other biopolymers, arbuscular mycorrhizal fungi and plant growth-promoting bacteria (Cristofano et al., 2021), each of which is discussed below.

4.1 | Humic substances

Humic substances are produced through decomposition processes and microbial activity (Popa et al., 2022). They act on the metabolism and morphology of plants by modulating biochemical and physiological processes, thereby increasing the absorption of nutrients and leading to greater growth. A greater absorption of nitrates, phosphates and sulphates has been observed, as evidenced by physiological and microarray studies. Humic substances influence the expression of genes involved in the absorption, transport and assimilation of these elements (Janin et al., 2012). For instance, Zanin et al. (2018) describe an increase in the expression of genes related to the transport and assimilation of nitrates (*Nitrate transporter 1: NRT1*, *Nitrate transporter 1: NRT2*).

Their ability to act as chelators and redox properties is especially important in the mobilization of some of these nutrients (Olaetxea et al., 2018). They stimulate the functioning of the plasmamembrane H^+ -ATPase (PM H^+ -ATPase), co-transport systems and calcium (Ca^{2+}) fluxes, and signaling dependent on Ca^{2+} -dependent protein kinase (CDPK) (Ramos et al., 2015). In this sense, higher expression levels of the PM H^+ -ATPase genes have been observed (Tavares et al., 2017). By activating secondary metabolism, increasing the production of reactive oxygen species (ROS), nitric oxide (NO) and acting on the metabolism of polyamines, they enhance plants' response to stress conditions (Ramos et al., 2015; Zanin et al., 2018). Furthermore, they act by modulating the expression of the genes of the antioxidant system enzymes, as well as the activity of these enzymes, therefore intervening in redox homeostasis (Aguiar et al., 2016; Canellas et al., 2020; García et al., 2016). Their action appears to involve complementary and interconnected signaling pathways related to hormones and secondary messengers (García et al., 2016; Olaetxea et al., 2018). Humic substances trigger transcriptional, post-transcriptional and post-translational modifications that promote molecular, biochemical and physiological processes (Shah et al., 2018). Souza et al. (2022), in *Zea mays*, describe how the application of humic substances acts by modifying membrane receptors and the subsequent signalling cascade of protein kinases and phosphatases, finally modifying the expression of different transcription factors related to the metabolism of phytohormones. The humic substances modulate positively the expression of the auxin, cytokine and brassinosteroid genes, and negatively those of ethylene, abscisic acid, gibberellins and jasmonic acid. By modulating the expression level of genes involved in the biosynthesis of auxins (*TAA1: Tryptophan Aminotransferase of Arabidopsis*, *YUC1: YUCCA Flavin Monooxygenase*, *TAR2.1: Tryptophan Aminotransferase 2.1*, *GH3.2: Gretchen Hagen3.2*, and *PIN9: PIN-Formed 9*) and cytokinins (*IPT2: Isopentenyl Transferase 2*, *IPT5: Isopentenyl Transferase 5*, *LOG3: Lonely Guy3*, and *LOG5: Lonely Guy5*), a commercial mixture of humic substances boosted the growth of shoots and roots and increased development of absorbent hairs of wheat seedlings *Triticum aestivum* (Rathor et al., 2024).

Furthermore, the activation of carbon (C), nitrogen (N) and sulfur (S) metabolic pathways is observed after the application of humic substances, as shown by transcriptomic and metabolomic analyses in *Brassica napus* (Zanin et al., 2019). Finally, the application of humic

substances leads to both increased microbial diversity and activity of these populations, contributing to the creation of a more favorable soil environment for plant development.

4.2 | Amino acids, protein hydrolysates and extracts from animal, plants and algae

The use of amino acids, protein hydrolysates and extracts from animals, plants and algae constitutes another source of biostimulants. These compounds come from byproducts generated in livestock, poultry and fish processing plants (Mikula et al., 2023), and from crop remains and residues after processing (Gupta et al., 2023). Pérez-Aguilar et al. (2023), through enzymatic hydrolysis of pork processing byproducts, obtained an extract of free amino acids that enhance the growth of *Lactuca sativa* and *Brassica rapa* seedlings. The application of hydrolysates obtained from soybeans, alfalfa, wheat, potatoes and other plants also shows positive effects on biomass production, yield and potassium (K), calcium (Ca) and magnesium (Mg) (Sun et al., 2024). These effects were related to the increase in enzymatic activities and antioxidant compounds such as glutathione (GSH) and phenolics, and improved resistance to stressors. In lettuce, foliar application of amino acids increased biomass production, chlorophyll content, and content of nitrogen (N), phosphorus (P), K and Mg, antioxidant enzymes, phenolic compounds and flavonoids (Navarro-León et al., 2022). Furthermore, its application could allow a reduction in fertilization (Navarro-León et al., 2022).

The application of seaweed extracts promotes plant growth (Carrasco-Gil et al., 2021). Vaghela et al. (2022) have shown the presence of active compounds such as inositol, mannitol, amino acids, polyamines, indole-3-acetic acid (IAA), etc., in the algae *Kappaphycus alvarezii* and *Sargassum wightii*. Seaweed extracts improve plant tolerance to abiotic and biotic stress, nutrient use, health status, and plant growth, productivity and quality. The action of these extracts occurred at both physiological and molecular levels, involving cell signalling processes, ROS production and secondary metabolites. Also, seeds, roots or leaf extracts can be used as biostimulant raw material. *Moringa oleifera* L. leaf extract is a biostimulant that improves photosynthesis levels, the antioxidant system (enzymatic and non-enzymatic), nutrient absorption, and the capacity to accumulate photosynthates, all of which serve to increase the quality of the final product (Yuniati et al., 2022). Chitin and chitosan, obtained from insects, fish bones, molluscs and fungi, are also used for their beneficial action on crop yield and quality. They promote growth, photosynthetic activity, mineral nutrition and plant defence against biotic and abiotic stressors, including the antioxidant enzymes activities and expression of defence genes (Shahrajabian et al., 2021).

4.3 | Microorganisms

Regarding the use of microorganisms as biostimulants, the plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF) and *Trichoderma* spp. are the most studied. The application of

these inocula can consist of a single strain or a mixture of microorganisms that show additive or synergistic effects. The stimulatory effects of AMF include the modulation of root architecture, improved nutrient uptake, translocation and assimilation of macro- and micronutrients, enhancement of photosynthesis, regulation of plant hormones, and modulation of the microbial community in the rhizosphere (Del Buono 2021). These positive effects on crops are especially evident under stress conditions. Increased nutrient absorption was not only due to increased area of the absorption surface represented by the hyphae, but also to the release of enzymes that act by mobilizing them.

The inoculation of AMF in field crops allows increased absorption of P, N and Zn and yield (Ganugi et al., 2021). Saia et al. (2019) showed that AMF and *Trichoderma koningii*, regardless of water regimes, increase P, Mg, Fe, Mn and Zn uptake, phenolic compound content and plant yield. The AMF improve the roots' hydraulic conditions of the roots, and, under water stress, can regulate the expression of genes involved in the biosynthesis of ABA, antioxidant enzymes, and response to that stress, including the aquaporin genes in roots and those involved in the synthesis of lipoxygenase and terpenoids (Chitarra et al., 2016). In addition, there is also evidence of positive interactions between the AMF and bacteria (Battini et al., 2017).

Application of PGPR has also been shown to increase growth and mineral nutrition, resistance to abiotic stress and pathogen attack, and increased yield. At the level of mineral nutrition, PGPR act by increasing the levels of atmospheric nitrogen fixation. The rhizobacteria that improve plant development have the capacity to activate the ion transport systems within the roots or directly improve nutrient availability in the rhizosphere (Khosro et al., 2024). There are two fundamental forms of bacterial activity that can be taken into account when seeking to improve nutrition delivery. One of the main impacts of PGPR on plant nutrition is phosphate solubility. Several PGPR, including *Pseudomonas*, *Bacillus*, and *Rhizobium*, are able to dissolve insoluble forms of phosphate. The release of low molecular weight organic acids and phosphatases and phytases, which break down the organic forms of phosphate compounds, make the external environment more acidic. These acids chelate the cations attached to the phosphate. They also intervene by mobilizing Fe, especially when the soils are calcareous, through releasing siderophores that facilitate absorption. Therefore, mineral nutrition increases when, as a consequence of this inoculation, the release of auxin induces changes in the roots' architecture and, thus, the absorption surface (Tamariz-Angeles et al., 2021). They also produce an improvement in biological N₂ fixation, mineral solubilization and an increase in the plant's access to nutrients under adverse environmental conditions. Furthermore, microbial inocula produce volatile organic compounds (VOCs), improving stress tolerance (Bhadrecha et al., 2023). PGPR induce the biosynthesis of plant hormones, and contribute to stimulating growth, nutrient absorption, delaying leaf senescence, fruit and flower formation, seed ripening and the regulation of dormancy (Khosro et al., 2024). The modification of the cell wall induced by the plant-microbe association and the increase in soluble sugar content improves the water retention capacity and increase the plant's tolerance to osmotic and ionic stress. Enrichment with exopolysaccharides

and lipopolysaccharide-proteins modifies the cell wall by forming a protective biofilm on the surface of the root, which provides greater resistance under extreme environmental stresses (Ansari et al., 2019). Inoculation with PGPR (specifically, the AKMP7 strain of *Pseudomonas putida*) is very effective for thermotolerance since it reduces the formation of ROS and thus the oxidative damage to membranes, with the activation of the antioxidant response of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (Kaushal et al., 2023). Furthermore, improved accumulation of such metabolites as proline, soluble sugars, starch, proteins, amino acids and chlorophylls has also been observed after such inoculation. Similarly, cold-stressed plants also recovered after the application of PGPR through the elimination of ROS, membrane stability, and enhanced stress-responsive gene expression (Kaushal et al., 2023). Thus, the positive effects of microbial biostimulants in improving abiotic stress tolerance are possibly due to their direct effect on nitrogen fixation and mineral solubilization, root growth, improved water availability, and the production of metabolites and hormones, as well as the positive regulation of enzymatic activities that are involved in improving plant nutritional homeostasis, osmotic adjustment and ROS regulation. In short, PGPR increase the availability of mineral nutrients, regulate phytohormone levels and carry out an authentic biological control of phytopathogens. They produce and release hormones, secondary metabolites, antibiotics, and other signalling compounds, and modify the physiology of the entire plant, thereby improving nutrient absorption and promoting growth (Kaushal et al., 2023; Kumari et al., 2023). The productivity of a given PGPR can be further increased by optimizing it and adapting it to local soil conditions. They are expected to replace the use of synthetic growth regulators, herbicides and chemical fertilizers. Therefore, the development of more effective rhizobacteria is a current challenge. Studies on the effects that these microbial inoculants may have on human health are also needed.

Biostimulants may be key in the mineral nutrition processes of crop plants, allowing greater availability of mineral nutrients and better adaptation to stress conditions. The development of new and effective biostimulants requires good knowledge of their performance at physiological and molecular levels, as well as of the complex interactions that can occur between them. These interactions may be key, as studies of microbial consortium or combinations of microorganisms and humic substances have shown. Furthermore, testing under field conditions, and therefore subject to highly variable conditions that are different from those in the laboratory, is also necessary.

5 | STRATEGIES FOR BIOFORTIFICATION

The insufficient intake of essential mineral nutrients necessary for human health, also known as hidden hunger, affects approximately two billion people worldwide and stems from diets lacking in vitamins and minerals such as iron (Fe), calcium (Ca), zinc (Zn), and selenium (Se) (Banerjee et al., 2023). The deficiencies lead to severe health disorders, highlighting the urgent need for nutrient-rich food production beyond mere calorie provision (Prasad & Shivay, 2020). Therefore,

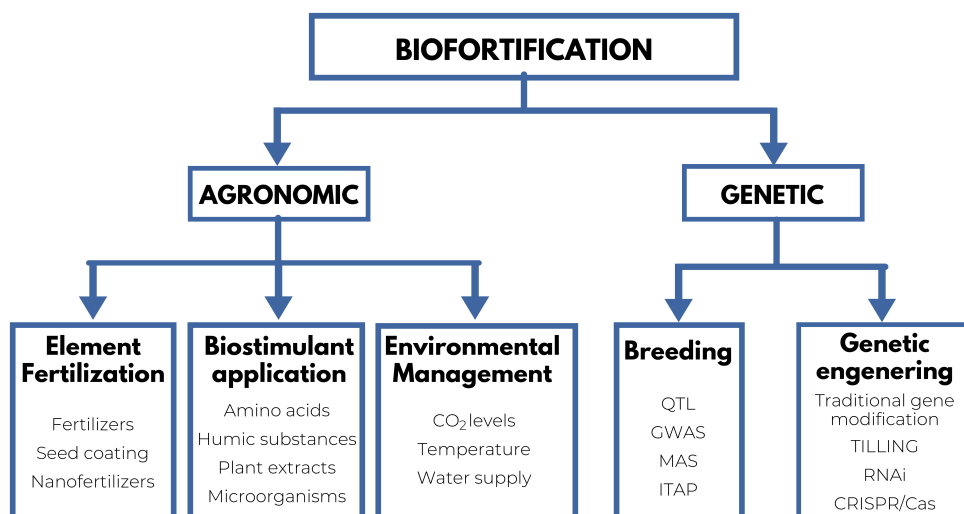


FIGURE 2 Scheme of strategies for biofortification: agronomic, including the applications of fertilizers, biostimulants, and the management of environmental condition, and genetic background through breeding and the generation of genetically modified organisms.

United Nations Sustainable Development Goals underscore the importance of ending global hunger and reducing malnutrition by 2030, identifying nutrient deficiencies and implementing biofortification programs. The process of biofortification enhances the nutritional value of food crops by increasing their content of specific mineral nutrients (White & Brown, 2010) (Figure 2), but also contributes to plant physiology by enhancing nutrient availability, stress tolerance, and metabolic efficiency. Biofortification is especially beneficial in regions where people have limited access to diverse diets and nutritional supplements, targeting staple crops widely consumed by populations at higher risk of malnutrition (Sharma & Verma, 2019).

5.1 | Agronomic biofortification

Agronomic biofortification enhances the nutrient content of food crops through strategic applications of fertilizers, biostimulants, and the management of environmental conditions. This approach has lower technical requirements and bypasses the complexities and regulatory challenges associated with genetically modified organisms (GMOs) (Vičko & Ohnoutková, 2019).

5.1.1 | Element Fertilization

Element fertilization directly supplies crops with essential nutrients, aiming to boost their accumulation in the edible parts. This method has been successful with nutrients like Zn, Se, iodine (I), and Ca (D'Imperio et al., 2016; Wakeel et al., 2018; Izydorczyk et al., 2021). Challenges exist, however, with nutrients like Fe due to their limited bioavailability to plants (Wakeel et al., 2018). Some successful experiments have been carried out with the joint application of two elements, such as Se and I, with a synergistic effect (Consentino et al., 2023). Application techniques range from soil to foliar methods, with the latter, sometimes in combination with soil application, proving more effective for targeting nutrient localization in crops like

cereals and vegetables (Sharma & Verma, 2019; Pradhan et al., 2020; Izydorczyk et al., 2021). Recently, new application techniques have been developed, such as the use of surfactants, adjuvants, the introduction of nutrients in seed coatings, and the use of microparticles or nanoparticles. Indeed, nanofertilizers offer a sustainable way to enhance nutrient delivery and uptake by plants, reducing the need for excessive fertilizer use and mitigating environmental impacts (Ahmed et al., 2024). Some examples are Zn nanoparticles and nanomaterial-enhanced fertilizers, such as hydroxylapatite, silica, and chitosan nanoparticles (Sánchez-Palacios et al., 2023).

5.1.2 | Biostimulants and Other Compounds

Biostimulants, encompassing a variety of compounds from amino acids to humic acids, serve to enhance plant growth, nutrient uptake, and stress resilience independently of their nutrient content. These substances play a crucial role in increasing the efficiency of nutrient use by the plant, potentially reducing the need for traditional fertilization (Ricci et al., 2019). Biostimulants also include extracts from hyper-accumulator species and the utilization of beneficial microorganisms, which can significantly enhance the bioavailability and uptake of nutrients like Se and Zn (Khan et al., 2019; Izydorczyk et al., 2021). This approach also leverages the natural interactions between plants and soil microbiota to foster a more nutrient-rich crop yield. Microorganisms can secrete metallophores or modify soil pH to increase the bioavailability of naturally occurring elements to plants (Mishra et al., 2023).

5.1.3 | Environmental Management

Modifying the environmental conditions under which crops are grown offers another avenue for agronomic biofortification. This method includes adjustments of CO₂ levels, temperature, and water supply, each of which can significantly impact the nutrient composition of the

resulting produce. For example, research has shown that Se accumulation can be enhanced in plants subjected to heat or drought stress, suggesting that controlled stress conditions can be beneficial for nutrient biofortification (Bocchini et al., 2018; Hawrylak-Nowak et al., 2018). Similarly, elevating CO₂ conditions or manipulating other environmental factors such as light and temperature has been shown to increase the accumulation of beneficial nutrients and compounds like ascorbate and glucosinolates in certain crops (Simkin, 2019; Wang et al., 2023).

5.2 | Genetic Biofortification

Genetic biofortification uses advanced breeding and genetic engineering techniques. This method is considered more efficient, sustainable, and environmentally friendly than agronomic approaches, as it reduces the reliance on excessive fertilizer use (Garg et al., 2018; Gupta et al., 2021).

5.2.1 | Biofortification Using Breeding Techniques

Traditional breeding methods involve hybridizing genotypes that exhibit desirable traits for nutrient accumulation with commercial genotypes to create new biofortified varieties. This process begins with the identification and characterization of genetic variability for nutrient uptake, transport, or accumulation within a species (White & Broadley, 2009). Techniques such as quantitative trait locus (QTL) mapping and genome-wide association studies (GWAS) are utilized to identify genetic markers linked to increased nutrient accumulation. Marker-assisted selection (MAS) leverages these markers to select and breed desired genotypes. Intron Targeted Amplified Polymorphism (ITAP) is a novel approach that employs bioinformatics to identify markers, further advancing the breeding process (Gupta et al., 2020). Initiatives such as those developed by HarvestPlus and CGIAR have generated multiple biofortified varieties through breeding that are currently used in developing countries (Mandal et al., 2023).

5.2.2 | Genetic Engineering Techniques

Genetic engineering surpasses traditional breeding by rapidly and precisely enhancing nutrient accumulation in specific target organs of plants. Traditional methods such as gene overexpression or heterologous expression have been used to enhance the rate of transcription or the gene copy number, thus leading to an increased accumulation of nutrients. Furthermore, it is feasible to introduce a down-regulated or knockout variant of a gene to decrease the synthesis of anti-nutrients or to alter a metabolic pathway (Dutt et al., 2019). As an alternative, the RNAi technique was also proved effective in silencing gene expression (Vlčko & Ohnoutková, 2019). Other techniques to generate genetic variation are TILLING and the recently developed CRISPR/Cas systems (Till et al., 2018; Bhambhani et al., 2021). All these techniques benefit from the current rise of artificial intelligence

to detect genes or regulatory regions that can be modified for biofortification (Khan et al., 2023). There are different approaches to using these techniques. One is to alter genes responsible for specific metabolic pathways to increase the production or reduce the degradation of target nutrients (Bhambhani et al., 2021). For example, overexpressing enzymes like phytoene synthase has led to the creation of “Golden Rice,” enriched in pro-vitamin A (Ye et al., 2000). In addition, it is possible to increase the accumulation of elicitors such as ascorbate, carotene and certain amino acids that promote the intestinal absorption of nutrients (Consentino et al., 2023). Another approach is to reduce the presence of anti-nutrients by targeting genes related to their synthesis, such as phytate and tannins, which can enhance intestinal absorption of nutrients. Thus, mutations in genes controlling phytic acid transport or biosynthesis, such as *SULTR* and *MRP*, have been developed to lower its concentration in crops (Cominelli et al., 2020). The third approach is to modify nutrient transporter genes. For instance, altering the expression of the *CAX1* transporter gene has shown higher Ca accumulation in *L. sativa*, *A. thaliana*, and *B. rapa* without adverse effects (Park et al., 2009; Yi et al., 2012; Navarro-León et al., 2018). Other transporters, such as *HMA4* and *IRT*, *VTL*, *VIT*, and *NRAMP* have been manipulated to enhance Zn and Fe content in crops (Blasco et al., 2019; Li et al., 2019; Narayanan et al., 2019; Wang et al., 2019).

6 | NANOTECHNOLOGIES FOR PLANT NUTRITION

Nanotechnology has gained considerable interest during the last years for its prospective applications across several biological domains, including medicine, microbiology, and plant sciences. Nanoscale materials show diverse shapes, compositions, and structures, providing great capacity to interface with biological systems (Bárcana et al., 2022). According to plant sciences, the effects of engineered nanomaterials, also called nanofertilizants, include improvements in germination percentage and speed, along with the elongation of root and shoot structures, as well as the enhancement of vegetative biomass (Szöllósi et al., 2020). These increases have been linked to identifiable physiological mechanisms governing plant water regulation, photosynthetic activity, and nitrogen metabolism (Singla et al., 2019; Tripathi et al., 2023).

Nanoparticles used as fertilizers are one of the most promising in this field but need to be investigated and developed (Yadav et al., 2023). Numerous nanoparticles, such as carbon nanotubes, and metals like Au, Ag, as well as metal oxides such as ZnO, Fe₂O₃, TiO₂, SiO₂, and Al₂O₃, exhibit remarkable beneficial properties for plants, but the most reported has been nano-SiO₂ and nano-ZnO particles (Shalaby et al., 2016). They have demonstrated capabilities in enhancing germination, plant growth, development, plant nutrition and water uptake. They also have shown several effects on stress alleviation (Aqeel et al., 2022). The interactions with biological systems strongly depend on their physical attributes and alterations in the surrounding environment (Gonzalez-Grandio et al., 2021). Due to their extensive

surface area per unit mass, nanoparticles are anticipated to exhibit greater biological activity compared to larger particles of identical chemical composition (Sozer and Kokini, 2009). Nanoparticles exhibit unique physico-chemical properties, in addition to their exceptionally large surface area. These properties include high surface energy and quantum confinement effects (Ma et al., 2010). Quantum confinement occurs because the small dimensions of nanoparticles restrict the movement of electrons, leading to discrete energy levels. As a result, the band gap energy increases. These exceptional characteristics make a markedly distinct plant fates in relation to their behaviors according to plant nutrition as they can improve nutrient delivery, control release of nutrients and enhance bioavailability.

Among these nanomaterials, *carbon nanotubes* (CNTs) stand out as particularly intriguing across biological domains due to their distinctive physical and chemical properties (Dresselhaus et al., 2004). Carbon nanotubes (CNTs) are nanostructures composed of carbon atoms arranged in a hexagonal structure, forming cylindrical tubes. They are categorized into single-walled carbon nanotubes (SWCNTs) and multi-walled carbon nanotubes (MWCNTs), depending on the number of concentric layers of rolled graphene sheets within the structure (De Volder et al., 2013). MWCNTs have typically an outer diameter ranging from 2 to 100 nanometers and an inner diameter of 1 to 3 nanometers, with lengths varying from 10 to 100 nanometers (He et al., 2013). Compared to SWCNTs, MWCNTs exhibit higher density and superior tensile strength (Shoukat and Khan, 2022), which makes them more suitable for plant treatments. Therefore, MWCNT have generated attention as a potential solution for several agronomic challenges. For instance, MWCNTs have been observed to increase biomass, seedling height, and antioxidant activity in *Thymus daenensis* (Samadi et al. 2020). Also, a positive effect on growth, total chlorophyll, carbon, and macronutrient and micronutrient contents in sugarcane micropropagation has been demonstrated (Sorcia-Morales et al. 2021). In broccoli, MWCNTs were reported to change lipid composition, rigidity and permeability of the root plasma membranes, which was related to the enhanced aquaporin presence, hence improving water uptake and transport (Martínez-Ballesta et al., 2016). Furthermore, the enhancement of secondary metabolism was observed in *Catharanthus roseus* callus after MWCNT supplementation (Ghasempour et al. 2019).

Concerns over the potential toxicity and adverse reactions associated with metal and synthetic nanoparticles have led to the exploration of alternative delivery systems. Biologically derived nanoparticles offer a promising approach for transporting drugs, proteins, nucleic acids, and other substances to tissues (Lang et al., 2021). These nanoparticles can be artificially synthesized (e.g., liposomes) or sourced from natural organisms such as plants, milk, and bacterial nanovesicles. These nanovesicles, released or extracted by both eukaryotic and prokaryotic cells, facilitate intercellular and cross-species communication by transporting bioactive cargo such as DNA, RNA, lipids, and proteins. Biologically sourced vesicles primarily enter host cells through endocytic pathways, including clathrin-mediated endocytosis or lipid raft-mediated pathways (Canas et al., 2016). Due to their ability to be internalized by cells and function as delivery vehicles,

research groups are actively developing and engineering biologically sourced nanovesicles for medical applications (Tan et al., 2018). In this way, the application as nanofertilizant has also been described by the ability to enter leaves through stomata or aqueous pores of the cuticle layer (Rios et al. 2021). Sustained release intensifies the use of the resources in the best possible way, along with improving overall environmental safety (Mishra et al., 2020). Also, Sinha et al. (2019) and Fernández et al. (2022) demonstrated the ability of chitosan to be a carrier of essential plant microbes.

6.1 | Nutrient release

Linking/encapsulating nutrients and bioactive compounds to/into nanoparticles have resulted in formulations with enhanced precision and targeted high efficiency of use, providing a large number of nanofertilizers (Chugh et al., 2021). The use of nanoparticles (NPs) of essential and nonessential elements as nanofertilizers to promote plant growth has already been documented, whether administered through foliar spraying or soil application (Achari and Kowshik, 2018). Due to their slow solubility, they have been described as sustained-release nanofertilizers, and higher efficacy should then be achieved via soil application. In addition, nanoparticles have been developed as intelligent delivery systems to enhance nutrient penetration and tissue targeting (Kaur et al., 2020). This has been attributed to their inherent characteristics, including size, shape, zeta potential, hydrophobicity/hydrophilicity, and the potential for surface functionalization (modification of its surface with specific chemical groups or molecules to achieve desired properties or functionalities) (Solanki et al., 2015). The unique properties of nanoparticles allow them to retain nutrients and facilitate their slow, controlled release. This improves nutrient utilization efficiency, which plays a critical role in determining crop productivity (Pradhan and Mailapalli, 2017).

Membrane vesicles purified from natural sources, such as plant material, are gaining significant attention as nanocarriers for transporting and delivering compounds into target cells (Yepes-Molina et al., 2020). These vesicles are primarily composed of lipids and proteins, including many transporters and channel proteins. Transmembrane proteins, in particular, have been implicated in the stability and delivery of entrapped molecules (Martínez-Ballesta et al., 2016). Among these membrane proteins are aquaporins (AQPs), which are notably present in membrane vesicles derived from plant material (Martínez-Ballesta et al., 2018). AQPs, functioning as water transporters, play crucial roles in adjusting membrane permeability, which is an important characteristic of the vesicles for encapsulating and delivery of nutrients (Martínez-Ballesta et al., 2016). Advancements in agriculture have seen the development of nanofertilizers containing plant membrane vesicles, with promising results reported in recent years (Rios et al., 2019; Rios et al., 2021). These efforts aim to increase crop production while reducing environmental impact by enhancing the efficient use of nutrients, water, and agrochemicals (Singh, 2021). Nano-liposomes, due to their similarity to vesicles, have been demonstrated to penetrate the leaf epidermis and move

throughout the plant (Karny et al., 2018). These liposomes were observed to associate with cell nuclei and maintain their release activity even after 48 hours. Similarly, the foliar application of a Fe liposomal formulation improved the growth of Fe-deficient seedlings, highlighting an enhanced method for increasing Fe delivery to plant leaves (Farshchi et al., 2021). Additionally, the nanoencapsulation of Zn in natural membranes has been shown to enhance fertilization efficiency in broccoli by requiring lower doses to achieve high tissue concentrations, facilitated by high penetrability into leaves and effective cell delivery (Rios et al., 2019). Subsequent research demonstrated that B and Fe, incorporated into natural nanovesicles, could penetrate through stomatal pores of nutrient-deficient almond leaves, suggesting that B could distribute widely within tree tissues through aqueous pores (Rios et al., 2020).

The addition of nanoparticles to biochar increases the resistance of plants to stress, depending on the properties and application rates of this material, as well as the type of soil and environmental conditions prevailing at the specific site. A combination of 20% biochar and 0.7% nanoparticles significantly increased the growth parameters, total nitrogen absorption, phosphorus and potassium and total chlorophyll in *Calathea insignis* (Hasnain et al., 2023). The application of biochar stimulates plant growth and improves resistance to abiotic/biotic stress. Biochar increases the phytohormone content in bean plants in terms of the increase of polyamines, abscisic acid (ABA), 1-aminocyclopropane-1-carboxylic acid, jasmonic acid and salicylic acid (Tripathi et al., 2023). The use of biochar can improve the properties of soil microorganisms since it allows for the formation of aggregates as well as the adsorption and remediation of contaminants. Thus, a combination of biochar, compost and magnetic nanoparticles improved grassland growth (Ohsowski et al., 2018).

6.2 | Mechanism of action

Recent studies in plants are trying to elucidate the responses at molecular, cellular, and tissue levels to nanoparticles. Nanoparticles' interaction with plants is multifaceted and depends on the type of nanoparticles, their size, shape, surface charge, and chemical composition (Ren et al., 2024). As nanoparticles can be absorbed by plant roots from the soil or through the leaves when applied as sprays, the process should involve the penetration of NPs through the root epidermis and cortex or through cuticle and stomata, entering the leaf tissues (Karny et al., 2018). Once inside the plant, nanoparticles can be translocated to different organs, including stems, leaves, and fruits, via the xylem and phloem.

Some nanoparticles can mimic or enhance the activity of plant hormones. For example, silver nanoparticles (AgNPs) have been shown to influence auxin pathways, promoting root and shoot growth (Guzmán-Báez et al., 2021) and improving the efficiency of photosynthesis by increasing chlorophyll content and the activity of photosynthetic enzymes (Dilnawaz et al., 2023). Also, it has been reported that nanoparticles can help plants tolerate abiotic stresses (e.g., drought, salinity, extreme temperatures) by enhancing antioxidant enzyme

activities and reducing oxidative stress (Al-Khayri et al., 2023). Nanoparticles can influence the expression of genes involved in growth, development, and stress responses as aquaporins. This modulation has been related to improved plant performance under salinity conditions (Martinez-Ballesta et al., 2020). Therefore, along with all the results obtained with nanoparticles in plants, there has been an increased interest in their effect on improving plant performance, not only as biostimulants but also for their effects on the plant's response under stressful environments, such as the increase in their water uptake and transport involving aquaporins (Martínez-Ballesta et al., 2016).

6.3 | Safety

It has been reported that safety of using nanoparticles (NPs) in crops must be thoroughly evaluated (Kah et al., 2019). Studies have suggested that the potential nanotoxicity of NPs may be linked to the detoxification mechanisms activated by plants in response to their presence (Wang et al., 2016). Available evidence suggests that the negative effects of some nanoparticles on plants' growth, physiology and yield are influenced by the type and size of the nanoparticles. However, the more robust evidence suggests that their toxicity is related to their concentration (Safiuddin et al., 2014).

To address concerns about toxicity, research is focusing on developing nanoparticles derived from biological materials. These natural nanoparticles, due to their biodegradability, can enhance plant tissue permeability and facilitate mineral release, representing a promising advancement in the field of plant nutrition (Bárcana et al., 2022).

7 | CHALLENGES AND FUTURE DIRECTIONS-

This review highlights the transformative potential of sustainable fertilization practices in modern mineral nutrition. Through the integration of biostimulants, micronutrient management, biofortification, and nanotechnologies, we demonstrate how these innovative approaches can enhance plant health, improve tolerance to contaminants, and promote more efficient nutrient use with the common edge of the involvement of the micronutrients. However, while significant advancements have been made, ongoing research and innovation, addressing future challenges and unlocking new opportunities for resilient plants, will be critical.

While biostimulants have shown promise in promoting plant growth and stress tolerance, their mechanisms of action are still not fully understood. Also, their effectiveness can vary greatly depending on soil types, climate conditions, and crop species. Therefore, more research is needed to understand how these products perform under different environmental stresses as climate change continues to alter agricultural landscapes, such as drought, salinity, and temperature extremes. Consequently, addressing challenges, such as investigating plant tolerance to abiotic stresses and understanding nutrient toxicity management through compartmentation strategies, is crucial. These efforts will play a vital role in sustaining plant productivity.

On the other hand, by unraveling the roles of ion-water channels, transporters, biothiols, and oxidative stress defense mechanisms, scientists are laying the groundwork for identifying plant species and cultivars capable of thriving in mineral nutrient-contaminated soils. However, much remains to be explored, and further research in this area is critical to fully understand these complex processes of plant physiology.

By enhancing the nutrient content in plants through agronomic or genetic methods, biofortification aims to reach around 1 billion people by 2030, potentially making a significant dent in global malnutrition. However, future research must address the multifaceted challenges of biofortification, from identifying nutrient-dense germplasm and optimizing crop nutrient content under changing climate conditions to understanding the socio-economic factors influencing consumer acceptance and market integration. Finally, nanotechnologies represent a cutting-edge advancement in fertilization, offering novel solutions to longstanding challenges in nutrient management. By utilizing nanoparticles and nanomaterials, fertilizers can be designed with precise control over nutrient release, ensuring that plants receive nutrients when they are most needed, thereby enhancing nutrient use efficiency. These nanofertilizers can also be engineered to improve the solubility and bioavailability of nutrients, which is especially important for micronutrients that are typically required in small amounts but are critical for plant health.

AUTHOR CONTRIBUTIONS

LEH, JMR, FE, AA and MC conceptualized the idea. LEH, JMR, FE, AA and MC wrote the manuscript. LEH, JMR and MC prepared figures. MC edited the manuscript. All authors reviewed the manuscript.

DATA AVAILABILITY STATEMENT

Data sharing does not apply to this article as no new data were created or analyzed in this article.

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REFERENCES

- Achari, G.A. & Kowshik, M. (2018) Developments on Nanotechnology in Agriculture: Plant Mineral Nutrition, Health, and Interactions with Soil Microflora. *Journal of Agricultural and Food Chemistry*, 22; 66(33) 8647–8661. doi: <https://doi.org/10.1021/acs.jafc.8b00691>.
- Aguiar, N.O., Medici L.O., Olivares, F.L., Dobbss, L.B., Torres-Netto, A., Silva S.F. & Canellas LP (2016) Metabolic profile and antioxidant responses during drought stress recovery in sugarcane treated with humic acids and endophytic diazotrophic bacteria. *Annals of Applied Biology*, 168, 203–213.
- Ahmed, N., Zhang, B., Chachar, Z., Li, J., Xiao, G., Wang, Q., Hayat, F., Deng, L., Narejo, M.-N., Bozdar, B. & Tu, P. (2024) Micronutrients and their effects on Horticultural crop quality, productivity and sustainability. *Scientia Horticulturae*, 323: 112512.
- Al-Khayri, J.M., Rashmi, R., Surya-Ulhas, R., Sudheer, W.N., Banadka, A., Nagella, P., Aldaej, M.I., Rezk, A.A., Shehata, W.F. & Almaghasla, M.I. (2023) The Role of Nanoparticles in Response of Plants to Abiotic Stress at Physiological, Biochemical, and Molecular Levels. *Plants (Basel)*, 7, 12(2), 292. doi: <https://doi.org/10.3390/plants12020292>
- Alloway, B.J. (2008) Micronutrients and crop production: An introduction. In: Alloway, B.J. (ed.), *Micronutrient Deficiencies in Global Crop Production*, Springer Science + Business Media B.V. pp. 1–39. ISBN 978-1-4020-6859-1
- Álvarez-Fernández, A., Díaz-Benito, P., Abadía, A., López Millán, A.F. & Abadía, J. (2014) Metal species involved in long distance metal transport in plants. *Frontiers in Plant Science*, 5, 105.
- Ansari, F.A., Ahmad, I. & Pichtel, J. (2019) Growth stimulation and alleviation of salinity stress to wheat by the biofilm forming *Bacillus pumilus* strain FAB10. *Appl Soil Ecol* 143, 45–54.
- Assunção, A.G.L., Cakmak, I., Clemens, S., González-Guerrero, M., Nawrocki, A. & Thomine, S. (2022) Micronutrient homeostasis in plants for more sustainable agriculture and healthier human nutrition. *Journal of Experimental Botany*, 73, 1789–1799.
- Aqeel, U., Aftab, T., Khan, M.M.A., Naeem, M. & Khan, M.N. (2022) A comprehensive review of impacts of diverse nanoparticles on growth, development and physiological adjustments in plants under changing environment. *Chemosphere*, 291. <https://doi.org/10.1016/j.chemosphere.2021.132672>.
- Bana, R.S., Jat, G.S., Grover, M., Bamboriya, S.D., Singh, D., Bansal, R., Choudhary, A. K., Kumar, V., Laing, A.M., Godara, S., Bana, R.C., Kumar, H., Kuri, B.R., Yadav, A., & Singh, T. (2022) Foliar nutrient supplementation with micronutrient-embedded fertilizer increases biofortification, soil biological activity and productivity of eggplant. *Scientific Reports*, 12, 5146.
- Banerjee, S., Roy, P., Nandi, S. & Roy, S. (2023) Advanced biotechnological strategies towards the development of crops with enhanced micronutrient content. *Plant Growth Regulation*, 100, 355–371.
- Barrameda-Medina, Y., Montesinos-Pereira, D., Romero, L., Blasco, B. & Ruiz, J.M. (2014a) Role of GSH homeostasis under Zn toxicity in plants with different Zn tolerance. *Plant Science*, 227, 110–121.
- Barrameda-Medina, Y., Montesinos-Pereira, D., Romero, L., Ruiz, J.M. & Blasco, B. (2014b) Comparative study of the toxic effect of Zn in *Lactuca sativa* and *Brassica oleracea* plants: I. Growth, distribution, and accumulation of Zn, and metabolism of carboxylates. *Environmental and Experimental Botany*, 107, 98–104.
- Bárzana, G., Garcia-Gomez, P. & Carvajal, M. (2022) Nanomaterials in plant systems: Smart advances related to water uptake and transport involving aquaporins. *Plant Nano Biology*, 1, 100005. <https://doi.org/10.1016/j.plana.2022.100005>
- Battini, F., Grønlund, M., Agnolucci, M., Giovannetti, M., Jakobsen, I. (2017) Facilitation of phosphorus uptake in maize plants by mycorrhizosphere bacteria. *Scientific Reports*, 7, 4686.
- Bhadrecha, P., Singh, S. & Dwibedi, V. (2023) A plant's major strength in rhizosphere: the plant growth promoting rhizobacteria. *Archives of Microbiology*, 205(5), 165.
- Bhambhani, S., Kondhare, K.R. & Giri, A.P. (2021) Advanced genome editing strategies for manipulation of plant specialized metabolites pertaining to biofortification. *Phytochemistry Reviews*, 1–19.
- Bhardwaj, R.L., Parashar, A., Parewa, H.P. & Vyas, L. (2024) An alarming decline in the nutritional quality of foods: the biggest challenge for future generations' health. *Foods*, 13, 877.
- Blasco, B., Navarro-León, E. & Ruiz, J.M. (2019) Study of Zn accumulation and tolerance of HMA4 TILLING mutants of *Brassica rapa* grown under Zn deficiency and Zn toxicity. *Plant Science*, 287: 110201.
- Bocchini, M., D'Amato, R., Ciancaleoni, S., Fontanella, M.C., Palmerini, C.A., Beone, G.M., Onofri, A., Negri, V., Marconi, G., Albertini, E. & Businelli, D. (2018) Soil selenium (Se) biofortification changes the physiological, biochemical and epigenetic responses to water stress in

- Zea mays L. by inducing a higher drought tolerance. *Frontiers in Plant Science*, 9, 389.
- Bolaños, L., Abreu, I., Bonilla, I., Camacho-Cristóbal J.J. & Reguera, M. (2023) What can boron deficiency symptoms tell us about its function and regulation? *Plants (Basel)*, 9;12(4):777. doi: <https://doi.org/10.3390/plants12040777>.
- Brusko, V., Garifullin, B., Geniyatullina, G., Kuryntseva, P., Galieva, G., Galitskaya, P., Selivanovskaya, S. & Dimiev, A.M. (2023) Novel biodegradable chelating agents for micronutrient fertilization. *Journal of Agricultural and Food Chemistry*, 71, 14979–14988.
- Busoms, S., Pérez-Martín, L., Llimós, M., Poschenrieder, C. & Martos, S. (2021) Genome-wide association study reveals key genes for differential lead accumulation and tolerance in natural *Arabidopsis thaliana* accessions. *Frontiers in Plant Science*, 12, 1–17.
- Cakmak, I., Brown, P., Colmenero-Flores, J.M., Husted, S., Kutman, B.Y., Nikolic, M., Rengel, Z., Schmidt, S.B. & Zhao, F.J. (2023) Chapter 7 Micronutrients. In: Rengel, Z., Cakmak, I. & White, P.B. (eds), *Marschner's Mineral Nutrition of Plants* (Fourth Edition), Academic Press. pp. 283–385. eBook ISBN: 9780323853521
- Canas, M.A., Gimenez, R., Fabrega, M.J., Toloza, L., Baldoma, L. & Badia, J. (2016) Outer membrane vesicles from the probiotic *Escherichia coli* nissle 1917 and the commensal ECOR12 enter intestinal epithelial cells via clathrin-dependent endocytosis and elicit differential effects on DNA damage. *PLoS One*, 11 (8) Article e0160374.
- Canellas, L.P., Canellas, N.O.A., Irineu, L.E., Olivares, F.L. & Piccolo, A. (2020) Plant chemical priming by humic acids. *Chemical and Biological Technologies in Agriculture*, 7, 12.
- Carrasco-Gil, S., Allende-Montalbán, R., Hernández-Apaolaza, L. & Lucena, J.J. (2021) Application of Seaweed Organic Components Increases Tolerance to Fe Deficiency in Tomato Plants. *Agronomy*, 11, 507.
- Carrasco-Gil, S., Ortega-Villasante, C., Sobrino-Plata, J., Barón-Sola, Á., Millán, R. & Hernández, L.E. (2023) Attenuation of mercury phytotoxicity with a high nutritional level of nitrate in alfalfa plants grown hydroponically. *Plant Stress*, 7, 100131.
- Catarecha, P., Segura, M.D., Franco-Zorrilla, J.M., García-Ponce, B., Lanza, M., Solano, R., Paz-Ares, J. & Leyva, A. (2007) A mutant of the *Arabidopsis* phosphate transporter PHT1;1 displays enhanced arsenic accumulation. *Plant Cell*, 19, 1123–1133.
- Chary, N.S., Kamala, C.T. & Raj, D.S.S. (2008) Assessing risk of heavy metals from consuming food grown on sewage irrigated soils and food chain transfer. *Ecotoxicology and Environmental Safety*, 69, 513–524.
- Chitarra, W., Pagliarani, C., Maserti, B., Lumini, E., Siciliano, I., Cascone, P., Schuber A., Gambino, G., Balestrini, R. & Guerrieri, E. (2016) Insights on the impact of arbuscular mycorrhizal symbiosis on tomato tolerance to water stress. *Plant Physiology*, 171, 00307.
- Chugh, G., Siddique, K.H.M. & Solaiman, Z.M. (2021) Nanobiotechnology for agriculture: smart technology for combating nutrient deficiencies with nanotoxicity challenges. *Sustainability*, 13. <https://doi.org/10.3390/su13041781>
- Cominelli, E., Pilu, R. & Sparvoli, F. (2020) Phytic acid and mineral biofortification strategies: From plant science to breeding and biotechnological approaches. *Plants*, 9, 553.
- Consentino, B.B., Ciriello, M., Sabatino, L., Vultaggio, L., Baldassano, S., Vasto, S., Roupael, Y., La Bella, S. & De Pascale, S. (2023) Current Acquaintance on Agronomic Biofortification to Modulate the Yield and Functional Value of Vegetable Crops: A Review. *Horticulturae*, 9, 219.
- Cristofano, F., El-Nakhel, C., Roupael, Y. (2021) Biostimulant substances for sustainable agriculture: origin, operating mechanisms and effects on Cucurbits, leafy greens, and nightshade vegetables species. *Biomolecules*, 11, 1103.
- D'Imperio, M., Renna, M., Cardinali, A., Buttaro, D., Santamaria, P. & Serio, F. (2016) Silicon biofortification of leafy vegetables and its bioaccessibility in the edible parts. *Journal of Science of Food and Agriculture*, 96, 751–756.
- DalCorso, G., Fasani, E., Manara, A., Visioli, G. & Furini, A. (2019) Heavy metal pollutions: State of the art and innovation in phytoremediation. *International Journal of Molecular Science*, 20, 3412.
- Dalcorso, G., Manara, A., Piasentin, S. & Furini, A. (2014) Nutrient metal elements in plants. *Metallomics*, 6, 1770–1788.
- De Volder, M.F.L., Tawfick, S.H., Baughman, R.H. & Hart, A.J. (2013) Carbon nanotubes: present and future commercial applications. *Science*, 339, 535–539.
- Del Buono, D. (2021) Can biostimulants be used to mitigate the effect of anthropogenic climate change on agriculture? It is time to respond. *Science of the Total Environment*, 751, 141763.
- Del Río, L.A. (2015) ROS and RNS in plant physiology: An overview. *Journal of Experimental Botany*, 66, 2827–2837.
- Dhaliwal, S.S., Sharma, V. & Shukla, A.K. (2022) Chapter One - Impact of micronutrients in mitigation of abiotic stresses in soils and plants—A progressive step toward crop security and nutritional quality. *Advances in Agronomy* 173, 1–78.
- Dilnawaz, F., Kalaji, M.H. & Misra, A.N. (2023) Nanotechnology in improving photosynthesis under adverse climatic conditions: Cell to Canopy action. *Plant Nano Biology*. 4, 100035. <https://doi.org/10.1016/j.plana.2023.100035>.
- Dimkpa, C.O. & Bindraban, P.S. (2016) Fortification of micronutrients for efficient agronomic production: a review. *Agronomy for Sustainable Development*, 36(1), 7.
- Dresselhaus, M.S., Dresselhaus, G. & Jorio, A. (2004) Unusual properties and structure of carbonnanotubes. *Annual Review of Material Research*, 34, 247–278. <https://doi.org/10.1146/annurev.matsci.34.040203.114607>
- Dutt, S., Manjul, A.S., Chauhan, M., Changan, S.S., Raigond, P., Singh, B. & Chakrabarti, S.K. (2019) Biotechnology for nutritional and associated processing quality improvement in potato. In: Jaiwal, P., Chhillar, A., Chaudhary, D., Jaiwal, R. (eds) *Nutritional Quality Improvement in Plants. Concepts and Strategies in Plant Sciences*. Springer, Cham. 10.1007/978-3-319-95354-0_15 pp. 429–483.
- Ebbisa, A. (2022) Mechanisms underlying cereal/legume intercropping as nature-based biofortification: A review. *Food Production, Processing and Nutrition*, 4, 19.
- Farshchi, H.K., Azizi, M., Teymouri, M., Nikpoor, A.R. & Jaafari, M.R. (2021) Synthesis and characterization of nanoliposome containing Fe₂⁺ element: A superior nano-fertilizer for ferrous iron delivery to sweet basil. *Scientia Horticulturae*, 283, 110110
- Fernández, V. & Brown, P.H. (2013) From plant surface to plant metabolism: the uncertain fate of foliar-applied nutrients. *Frontiers in Plant Science*, 4, 289.
- Fernández, M., Pagnussat, L.A., Borrajo, M.P., Perez-Bravo, J.J., Francois, N.J. & Creus C.M. (2022) Chitosan/starch beads as bioinoculants carrier: Long-term survival of bacteria and plant growth promotion. *Applied Microbiology and Biotechnology* 106, 7963–7972.
- Fernández, S., Poschenrieder, C., Marcenò, C., Gallego, J.R., Jiménez-Gámez, D., Bueno A. & Afif, E. (2017) Phytoremediation capability of native plant species living on Pb-Zn and Hg-As mining wastes in the Cantabrian range, north of Spain. *Journal of Geochemical Exploration*, 174, 10–20.
- Fernández-Caliani, J.C., Barba-Brioso, C., González, I. & Galán, E. (2009) Heavy metal pollution in soils around the abandoned mine sites of the Iberian pyrite belt (Southwest Spain). *Water Air Soil Pollution*, 200, 211–226.
- Ganugi, P., Martinelli, E. & Lucini, L. (2021) Microbial biostimulants as a sustainable approach to improve the functional quality in plant-based foods: A review. *Current Opinion of Food Science*, 41, 217–223.
- García, A.C., Olaetxea, M., Santos, L.A., Mora, V., Baigorri, R., Fuentes, M., Zamarreño, A.M., Berbara, R.L. & Garcia-Mina, J.M. (2016) Involvement of hormone and ROS signalling pathways in the beneficial action of humic substances on plants growing under normal and stressing conditions. *BioMed Research International*, 2016, 3747501.

- García de la Torre, V.S., Coba de la Peña, T., Pueyo, J.J. & Lucas, M.M. (2021) Cadmium-tolerant and -sensitive cultivars identified by screening of *Medicago truncatula* germplasm display contrasting responses to cadmium stress. *Frontiers in Plant Science*, 12, 1–17.
- Garg, M., Sharma, N., Sharma, S., Kapoor, P., Kumar, A., Chunduri, V. & Arora, P. (2018) Biofortified crops generated by breeding, agronomy, and transgenic approaches are improving lives of millions of people around the world. *Frontiers of Nutrition*, 5, 12.
- Ghasempour, M., Iranbakhsh, A., Ebadi, M. & Ardebili, Z.O. (2019) Multi-walled carbon nanotubes improved growth, anatomy, physiology, secondary metabolism, and callus performance in *Catharanthus roseus*: an in vitro study. *3 Biotech*, 9(11), 404. doi: <https://doi.org/10.1007/s13205-019-1934-y>.
- Gisbert, C., Clemente, R., Navarro-Aviñó, J., Baixauli, C., Ginér, A., Serrano, R., Walker, D.J. & Bernal, M.P. (2006) Tolerance and accumulation of heavy metals by Brassicaceae species grown in contaminated soils from Mediterranean regions of Spain. *Environmental and Experimental Botany*, 56, 19–27.
- Gnanaprakasam, P.D. & Vanisree, A.J. (2022) Recurring detrimental impact of agrochemicals on the ecosystem, and a glimpse of organic farming as a possible rescue. *Environmental Science of Pollution Research*, 29, 75103–75112.
- Gonzalez-Grandio, E., Demirer, G.S., Jackson, C.T., Yang, D., Ebert, S., Molawi, K., Keller, H. & Landry, M.P. (2021) Carbon nanotube biocompatibility in plants is determined by their surface chemistry. *Journal of Nanobiotechnology*, 19. <https://doi.org/10.1186/s12951-021-01178-8>
- Gupta, A.P., Upadhyay, P., Sen, T. & Dutta, J. (2023) Agricultural waste as a resource: the lesser travelled road to sustainability. *Agric. Agriculture Waste Management and Bioresource*, 1–20.
- Gupta, P.K., Balyan, H.S., Sharma, S. & Kumar, R. (2020) Genetics of yield, abiotic stress tolerance and biofortification in wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics*, 133: 1569–1602.
- Gupta, P.K., Balyan, H.S., Sharma, S. & Kumar, R. (2021) Biofortification and bioavailability of Zn, Fe and Se in wheat: present status and future prospects. *Theoretical and Applied Genetics*, 134: 1–35.
- Guzmán-Báez, G.A., Trejo-Téllez, L.I., Ramírez-Olvera, S.M., Salinas-Ruiz, J., Bello-Bello, J.J., Alcántar-González, G., Hidalgo-Contreras, J.V. & Gómez-Merino, F.C. (2021) Silver nanoparticles increase nitrogen, phosphorus, and potassium concentrations in leaves and stimulate root length and number of roots in tomato seedlings in a hormetic manner. *Dose Response*, 19(4), 15593258211044576. doi: <https://doi.org/10.1177/15593258211044576>.
- Hasnain, M., Munir, N., Abideen, Z., Zulfiqar, F., Koyro, H.W., El-Naggar, A., Caçador, I., Duarte, B., Rinklebe, J. & Yong, J.W.H. (2023) Biochar-plant interaction and detoxification strategies under abiotic stresses for achieving agricultural resilience: A critical review. *Ecotoxicological Environmental Safety*, 249, 14408.
- Hawrylak-Nowak, B., Dresler, S., Rubinowska, K., Matraszek-Gawron, R., Woch, W. & Hasanuzzaman, M. (2018) Selenium biofortification enhances the growth and alters the physiological response of lamb's lettuce grown under high temperature stress. *Plant Physiology and Biochemistry*, 127: 446–456.
- He, H., Pham-Huy, L.A., Dramou, P., Xiao, D., Zuo, P. & Pham-Huy, C. (2013) Carbon nanotubes: applications in pharmacy and medicine. *BioMed Research International*, 578290.
- Hernández, L.E., Sobrino-Plata, J., Montero-Palmero, M.B., Carrasco-Gil, S., Flores-Cáceres, M.L., Ortega-Villasante, C. & Escobar, C. (2015) Contribution of glutathione to the control of cellular redox homeostasis under toxic metal and metalloid stress. *Journal of Experimental Botany*, 66, 2901–2911.
- Izdyrczyk, G., Ligas, B., Mikula, K., Witek-Krowiak, A., Moustakas, K. & Chojnacka, K. (2021) Biofortification of edible plants with selenium and iodine – A systematic literature review. *Science of The Total Environment*, 754, 141983.
- Jannin, L., Arkoun, M., Ourry, A., Laïne, P., Goux, D., & Garnica, M. (2012) Microarray analysis of humic acid effects on Brassica napus growth: involvement of N C and S metabolisms. *Plant and Soil*, 359, 297–319.
- Jogawat, A., Yadav, B., Chhaya, A. & Narayan, O.P. (2021) Metal transporters in organelles and their roles in heavy metal transportation and sequestration mechanisms in plants. *Physiologia Plantarum*, 173, 259–275.
- Kabata-Pendias, A. (2000) *Trace Elements in Soils and Plants* (4th ed.). CRC Press. <https://doi.org/10.1201/b10158>.
- Kah, M., Tufenkji, N. & White, J.C. (2019) Nano-enabled strategies to enhance crop nutrition and protection. *Natural Nanotechnology*, 14, 532–540. <https://doi.org/10.1038/s41565-019-0439-5>
- Karny, A., Zinger A., Kajal A., Shainsky-Roitman, J. & Schroeder, A. (2018) Therapeutic nanoparticles penetrate leaves and deliver nutrients to agricultural crops. *Scientific Reports*, 8, 7589. <https://doi.org/10.1038/s41598-018-25197-y>
- Kaur, P., Choudhary, R., Pal, A., Mony, C. & Adholeya, A. (2020). Polymer-metal nanocomplexes based delivery system: A boon for agriculture revolution. *Current Topics in Medicinal Chemistry*, 20, 1009–1028. <https://doi.org/10.2174/1568026620666200330160810>
- Kaushal, P., Ali, N., Saini, S., Pati, P.K. & Pati, A.M. (2023) Physiological and molecular insight of microbial biostimulants for sustainable agriculture. *Frontiers in Plant Science*, 14, 41413.
- Khan, A., Singh, J., Upadhyay, V.K., Singh, A.V. & Shah, S. (2019) *Microbial Biofortification: A Green Technology Through Plant Growth Promoting Microorganisms*. Sustainable Green Technologies for Environmental Management. Springer Singapore, Singapore, pp. 255–269.
- Khan, S., Kaur, K., Kumar, V. & Tiwari, S. (2023) Iron transport and homeostasis in plants: current updates and applications for improving human nutrition values and sustainable agriculture. *Plant Growth Regulation*, 100, 373–390.
- Khoso, M.A., Wagan, S., Alam, I., Hussain, A., Ali, Q., Saha, S., Poudel, T.R., Manghwar, H. & Liu, F. (2024) Impact of plant growth-promoting rhizobacteria (PGPR) on plant nutrition and root characteristics: Current perspective. *Plant Stress*, 11, 100341.
- Kumari, M., Swarupa, P., Kesari, K.K. & Kumar, A. (2023) Microbial Inoculants as Plant Biostimulants: A Review on Risk Status. *Life* 13, 12.
- Lacalle, R.G., Bernal, M.P., Álvarez-Robles, M.J. & Clemente, R. (2023) Phytostabilization of soils contaminated with As, Cd, Cu, Pb and Zn: Physicochemical, toxicological and biological evaluations. *Soil & Environmental Health*, 1, 100014.
- Lang, C., Mission, E.G., Ahmad-Fuaad, A.A-H. & Shaalan, M. (2021). Nanoparticle tools to improve and advance precision practices in the Agrifoods Sector towards sustainability - A review. *Journal of Cleaner Production*, 293. Elsevier Ltd. <https://doi.org/10.1016/J.JCLEPRO.2021.126063>
- Lešková, A., Javot, H. & Giehl, R.F.H. (2022) Metal crossroads in plants: Modulation of nutrient acquisition and root development by essential trace metals. *Journal of Experimental Botany*, 73, 1751–1765.
- Li, J., Martin, C. & Fernie, A. (2024) Biofortification's contribution to mitigating micronutrient deficiencies. *Nature Food*, 5, 19–27.
- Li, S., Liu, X., Zhou, X., Li, Y., Yang, W. & Chen, R. (2019) Improving zinc and iron accumulation in maize grains using the zinc and iron transporter ZmZIP5. *Plant Cell Physiology*, 60: 2077–2085.
- Lilay, G.H., Thiébaud, N., du Mee, D., Assunção, A.G.L., Schjoerring, J.K., Husted, S. & Persson, D.P. (2024) Linking the key physiological functions of essential micronutrients to their deficiency symptoms in plants. *New Phytologist*, 242, 881–902.
- López-Rayo, S., Nadal, P. & Lucena, J.J. (2015) Reactivity and effectiveness of traditional and novel ligands for multi-micronutrient fertilization in a calcareous soil. *Frontiers in Plant Science*, 6, 752
- Loscos, J., Naya, L., Ramos, J., Clemente, M.R., Matamoros, M.A. & Becana, M. (2006) A reassessment of substrate specificity and activation of phytochelatin synthases from model plants by physiologically relevant metals. *Plant Physiology*, 140, 1213–1221.

- Lu, Y., Li, T., Li, R., Zhang, P., Li, X.X., Bai, Z. & Wu, J. (2024) Role of SbNRT1.1B in cadmium accumulation is attributed to nitrate uptake and glutathione-dependent phytochelatin biosynthesis. *Journal of Hazard Material*, 479, 135655.
- Ma, X., Geiser-Lee, J., Deng, Y. & Kolmakov, A. (2010) Interactions between engineered nanoparticles (ENPs) and plants: phytotoxicity, uptake and accumulation. *Science of Total Environment*, 408(16), 3053–3061.
- Mandal, S., Gupta, S.K., Ghorai, M., Patil, M.T., Biswas, P., Kumar, M., Radha, A., Gopalakrishnan, A.V., Mohture, V.M., Rahman, M.D.H., Prasanth, D.A., Mane, A.B., Jha, N.K., Jha, S.K., Lal, M.K., Tiwari, R.K. & Dey, A. (2023) Retraction Note: Plant nutrient dynamics: a growing appreciation for the roles of micronutrients. *Plant Growth Regulation*, 1–2.
- Márquez-García, B., Horemans, N., Torronteras, R. & Córdoba, F. (2012) Glutathione depletion in healthy cadmium-exposed *Erica andevalensis*. *Environmental and Experimental Botany*, 75, 159–166.
- Martinez-Ballesta, M.C., Chelbi, N., Lopez-Zaplana, A. & Carvajal, M. (2020) Discerning the mechanism of the multiwalled carbon nanotubes effect on root cell water and nutrient transport. *Plant Physiology and Biochemistry*, 146, 23–30
- Martínez-Ballesta, M.C., Zapata, L., Chalbi, N. & Carvajal, M. (2016) Multiwalled carbon nanotubes enter broccoli cells enhancing growth and water uptake of plants exposed to salinity. *Journal of Nanobiotechnology*, 14, 42. <https://doi.org/10.1186/s12951-016-0199-4>
- Martínez-Ballesta, M.C., García-Gomez, P., Yepes-Molina, L., Guarnizo, A.G., Teruel, J.A. & Carvajal, M. (2018) Plasma membrane aquaporins mediate vesicle stability in broccoli. *PlosOne*, 8. DOI: <https://doi.org/10.1371/journal.pone.0192422>
- Martínez-Cortijo, J. & Ruiz-Canales, A. (2018) Effect of heavy metals on rice irrigated fields with waste water in high pH Mediterranean soils: The particular case of the Valencia area in Spain. *Agricultural Water Management*, 210, 108–123.
- Martos, S., Gallego, B., Sáez, L., López-Alvarado, J., Cabot, C. & Poschenrieder, C. (2016) Characterization of zinc and cadmium hyperaccumulation in three *Noccaea* (Brassicaceae) populations from non-metalliferous sites in the eastern pyrenees. *Frontiers in Plant Science*, 7, 1–13.
- Merchant, S.S. (2010) The elements of plant micronutrients. *Plant Physiology*, 154, 512–515.
- Mikula, K., Izydorczyk, G., Skrzypczak, D., Mironiuk, M., Moustakas, K., Witek-Krowiak, A. & Chojnacka, K. (2020) Controlled release micronutrient fertilizers for precision agriculture - A review. *The Science of the total environment*, 712, 136365.
- Mikula, K., Konieczka, M. & Taf, R. (2023) Tannery waste as a renewable source of nitrogen for production of multicomponent fertilizers with biostimulating properties. *Environmental Science of Pollution Research*, 30, 8759–8777.
- Mishra, A., Saini, R.K. & Bajpai, A.K. (2020) Polymer Formulations for Pesticide Release. In *Controlled Release of Pesticides for Sustainable Agriculture*; Springer: Cham, Switzerland, 185–206.
- Mishra, P., Mishra, J. & Arora, N.K. (2023) Biofortification revisited: Addressing the role of beneficial soil microbes for enhancing trace elements concentration in staple crops. *Microbiology Research*, 275, 127442.
- Muszyńska, E. & Labudda, M. (2019) Dual role of metallic trace elements in stress biology—from negative to beneficial impact on plants. *International Journal of Molecular Science*, 20(13), 3117.
- Mykolenko, S., Liedienov, V., Kharytonov, M., Makieieva, N., Kuliush, T., Queralt, I., Marguá, E., Hidalgo, M., Pardini, G. & Gispert, M. (2018) Presence, mobility and bioavailability of toxic metal(oids) in soil, vegetation and water around a Pb-Sb recycling factory (Barcelona, Spain). *Environmental Pollution*, 237, 569–580.
- Narayanan, N., Beyene, G., Chauhan, R.D., Gaitán-Solís, E., Gehan, J., Butts, P., Siritunga, D., Okwuonu, I., Woll, A., Jiménez-Aguilar, D.M., Boy, E., Grusak, M.A., Anderson, P. & Taylor, N.J. (2019) Biofortification of field-grown cassava by engineering expression of an iron transporter and ferritin. *Nature Biotechnology*, 37, 144–151.
- Navarro-León, E., López-Moreno, F.J., Borda, E., Marín, C., Sierras, N., Blasco, B. & Ruiz, J.M. (2022) Effect of l-amino acid-based biostimulants on nitrogen use efficiency (NUE) in lettuce plants. *Journal of the Science of Food and Agriculture*, 102, 7098–7106.
- Navarro-León, E., Ruiz, J.M., Graham, N. & Blasco, B. (2018) Physiological profile of CAX1a TILLING mutants of *Brassica rapa* exposed to different calcium doses. *Plant Science*, 272, 164–172.
- Neri, A., Francin, A., Giovannelli, A., Traversari, S. & Sebastiani, L. (2024) Differences in mineral and osmotic balances enhance zinc translocation in an aquaporin overexpressing poplar. *Plant Physiology and Biochemistry*, 208, 108528.
- Noman, M., Ahmed, T., Wang, J. & White, J.C. (2022) Micronutrient–microbiome interplay: a critical regulator of soil–plant health. *Trends in Microbiology*, 32, 319–320.
- Ohsowski, B.M., Dunfield, K., Klironomos, J.N. & Hart, M.M. (2018) Plant response to biochar, compost, and mycorrhizal fungal amendments in post-mine sandpits. *Restoration Ecology*, 26, 63–72.
- Olaetxea, M., De Hita, D., García, C.A., Fuentes, M., Baigorri, R., Mora, V., Garnica, M., Urrutia, O., Erro, J., Zamarreño, A.M., Berbara, R.L. & García-Mina, J.M. (2018) Hypothetical framework integrating the main mechanisms involved in the promoting action of rhizospheric humic substances on plant root- and shoot- growth. *Applied of Soil Ecology*, 123, 521–537,
- Paape, T., Heiniger, B., Santo-Domingo M., Clear, M.R., Lucas, M.M. & Pueyo, J.J. (2022) Genome-wide association study reveals complex genetic architecture of cadmium and mercury accumulation and tolerance traits in *Medicago truncatula*. *Frontiers in Plant Science*, 12, 1–20.
- Palma, J.M., Gupta, D.K. & Corpas, F.J. (2013) Metalloenzymes involved in the metabolism of reactive oxygen species and heavy metal stress. In: Gupta DK, Corpas FJ, Palma JM (eds) *Heavy Metal Stress in Plants*. Springer-Verlag, Berlin Heidelberg, pp. 1–17
- Park, S., Elless, M.P., Park, J., Jenkins, A., Lim, W., Chambers, I.V. E. & Hirschi, K.D. (2009) Sensory analysis of calcium-biofortified lettuce. *Plant Biotechnology Journal*, 7, 106–117.
- Pérez-Aguilar, H., Lacruz-Asaro, M. & Arán-Ais F. (2023) Evaluation of biostimulants based on recovered protein hydrolysates from animal by-products as plant growth enhancers. *Journal of Plant Science and Phytopathology*, 7, 042–047.
- Popa, D.G., Lupu, C., Constantinescu-Aruxandei, D. & Oancea, F. (2022) Humic Substances as Microalgal Biostimulants— Implications for Microalgal Biotechnology. *Marine Drugs*, 20, 327.
- Pradhan, S. & Mailpalli, D.R. (2017) Interaction of engineered nanoparticles with the agri-environment. *Journal of Agriculture and Food Chemistry*, 65, 8279–8294. <https://doi.org/10.1021/acs.jafc.7b02528>
- Pradhan, S.K., Pandit, E., Pawar, S., Pradhan, A., Behera, L., Das, S.R. & Pathak, H. (2020) Genetic regulation of homeostasis, uptake, biofortification and efficiency enhancement of iron in rice. *Environmental and Experimental Botany*, 177, 104066
- Prasad, R. & Shivay, Y.S. (2020) Agronomic biofortification of plant foods with minerals, vitamins and metabolites with chemical fertilizers and liming. *Journal of Plant Nutrition*, 43, 1534–1554.
- Ramos, A.C., Dobbss, L.B., Santos, L.A., Fernandes, M.S., Olivares, F.L., Aguiar, N.O. & Canellas, L.P. (2015) Humic matter elicits proton and calcium fluxes and signaling dependent on Ca²⁺-dependent protein kinase (CDPK) at early stages of lateral plant root development. *Chemical and Biological Technologies in Agriculture*, 2, 3.
- Rathor, P., Upadhyay, P., Ullah, A., Gorim, L.Y. & Thilakarathna, M.S. (2024) Humic acid improves wheat growth by modulating auxin and cytokinin biosynthesis pathways. *AoB PLANTS*, 16 (2), 2.
- Ren, J., Zhang, Z. & Geng, S. (2024) Molecular mechanisms of intracellular delivery of nanoparticles monitored by an enzyme-induced proximity labeling. *Nano-Micro Letters*, 16, 103 <https://doi.org/10.1007/s40820-023-01313-0>

- Ricci, M., Tilbury, L., Daridon, B. & Sukalac, K. (2019) General principles to justify plant biostimulant claims. *Frontiers in Plant Science*, 10, 494.
- Rios, J.J., Garcia-Ibañez, P. & Carvajal, M. (2019) The use of biovesicles to improve the efficiency of Zn foliar fertilization. *Colloids and Surfaces B: Biointerfaces*, 173, 899–905.
- Rios, J.J., Lopez-Zaplana, A., Barzana, G., Martinez-Alonso, A., Carvajal, M. (2021) Foliar application of boron nanoencapsulated in almond trees allows B movement within tree and implements water uptake and transport involving aquaporins. *Frontiers in Plant Science*, 12, 2373. DOI=<https://doi.org/10.3389/fpls.2021.752648>
- Rios, J.J., Yepes-Molina, L., Martinez-Alonso, A. & Carvajal, M. (2020) Nanobiofertilisation as a novel technology for highly efficient foliar application of Fe and B in almond trees. *Royal Society Open Science*, <https://doi.org/10.1098/rsos.200905>
- Rodrigo-Moreno, A., Poschenrieder, C. & Shabala, S. (2013) Transition metals: A double edge sword in ROS generation and signaling. *Plant Signal and Behaviour*, 8(3), e23425.
- Rodríguez-Serrano, M., Romero-Puertas, M.C., Pazmino, D.M., Testillano, P.S., Risueno, M.C., Del Río, L.A. & Sandalio, L.M. (2009) Cellular response of pea plants to cadmium toxicity: Cross talk between reactive oxygen species, nitric oxide, and calcium. *Plant Physiology*, 150, 229–243.
- Rudnicki, R., Biczkowski, M., Wiśniewski, Ł., Wiśniewski, P., Bielski, S. & Marks-Bielska, R. (2023) Towards Green Agriculture and Sustainable Development: Pro-Environmental Activity of Farms under the Common Agricultural Policy. *Energies* 16, 1770.
- Sachdev, S., Ansari, S.A., Ansari, M.I., Fujita, M. & Hasanuzzaman, M. (2021) Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. *Antioxidants*, 10, 277.
- Safiuddin, M., Gonzalez, M., Cao, J.W. & Tighe, S.L. (2014) State-of-the-art report on use of nano-materials in concrete. *International Journal of Pavement Engineering*, 15, 940–949. <https://doi.org/10.1080/10298436.2014.893327>
- Saia, S., Colla, G., Raimondi, G., Di Stasio, E., Cardarelli, M., Bonini, P., Vitaglione, P., De Pascale, S. & Roupael, Y. (2019) An endophytic fungi-based biostimulant modulated lettuce yield, physiological and functional quality responses to both moderate and severe water limitation. *Scientia Horticulturae*, 256, 108595.
- Samadi, S., Saharkhiz, M.J., Azizi, M., Samiei, L. & Ghorbanpour, M. (2020) Multi-walled carbon nanotubes stimulate growth, redox reactions and biosynthesis of antioxidant metabolites in *Thymus daenensis* celak. *In vitro*. *Chemosphere*, (249), 126069, <https://doi.org/10.1016/j.chemosphere.2020.126069>.
- Sánchez-Palacios, J.T., Henry, D., Penrose, B. & Bell, R. (2023) Formulation of zinc foliar sprays for wheat grain biofortification: a review of current applications and future perspectives. *Frontiers in Plant Science*, 14, 1247600.
- Sandalio, L.M., Espinosa, J., Shabala, S., León, J. & Romero-Puertas, M.C. (2023) Reactive oxygen species- and nitric oxide-dependent regulation of ion and metal homeostasis in plants. *Journal of Experimental Botany*, 74, 5970–5988.
- Santos, J.L., Malvar, J.L., Martín, J., Aparicio, I. & Alonso, E. (2020) Distribution of metals in sediments of the Guadiamar river basin 20 years after the Aznalcollar mine spill: Bioavailability and risk assessment. *Journal of Environmental Management*, 260, 110146
- Sanz-Fernández, M., Rodríguez-González, A., Sandalio, L.M. & Romero-Puertas, M.C. (2021) Role of potassium transporter KUP8 in plant responses to heavy metals. *Physiologia Plantarum*, 173, 180–190.
- Schjørring, J.K. & Cakmak, I. (2014) Plant mineral nutrition for nutrient and food security *Physiologia Plantarum*, 151(3), 199. doi: <https://doi.org/10.1111/ppl.12215>. PMID: 24773189.
- Shah, Z.H., Rehman, H.M., Akhtar, T., Alsamadany, H., Hamooh, B.T., Mujtaba, T., Daur I., Al Zahrani, Y., Alzahrani, H.A.S., Ali, S., Yang, S.H. & Chung, G. (2018) Humic substances: determining potential molecular regulatory processes in plants. *Frontiers in Plant Science*, 9, 263.
- Shahrajabian, M.H., Chaski, C., Polyzos, N., Tzortzakis, N. & Petropoulos, S.A. (2021) Sustainable Agriculture Systems in Vegetable Production Using Chitin and Chitosan as Plant Biostimulants. *Biomolecules*, 11, 819.
- Shalaby, T.A., Bayoumi, Y., Abdalla, N., Taha, H., Alshaal, T., Shehata, S., Amer, M., Domokos-Szabolcsy, É. & El-Ramady, H. (2016). Nanoparticles, soils, plants and sustainable agriculture. In: Ranjan, S., Dasgupta, N., Lichtfouse, E. (eds) *Nanoscience in Food and Agriculture 1. Sustainable Agriculture Reviews*, vol 20. Springer, Cham. https://doi.org/10.1007/978-3-319-39303-2_10
- Sharma, A. & Verma, R.K. (2019) *Biofortification: A Promising Approach Toward Eradication of Hidden Hunger*. Microbial Interventions in Agriculture and Environment. Springer Singapore, Singapore, pp. 313–327.
- Shoukat, R. & Khan, M.I. (2022) Carbon nanotubes/nanofibers (CNTs/CNFs): a review on state of the art synthesis methods. *Microsystems Technology*, 28, 885–901.
- Simkin, A.J. (2019) Genetic engineering for global food security: Photosynthesis and biofortification. *Plants*, 8, 586.
- Singla, R., Kumari, A. & Yadav, S.K. (2019) Impact of Nanomaterials on Plant Physiology and Functions. In: Husen, A., Iqbal, M. (eds) *Nanomaterials and Plant Potential*. Springer, 349–377. Cham. https://doi.org/10.1007/978-3-030-05569-1_14
- Sinha, T., Bhagwatwar, P., Krishnamoorthy, C. & Chidambaram, R. (2019) *Polymer based micro and nanoencapsulation of agrochemicals*. In *Polymers for Agri-Food Applications*; Springer: Cham, Switzerland, 5–28.
- Sobrinho-Plata, J., Barón-Sola, Á., Ortega-Villasante, C., Ortega-Campayo, V., González-Berrocá, C., Conesa-Quintana, C., Carrasco-Gil, S., Muñoz-Pinilla, M., Abadía, J., Álvarez-Fernández, A. & Hernández, L.E. (2021) Sulphur and biothiol metabolism determine toxicity responses and fate of mercury in *Arabidopsis*. *Environmental and Experimental Botany*, 182, 104302.
- Sobrinho-Plata, J., Herrero, J., Carrasco-Gil, S., Pérez-Sanz, A., Lobo, C., Escobar, C., Millán, R. & Hernández, L.E. (2013) Specific stress responses to cadmium, arsenic and mercury appear in the metallophyte *Silene vulgaris* when grown hydroponically. *RSC Advances*, 3, 4736–4744.
- Sobrinho-Plata, J., Meyssen, D., Cuypers, A., Escobar, C. & Hernández, L.E. (2014) Glutathione is a key antioxidant metabolite to cope with mercury and cadmium stress. *Plant and Soil*, 377, 369–381.
- Solanki, A.R., Kamath, B.V. & Thakore, S. (2015) Carbohydrate crosslinked biocompatible polyurethanes: Synthesis, characterization, and drug delivery studies. *Journal of Applied Polymer Science*, 132. <https://doi.org/10.1002/app.42223>.
- Sorcía-Morales, M., Gómez-Merino, F.C., Sánchez-Segura, L., Spinoso-Castillo, J.L. & Bello-Bello, J.J. (2021) Multi-walled carbon nanotubes improved development during *in vitro* multiplication of sugarcane (*Saccharum* spp.) in a semi-automated bioreactor. *Plants (Basel)* 10(10), 2015. doi: <https://doi.org/10.3390/plants10102015>.
- Souza, A.C., Olivares, F.L., Peres, L.E.P., Piccolo, A. & Canellas, L.P. (2022) Plant hormone crosstalk mediated by humic acids. *Chemical and Biological Technologies in Agriculture*, 9, 29.
- Sozer, N. & Kokini, J.L. (2009) Nanotechnology and its applications in the food sector. *Trends in Biotechnology*, 27(2), 82–89. doi: <https://doi.org/10.1016/j.tibtech.2008.10.010>.
- Srivastava, V., Sarkar, A., Singh, S., Singh, P., de Araujo, A.S.F. & Singh, R.P. (2017) Agroecological responses of heavy metal pollution with special emphasis on soil health and plant performances. *Frontiers in Environmental Sciences*, 5, 1–19.
- Sun, W., Shahrajabian, M.H., Kuang, Y. & Wang, N. (2024) Amino acids biostimulants and protein hydrolysates in agricultural sciences. *Plants*, 13, 210.
- Szóllósi, R., Molnár, Á., Kondak, S. & Kolbert, Z. (2020) Dual effect of nanomaterials on germination and seedling growth: stimulation vs phytotoxicity. *Plants (Basel)*, 9, 1745, <https://doi.org/10.3390/plants9121745>

- Tamariz-Angeles, C., Huamán, G.D., Palacios-Robles, E., Olivera-Gonzales, P. & Castañeda-Barreto, A (2021). Characterization of siderophore-producing microorganisms associated to plants from high-Andean heavy metal polluted soil from Callejón de Huaylas (Ancash, Perú). *Microbiological Research*, 250, 126811.
- Tan, K., Li, R., Huang, X. & Liu, Q. (2018) Outer membrane vesicles: current status and future direction of these novel vaccine adjuvants. *Frontiers of Microbiology*, 9 p. 783.
- Tavares, O.C.H., Santos, L.A., Ferreira, L.M., Sperandio, M.V.L., da Rocha, J.G., García, C., Dobbss, L.B., Berbara, R.L.L., de Souza, S.R. & Fernandes, M.S. (2017), Humic acid differentially improves nitrate kinetics under low- and high-affinity systems and alters the expression of plasma membrane H⁺-ATPases and nitrate transporters in rice. *Annals of Applied Biology*, 170, 89–103.
- Till, B.J., Datta, S. & Jankowicz-Cieslak, J. (2018) *TILLING: The Next Generation*. Springer, Cham, pp. 139–160.
- Tripathi, S., Mahra, S.J.V., Tiwari, K., Rana, S., Tripathi, D.K., Sharma, S. & Sahi, S. (2023) Recent Advances and Perspectives of Nanomaterials in Agricultural Management and Associated Environmental Risk: A Review. *Nanomaterials*, 13, 1604.
- Uraguchi, S., Tanaka, N., Hofmann, C., Abiko, K., Ohkama-Ohtsu, N., Weber, M., Kamiya, T., Sone, Y., Nakamura, R., Takanezawa, Y., Kiyono, M., Fujiwara, T. & Clemens, S. (2017) Phytochelatin synthase has contrasting effects on cadmium and arsenic accumulation in rice grains. *Plant and Cell Physiology*, 58, 1730–1742.
- Vaghela, P., Kumar Das, A., Trivedi, K., Vijay-Anand, K.G., Shinde, P. & Ghosh, A. (2022) Characterization and metabolomics profiling of *Kappaphycus alvarezii* seaweed extract. *Algal Research*, 66, 102774.
- Vangronsveld, J., Van Assche, F. & Clijsters, H. (1995) Reclamation of a bare industrial area contaminated by non-ferrous metals: In situ metal immobilization and revegetation. *Environmental Pollution*, 87, 51–59.
- Vázquez, S., Goldsbrough, P. & Carpena, R.O. (2009) Comparative analysis of the contribution of phytochelatin to cadmium and arsenic tolerance in soybean and white lupin. *Plant Physiology and Biochemistry*, 47, 63–67.
- Vlčko, T. & Ohnoutková, L. (2019) Recent advances and perspectives in crop biofortification. *Biolgia Plantarum*, 63, 586–593
- Wakeel, A., Farooq, M., Bashir, K. & Ozturk, L. (2018) Micronutrient Malnutrition and Biofortification: Recent Advances and Future Perspectives. *Plant Micronutrient Use Efficiency*. Academic Press, pp. 225–243
- Wang, M., Li, Y., Yang, Y., Tao, H., Mustafa, G., Meng, F., Sun, B., Wang, J., Zhao, Y., Zhang, F., Cheng, K. & Wang, Q. (2023) Biofortification of health-promoting glucosinolates in cruciferous sprouts along the whole agro-food chain. *Trends Food Science and Technology*, 140, 104164.
- Wang, N., Qiu, W., Dai, J., Guo, X., Lu, Q., Wang, T., Li, S., Liu, T. & Zuo, Y. (2019) AhNRAMP1 enhances manganese and zinc uptake in plants. *Frontiers in Plant Science*, 10: 415.
- Wang, Z., Xu, L., Zhao, J., Wang, X., White, J.C. & Xing, B. (2016) CuO nanoparticle interaction with *Arabidopsis thaliana*: toxicity, parent-progeny transfer, and gene expression. *Environmental Science & Technology*, 50(11), 6008–6016.
- White, P.J. & Broadley, M.R. (2009) Biofortification of crops with seven mineral elements often lacking in human diets – iron, zinc, copper, calcium, magnesium, selenium and iodine. *New Phytologist*, 182: 49–84.
- White, P.J. & Brown, P.H. (2010) Plant nutrition for sustainable development and global health. *Annals of Botany*, 105, 1073–1080.
- White, P.J., George, T.S., Dupuy, L.X., Karley, A.J., Valentine, T.A., Wiesel, L. & Wishart J. (2013) Root traits for infertile soils. *Frontiers in Plant Science*, 4, 193.
- Yadav, A., Yadav, K. & Abd-Elsalam, K.A. (2023) Nanofertilisers: Types, delivery and advantages in agricultural sustainability. *Agrochemicals*, 2(2), 296–336. doi: <https://doi.org/10.3390/agrochemicals2020019>.
- Yamaji, N. & Ma, J.F. (2021) Metalloid transporters and their regulation in plants. *Plant Physiology*, 187, 1929–1939.
- Ye, X., Al-Babili, S., Klöti, A., Zhang, J., Lucca, P., Beyer, P. & Potrykus, I. (2000) Engineering the provitamin A (beta-carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. *Science*, 287:303–5.
- Yepes-Molina, L., Martínez-Ballesta, M.C. & Carvajal, M. (2020) Plant plasma membrane vesicles interaction with keratinocytes reveals their potential as carriers. *Journal of Advanced Research*, 8(23), 101–111. doi: <https://doi.org/10.1016/j.jare.2020.02.004>.
- Yi, G.H., Lee, H.S., Sohn, J.K. & Kim, K.M. (2012) Physico-chemical properties of *Arabidopsis* Ca²⁺/H⁺ antiporter transgenic rice grain. *Bioscience Research*, 9, 8–16.
- Yuniati, N., Kusumiyati, K., Mubarak, S. & Nurhadi, B. (2022) The role of moringa leaf extract as a plant biostimulant in improving the quality of agricultural products. *Plants*, 11, 2186.
- Zanin, L., Tomasi, N., Cesco, S., Varanini, Z. & Pinton, R. (2019) Humic substances contribute to plant iron nutrition acting as chelators and biostimulants. *Frontiers in Plant Sciences*, 10, 675.
- Zanin, L., Tomasi, N., Zamboni, A., Segal, D., Varanini, Z. & Pinton, R. (2018) Water-extractable humic substances speed up transcriptional response of maize roots to nitrate. *Environmental and Experimental Botany*, 147, 167–178.
- Zhao, F.J., Tang, Z., Song, J.J., Huang, X.Y. & Wang, P. (2022) Toxic metals and metalloids: Uptake, transport, detoxification, phytoremediation, and crop improvement for safer food. *Molecular Plants*, 15, 27–44.
- Zhu, C., Kobayashi, K., Loladze, I., Zhu, J., Jiang, Q., Xu, X., Liu, G., Seneweera, S., Ebi, K.L., Drewnowski, A., Fukagawa, N.K. & Ziska, L.H. (2018) Carbon dioxide (CO₂) levels this century will alter the protein, micronutrients, and vitamin content of rice grains with potential health consequences for the poorest rice-dependent countries. *Science Advances*, 4, eaaq1012.

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