

Viewpoints

The potential of arbuscular mycorrhizal fungi to enhance metallic micronutrient uptake and mitigate food contamination in agriculture: prospects and challenges

Summary

Optimizing agroecosystems and crops for micronutrient uptake while reducing issues with inorganic contaminants (metal(loid)s) is a challenging task. One promising approach is to use arbuscular mycorrhizal fungi (AMF) and investigate the physiological, molecular and epigenetic changes that occur in their presence and that lead to changes in plant metal(loid) concentration (biofortification of micronutrients or mitigation of contaminants). Moreover, it is important to understand these mechanisms in the context of the soil microbiome, particularly those interactions of AMF with other soil microbes that can further shape crop nutrition. To address these challenges, a two-pronged approach is recommended: exploring molecular mechanisms and investigating microbiome management and engineering. Combining both approaches can lead to benefits in human health by balancing nutrition and contamination caused by metal(loid)s in the agro-ecosystem.

Introduction

Current agriculture is facing key challenges to meet the increasing food demands of a rising human population while having to decrease the environmental footprint of food production. In the interest of achieving greater sustainability, agriculture should strive to decrease dependency on synthetic fertilizers due to: (1) unacceptable environmental impacts from excess application; (2) rising prices of energy; and (3) scarcity of certain resources that will decrease availability, with costs likely increasing. Agriculture is therefore looking for alternatives to preserve or enhance yield and product quality and to protect the environment. Arbuscular mycorrhizal fungi (AMF) are obligate biotrophs in symbiotic partnership with plant roots and have a fundamental role in agriculture. They are widely recognized as fundamental actors to enhance crop nutrition, especially in terms of macronutrients and

play a role in plant water acquisition, protection against pathogens and tolerance to metal(oid)s (Sosa-Hernández *et al.*, 2019; Janeeshma & Puthur, 2020; Wang *et al.*, 2022).

To date, little effort has been devoted to exploring the potential role of AMF in supplying metallic micronutrients to plants and in controlling the uptake of metallic contaminants (Lehmann & Rillig, 2015; Ferrol *et al.*, 2016). Metallic nutrients such as iron (Fe), zinc (Zn), copper (Cu) or manganese (Mn) are critical to plants, as they are required for several biological processes including, for example, photosynthesis, enzymatic metabolism, reproduction and plant defence against pathogens. As such, their availability can boost agricultural production and crop quality (Bouis & Welch, 2010; Jaiswal *et al.*, 2022). Globally, many of these elements are scarce in agricultural products and animal diets (including humans; Nair *et al.*, 2016), and aspects of soil chemistry (high pH and low organic matter, common in many agricultural fields) limit the available pool of micronutrients. As a result, plant demand cannot always be satisfied, and micronutrients thus become a limiting factor for plant production (yields) or quality (nutrient content). Micronutrients are essential in human and animal diets, with deficiencies causing serious health issues, including a compromised immune system, impaired growth and increased susceptibility to diseases (Alloway, 2013).

To deal with micronutrient scarcity, agriculture mainly relies on commercial fertilizers like chelated metals (soluble compounds in which a metallic micronutrient is bound to a ligand, facilitating the nutrient availability and uptake by crops) or inorganic salts (sulfates and oxides) to supply micronutrients to crops (Shuman, 2005; Montalvo *et al.*, 2016). As an alternative to this option, which depends on nonrenewable and declining resources, soil microorganisms such as AMF and bacteria could mobilize soil stocks of micronutrients (Hesterberg, 1998; Yadav *et al.*, 2017; Basu *et al.*, 2021), thus offering a more sustainable solution. Within this context, AMF have received less attention (Fig. 1) compared with bacteria. The current trends to rely less on chelates and synthetic fertilizers are highlighted by a stabilization in the number of peer-reviewed articles on these compounds (much lower increasing trends than for bacteria and AMF since 2015), and a remarkable increase in the number of publications employing fungal and bacterial models to supply micronutrients to crops are evident; particularly with bacteria due to their potential to deliver micronutrients to plants in agricultural production.

On the contrary, some other metallic trace elements, such as cadmium (Cd), lead (Pb), mercury (Hg) or arsenic (As, not a metal but a metalloid, but we include it here due to related fate and consequences in agroecosystems) can be both harmful to plant production and toxic for people and livestock. These metal(loid)s are thus undesirable, with food agencies world-wide calling for decreasing contents in our diets (EFSA Panel on Contaminants in the Food Chain (CONTAM), 2009, 2010, 2012; EFSA, 2012).

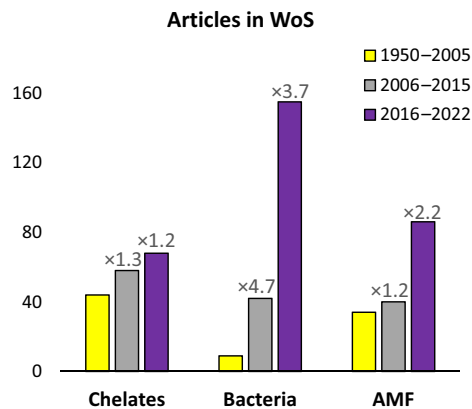


Fig. 1 Number of articles published and indexed in Web of Science (WoS) in different periods for chelates, bacteria and arbuscular mycorrhizal fungi (AMF) in relation to metallic micronutrient in soil and plants until 2023. Grey numbers on top of columns are the times-fold increase relative to the previous period. Search: Topic 'micronutrients and soils and plants and (chelate* not sideroph*)/bacteria/(arbus* or mycorrh*)', only the articles were selected because they better represent scientific activity and innovation, patents are only applicable to chelates.

The presence of metal(loid)s at high concentrations in crops poses a significant ecotoxicological risk to human health and agrosystems. Generally, both essential metals and pollutants are ubiquitous in the soil and it is a great challenge to enhance micronutrient plant uptake (biofortification) while confining the contaminants in the soil to mitigate exposure (immobilization). Interestingly, contaminants like Cd and As are taken up by plants through transporters of chemically analogous nutrients such as Zn or P/Si, respectively (Chaney, 2010; Zhao *et al.*, 2010).

Arbuscular mycorrhizal fungi are expected to have an active role in regulating the balance between micronutrient uptake and contaminant avoidance in plants, aspects fundamental for feeding the world population (Cakmak *et al.*, 2023). The priority in many agricultural soils will naturally be micronutrient enhancement because contaminants do not pose a substantial risk, but in some cases, the priority will be decreasing contaminant uptake. In order to devise promising 'AM-assisted strategies', we need to screen for interesting fungal activities and traits (e.g. ability to mobilize micronutrients from soil and transport them to the plant), connect these activities with AMF genetics and genomic signatures, and evaluate whether these findings align with our targets (e.g. balance between biofortification and mitigation in each specific scenario). Altogether, these analyses will highlight the complex links between plant–fungus–metal interactions and local environmental conditions and how they can be harnessed to achieve safe and nutritious food.

AMF contribute to metallic micronutrient uptake in plants

Arbuscular mycorrhizal fungi have demonstrated potential to mine micronutrients from soils and directly deliver them to crops (Lehmann & Rillig, 2015; Ferrol *et al.*, 2016). This potential stems from the capacity of AMF to increase the volume explored in soil that is accessible to root uptake (Chandrasekaran, 2020).

As availability of metallic nutrients is limited by diffusion, enhancing the volume of exploration increases the phytoavailable pool (Rengel & Marschner, 2005; Degryse *et al.*, 2009). AMF can also release substances (similar to siderophores, organic acids and phenols) that mobilize metals (Fe, Zn) in soil (Winkelmann, 2007; Haselwandter *et al.*, 2020) in ways similar to chelates, making these metals more soluble and transferable to fungi and plants when complexed by organic substances (Ahmed & Holmström, 2014).

The genome of several AMF have genes with homology to those involved in metal-ligand biosynthesis and in metal transport (Tamayo *et al.*, 2014; Haselwandter *et al.*, 2020). How these genes are regulated in the presence of multiple metals is unknown, and although gene homologues are found in several AMF species (as well as in some Mucoromycotina), their expression, regulation and occurrence and copy number within the genomes of Glomeromycotina have yet to be investigated. For this, the recently available chromosome-level genome datasets from model AMF are important resources for making comparisons (Yildirim *et al.*, 2022; Manley *et al.*, 2023; Sperschneider *et al.*, 2023). For example, gene expression may shift with varying levels of acidity in the surroundings of AMF hyphae (Bago & Azcón-Aguilar, 1997; Wang *et al.*, 2022) as a means to enhance micronutrient availability (Rengel, 2015), as seen in the rhizosphere of plants. Overall, the occurrence and relative importance of these different mechanisms via which AMF can realistically promote metallic micronutrient uptake at the plant–soil interface, as well as the identification and regulation of the fungal and plant gene families involved in these mechanisms, still await detailed study (Fig. 2a).

AMF can mitigate the presence of metallic contaminants in crops

The presence of contaminants in staple foods can impact human and animal health even if metal(loid)s are present at a low range, for example, trace amounts. Decreasing contamination levels for priority contaminants such as Cd, Pb, Hg or As in wheat, maize, coffee, rye or rice is thus of obvious benefit for human and ecosystem health, preventing metal-associated chronic illnesses (EFSA Panel on Contaminants in the Food Chain (CONTAM), 2009, 2012; EFSA, 2012) and reducing transfer of toxins along food chains.

There are several mechanisms in AMF that have been linked to immobilization of metal(loid)s in soils, restricting the transfer to plants, particularly for As, Cd, Hg and Pb (Xu *et al.*, 2008; Yang *et al.*, 2015; Cozzolino *et al.*, 2016; Debeljak *et al.*, 2018; Liu *et al.*, 2018; Baghaie *et al.*, 2019; Alam *et al.*, 2020; Riaz *et al.*, 2021; Cakmak *et al.*, 2023; Li *et al.*, 2022). Hyphae of AMF potentially contribute to metal immobilization in soils through the secretion of proteinaceous substances, which may form stable complexes with metals and decrease their phyto-availability (González-Chávez *et al.*, 2004; Wang *et al.*, 2019; Chen *et al.*, 2022). The nature of these proteins is currently unknown, and their identification may kick-start with investigations of gene regulation under these conditions using chromosome-level genome datasets from model AMF (Yildirim *et al.*, 2022; Manley *et al.*, 2023; Sperschneider *et al.*, 2023).

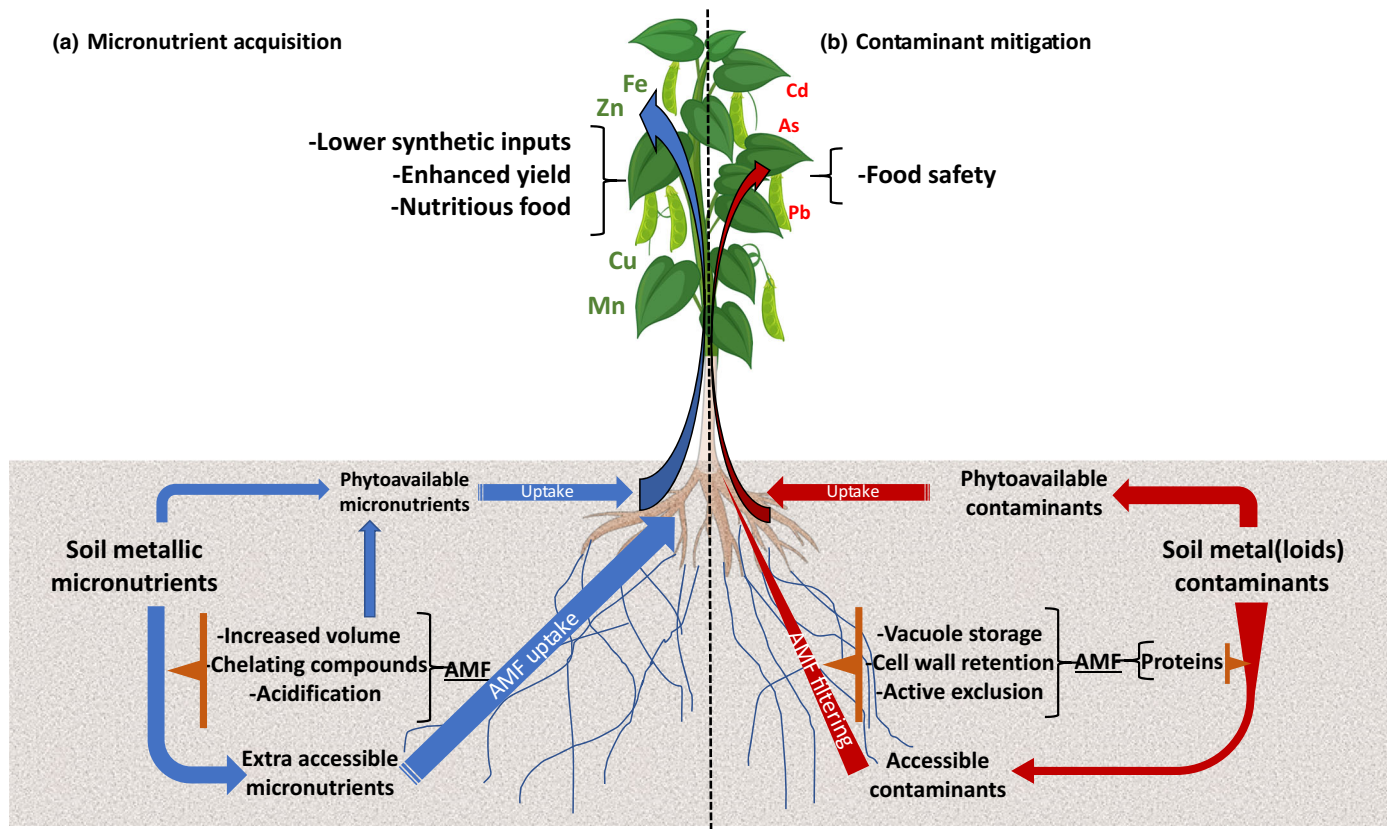


Fig. 2 Left side (a), processes in crops to obtain micronutrients from soils with special focus on those related to enhanced uptake through arbuscular mycorrhizal fungi (AMF) (blue lines belowground represents the mycelium). Right side (b), processes of metal(loid) uptake in plants from soils with emphasis on mitigating effects of AMF (blue lines belowground, the mycelium).

AMF can enhance plant growth and, concomitantly, lead to a potential dilution effect of the contaminants in edible plant parts. AMF can sequester contaminants in their intraradical and extraradical structures by retention in the hyphal/spore wall and by vacuole storage, reducing root-to-shoot metal(loid)s translocation and plant uptake (Jankong & Visoottiviset, 2008; Zhang *et al.*, 2010; Li *et al.*, 2016). The dominant mechanism likely depends on the particular context of fungal strain, plant and metal. For example, in the symbiosis *Trifolium subterraneum* and *Glomus mosseae* in a Cd-polluted soil, the association enhanced the accumulation of Cd in roots but blocked the translocation to shoots (Joner & Leyval, 1997), while in Zn-contaminated soil with tomato and soil inoculum, the Zn was immobilized outside of the root (Watts-Williams *et al.*, 2013). Active exclusion mechanisms in the extraradical mycelium to tolerate metal(loid)s have also been described in AMF that should assist in mitigating root contaminant uptake (González-Chávez *et al.*, 2011; Tamayo *et al.*, 2014). All these features for immobilization of metallic contaminants in soil with AMF have been broadly applied to scenarios involving contaminated soil (Liu *et al.*, 2005; De Oliveira *et al.*, 2020), in the context of site remediation. But in terms of food safety, the same principles should be of interest in agriculture (Fig. 2b; Cakmak *et al.*, 2023). However, more research into the specific contexts of effects is needed to understand effects of AMF on crops, because enhancement of uptake of contaminants with some AM fungal species/ecotypes has also been reported (Chen *et al.*, 2005, 2007;

Smith *et al.*, 2010; Adeyemi *et al.*, 2021), giving contrasting results that need to be resolved before confidently applying AMF to mitigate contamination of metal(loid)s in crops.

The abovementioned strain-specific phenotypic variability in metal(loid) immobilization is likely a direct reflection of their genetics and genome content. Specifically, high intra- and inter-specific variability in both phenotype and genotype is a hallmark of AMF (Mathieu *et al.*, 2018), and it is thus plausible that significant differences in the sequestration and retention of metals exist among AMF strains. For example, phylogenetically distinct strains of the model species *Rhizophagus irregularis* significantly vary in genome and chromosome size, as well as in gene and repeat content (Yildirim *et al.*, 2022; Sperschneider *et al.*, 2023). This variability may also affect regulations of genes that directly interact with metals.

Traits and features in AMF to manage micronutrients and contaminants in agriculture

Even if many processes of interest in the management of metals in agroecosystems have been described phenomenologically (enhancement or reduction in uptake of specific metal(oid)s), there is less information regarding the physiological and molecular mechanisms underpinning such effects. This knowledge is critical to correctly balance biofortification and mitigation depending on the target in each specific situation. Particularly relevant are the potential trade-offs between the two strategies shown in the

previous sections, that is, when AMF actively enhance plant uptake of micronutrients (Zn), the same processes may also promote uptake of analogous contaminants (Cd). Therefore, we need to clearly identify molecular, genetic and physiological mechanisms underpinning these effects. AMF display a high degree of functional diversity in terms of nutrient acquisition and supply to plants. For example, the amount of Zn delivered by the fungus differs between AM fungal species may reflect differences in gene content present within and among species of this group (Mathieu *et al.*, 2018).

Moreover, the same AMF individual does not deliver the same proportion of total Zn to different plant species, further highlighting that the individual genetic variability of both the AMF and plant involved in each symbiosis will shape the molecular interactions and metal(loid) uptake and distribution in the plant (Cavagnaro, 2008; Mathieu *et al.*, 2018). Particularly, AMF strains can be divided into two main genetic categories; some carry thousands of nuclei with one common genome (AMF homokaryons), while others carry nuclei derived from two parental strains (AMF dikaryons or heterokaryons). It will also be interesting to see how AMF heterokaryons interact with micronutrients and contaminants. These strains carry two parental nuclear genotypes (nucleotypes) in their mycelium (Ropars *et al.*, 2016) that vary in relative abundance (Kokkoris *et al.*, 2021) and expression (Sperschneider *et al.*, 2023), depending on strain and host identity and surrounding conditions. It is thus possible that parental genomes differ significantly in how they express genes relevant for micronutrient uptake or metal(loid) exclusion. Additionally, the potential coregulation of genes in the AMF–plant partnership needs to be addressed to optimize and synchronize metal uptake in plants (Li *et al.*, 2015; Forieri *et al.*, 2017). To shed light on this aspect, transcriptome analyses should be performed using RNA extracted from roots and extraradical hyphae of AMF when crops show enhanced or decreased metal(loid) uptake (Berruti *et al.*, 2016).

Variation in plant nutrient uptake via AMF should be more directly captured by extraradical hyphal abundance in the soil rather than by root colonization, since it is the soil-borne hyphae that acquire the nutrients and transport them to the plant (Smith & Read, 2010). The extraradical mycelium is, therefore, of paramount importance not only for exploration and exploitation of nutrient patches in the soil, but also for metal binding of metals to cell walls. Hyphal length densities in soil associated with plants are variable and depend on the identity of the fungus and on the plant genotype. Spore density might also contribute to reduced contaminant uptake, as AMF compartmentalize excess metal in their spores (Cornejo *et al.*, 2013). However, more research is required to understand the relationships between fungal traits and host metal uptake, also integrating potential coregulation of genes in AMF–plant interactions resulting in favourable traits regarding metal uptake. In this respect, as most mechanistic research in this area has been done with model AMF strains such as *R. irregularis*, expanding similar analyses to other Glomeromycotina lineages will be crucial to understand metal interaction and regulation in these prominent symbionts. Further understanding of the soil micronutrient use efficiency of various combinations of AMF and plant

species is also needed to increase micronutrient uptake in different crops and soil conditions.

Current literature highlights the need to unravel the functional spectrum of AMF to achieve nutritious and safe agricultural plant production, but reaching this goal will require a better understanding of the intricate genetic, molecular and physiological interactions that occur between the mycorrhizal partners in the presence of metals (Fig. 3). This is required to improve our understanding of the context dependence of effects and achieve deeper mechanistic insights into metal physiology in AM symbioses.

Exploiting microbiome approaches

Despite the potential of AMF to either increase micronutrient uptake in crops or mitigate food contamination, growing evidence indicates that AMF functioning is best understood in terms of their interaction with other soil organisms. For instance, some soil-beneficial symbiotic bacteria, such as rhizobium with legumes, benefit from micronutrient provision, because the symbiosis requires metals like Fe or Ni (González-Guerrero *et al.*, 2016) but, in turn, provides N to plants. On the contrary, plant growth-promoting rhizobacteria (PGPR) like some *Bacillus* and *Paenibacillus* have also been reported to increase the availability and supply of Fe to plants through siderophore production (Liu *et al.*, 2017). The same mechanisms should also function with other related metals (Zn and Cu), which could further benefit the provision of metallic micronutrients to the AMF and the crop. Regarding actinobacteria, some bacterial endophytes also produce siderophores and assist in the uptake of metals by crops. All these complex interactions between plants and microbiome could be addressed by transcriptome approaches to identify the function of genes that are activated/repressed or even coregulated in plants and microbes when different metal(loid)s are present in the soil or when specific traits regarding metal(loid)s are evident in plants (biofortification or contaminant exclusion).

Overall, consortia of different fungi, bacteria and other soil organisms may enhance the acquisition of micronutrients by plants

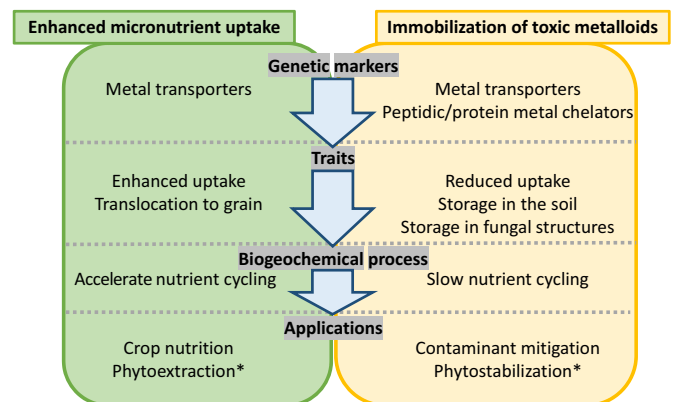


Fig. 3 Main genetic markers, traits, biochemical processes and applications that promote or are linked to enhanced uptake (left panel) or immobilization (right panel) of metals in terrestrial agroecosystems. *Phytoextraction uses plants to accumulate contaminants from soils while phytostabilization immobilizes contaminants in the soil and the rhizosphere.

and improve the production and nutritional value of food, as has been demonstrated for organic nitrogen (Rozmoš *et al.*, 2022). In parallel, many groups of bacteria have been shown to decrease availability of metallic contaminants and subsequent accumulation in plants, with mechanisms including biotransformation, biosorption and exopolysaccharide production (Manoj *et al.*, 2020). Integrative management of the soil microbiome, either using the indigenous soil reservoir or specific inocula, will thus very likely be crucial in achieving an optimum balance of crop metal uptake in agriculture. Such approaches may also entail microbiome engineering (Qiu *et al.*, 2019; Arif *et al.*, 2020; Bano *et al.*, 2021; Afridi *et al.*, 2022), including the production of complex inocula containing entire microbial communities through a process of experimental evolution, especially in situations where agroecosystems are far off the desired state.

Conclusions

Optimizing agroecosystems and crops for micronutrient uptake while reducing issues with contaminants is challenging. Here, we argue that there is significant potential to tackle these problems using AMF. Progress can be made by investigating physiological mechanisms and molecular changes that occur in the presence of these compounds at different levels of AMF biodiversity. While a focus on AMF is promising, we stress the importance of investigating these processes in the context of the soil microbiome. We thus believe a two-pronged approach, zooming into molecular mechanisms on the one hand, and exploring microbiome management and engineering on the other, could provide the synergies for real breakthroughs in order to balance nutrition and contamination when considering metal(loid)s in the agroecosystem.

Acknowledgements

EMJ was funded by the Humboldt Foundation (Fellowship for Experienced Researchers) and by COST Action 19116 Plantmetals (Short Term Scientific Mission). This work was supported by grant PID2021-1255210B-I00 funded by MCIN/AEI/10.13039/501100011033 and by 'ERDF A way of making Europe', by the 'European Union'. NC is a University of Ottawa Research Chair in Microbial Genomics, and his research on AMF genetics and genomics is supported by the Discovery Program of the Natural Sciences and Engineering Research Council (RGPIN2020-05643) and a Discovery Accelerator Supplements Program (RGPAS-2020-00033). Plant image for Fig. 2 was obtained from Freepik (by brgfx).

Competing interests

None declared.

Author contributions

EMJ and MCR conceptualized the idea. EMJ wrote the first draft of the manuscript with contributions from MCR. NF, NC and JMP

provided specific inputs and ideas in some parts of the manuscript. EMJ wrote the last version and created the figures. All the authors have edited the text.

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Key words: agriculture, arbuscular mycorrhizal fungi, biofortification, contamination, metalloids, metals, micronutrients, mitigation.

Received, 26 May 2023; accepted, 13 August 2023.