REVIEW

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Manganese (Mn) toxicity in plants a comprehensive overview: a review

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Manganese (Mn), an essential micronutrient necessary for plant growth and development, has serious phytotoxic effects when present in surplus concentrations. The higher concentration of Mn manifests as a reduction in photosynthetic activity and a gradual up regulation of oxidative stress, which results in reduced yield. Interestingly, Mn toxicity is a serious issue in acid soil, which is mainly encountered in sizable parts of the soil across the globe. In order to mitigate the detrimental influence of Mn on crop productivity, it is of significance to comprehend the diverse physiological aspects of Mn. Thus, such information is crucially important for the identification and development of Mn-tolerant genotypes. Hence, this review article precisely discusses the diverse physiological aspects of Mn toxicity in plants.

Key words: Acid soil, manganese, metal ion uptake, phytotoxicity, tolerance

Plants experience an array of abiotic stresses that seriously restrict their productivity and yield. In this context, the acidity of soils is a matter of serious concern which comprises about 40–50% of the total ice-free land, primarily in humid climates (Von Uexküll & Mutert, 1995). The low soil pH directly or indirectly affects the mineral uptake in plants, drastically limiting agriculture activities around the world. Moreover, acid soil results in the toxicity of plants on account of enhanced availability of metal ions (Fe, Mn, Al) and the deficiency of crucial elements required for plant growth (Ca, P, Mg, K, Mo, B) (Kochian *et al*., 2004; Chetry & Sharma, 2023). Mineral nutrients which have specific and essential functions in plant metabolism are classified as macronutrients and micronutrients. Manganese (Mn) is one of the 17 essential micronutrients required for the normal growth and development of plants. This metalloenzyme (Mn) cluster serves as an activator for several enzymes necessary for chlorophyll synthesis and the proper functioning of photosynthesis (Terry & Ulrich, 1974). However, Mn becomes toxic in poorly drained soil with low pH (Marschner, 1995; Pittman, 2005). Unlike aluminium (Al), excess Mn generally affects shoots more than roots in low-pH soil (Foy *et al*., 1978), as the accumulation of Mn has been predominantly reported in shoot rather than root systems (Page & Feller, 2005). The thresholds of Mn toxicity and tolerance vary significantly among plant species and among cultivars within a species (Foy *et al*., 1988). For example, rice is considered a Mn-tolerant species among the cereal crops, especially flooded or paddy rice (Lindon, 2001). Moreover, rice species have been reported to accumulate Mn in their leaves at concentrations as high as 5000 $\mu g \ g^{-1}$ DW without showing any toxic symptoms, which is remarkably high when compared with the Mn concentration recorded in barley with toxicity of 150 $\mu g \ g^{-1}$ DW (Vlamis & Williams, 1964).

Mn (II) the ubiquitously available form for plants, which can be easily oxidised to Mn (III) and Mn (IV) in the presence of an acidic environment (Marschner, 2011). The bioavailability of Mn depends on a range of environmental factors, *viz.,* soil acidity, redox potential, temperature and moisture, which gradually increase the concentration of Mn either individually or in a sequence (George *et al*., 2012). Mn toxicity results when the normal concentration of biologically available Mn is increased above the threshold level. Thus, the excess amount of Mn causes drastic physiological as well as biochemical changes in plants. Hence, an attempt was made to understand the phytotoxic effect of Mn in plants, which would provide insight into the physiological processes functioning during Mn toxicity as well as the detoxification mechanisms inbuilt in plants to sustain such abiotic stress.

Mn uptake in plants

The uptake of Mn depends on the soil pH as well as soil redox potential, as acid soil results in an increase in bioavailable Mn by promoting the reduction of soil-bound Mn (Mn^{3+} and Mn^{4+} to Mn^{2+}) (Goulding, 2016). Moreover, the uptake of Mn has been reported to be an active process where H^+-ATPases are used to create an electrochemical gradient across the plasma membrane of root cells (Rengel, 2000). The mechanism of Mn uptake has been depicted in two phases. (a) first phase consists of the absorption of Mn^{2+} via the negatively charged cell wall, which constitutes the apoplast of the root epidermal cells (b) second phase comprises Mn^{2+} transported to other parts via the symplastic pathway. It is interesting to note that the transporters associated with Mn uptake also compete with other divalent cations, such as Fe^{2+}, Zn^{2+}, Cu^{2+}, Cd^{2+}, Ca^{2+}, Co^{2+} and Ni^{2+}, because of their non-specificity and low requirement for Mn^{2+} for plant nutrition. Once Mn uptake from the soil takes place, diverse families of transport proteins are known to maintain Mn homeostasis, which have been classified as importers and exporters respectively. The importers mainly translocate Mn from the extracellular space into the cytosol, whereas the exporters are responsible for the exclusion of Mn from the cytosol into intracellular compartments. The natural resistance-associated macrophage protein (NRAMP) family, the zinc-regulated transporter/iron-regulated transporter (ZRT/IRT)-related protein (ZIP) family and the yellow stripe-like (YSL) family have members involved in the transport of Mn^{2+} into the cytosol. In contrast, the cation diffusion facilitator/metal transport protein (CDF/MTP)

family, the vacuolar iron transporter (VIT) family, the Ca^{2+}/cationantiporter (CaCA) superfamily, the bivalent cation transporter (BICAT) family and the P_{2A}-type ATPase family have members involved in the transport of Mn^{2+} out of the cytosol (Alejandro *et al*., 2020). The sequestration of surplus Mn in the vacuoles, endoplasmic reticulum, or Golgi bodies has key roles in Mn tolerance (Williams & Pittman, 2010). A variety of transporter proteins belonging to the family, *viz.,* cation exchanger (CAX), cation diffusion facilitator (CDF) and P_{2A}-type ATPase, mediate these processes, particularly in *Arabidopsis thaliana.* (Hirschi *et al*., 2000; Delhaize *et al*., 2007; Wu *et al*., 2002).

The accumulation of Mn was observed mainly in the shoot system, as discussed earlier, especially the leaves, where the highest level of Mn was available (Lidon, 2001). However, the accumulation of Mn at cellular levels was concentrated more in vacuoles than in the chloroplast, cell wall and endoplasmic reticulum (González & Lynch, 1999)

Phytotoxicity of Mn in plants

Mn toxicity limits plant productivity in acid soils after aluminium (Al), where it prevents the uptake and transport of various other essential plant nutrients because of their resemblance with the ionic radius and ligand binding ability (Clark, 1982). The common symptoms of Mn toxicity are marginal chlorosis and necrosis of leaves, which strongly vary depending on the plant species. For example, Mn restricts the number and size of nodules and causes bronze speckle in marigold or geranium, crinkle leaf necrosis in cotton, stem streak necrosis in potato, internal bark necrosis in apple, tip burn in carnation, and fruit cracking in muskmelon (Foy *et al*., 1978; Foy, 1983). Although a low concentration of Mn is a basic requirement for plant growth, the excess Mn in the soil not only harms plant productivity but also influences their yield and quality. Additionally, the excess concentration of Mn represents an important factor in environmental contamination, which causes various phytotoxic effects (Figure 1) (Pitman, 2005). Higher (Mn) concentrations are responsible for oxidative bursts with the production of reactive oxygen species (ROS) like superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH·) (Demirevska-

Kepova *et al*., 2004; Boojar & Goodarzi, 2008). To cope with these ROS, the combined action of enzymatic antioxidant systems like the production of superoxide dismutases, catalases, peroxidases and the synthesis of non-enzymatic antioxidants like ascorbate and glutathione is necessary (Sharma & Dietz, 2009). The threshold of Mn toxicity and the tolerance to excess Mn concentrations vary characteristically according to plant species and their cultivars (Foy *et al*., 1988).

Mn toxicity typically causes the oxidation of excess Mn^{2+} to Mn^{3+} in the apoplast, which in turn results in strong oxidative damage of proteins and lipids (Fecht-Christoffers *et al*., 2006). The visible symptoms of Mn toxicity, i.e., brown necrotic spots on the leaves, have been proposed to occur due to the accumulation of high levels of oxidised phenolics in the apoplast (Wissemeier & Horst, 1992). Mn toxicity in wheat results in reduced shoot fresh weight, leaf extension, and nodal root growth, which cause death of the seminal root system and early senescence of the lower leaves (Khabaz-Saberi *et al*., 2006).

Effects of Mn toxicity on photosynthesis

Mn, being an essential micronutrient for plants, forms an important component of the water-splitting complex of the photosystem II (PSII), which is bound to the D1 reaction centre protein of PSII, providing the necessary electrons that drive the electron transfer chain (ETC) of photosynthesis (Goussias *et al*., 2002). Mn plays an important role in both the structure and function of the photosynthetic apparatus. It is actively imported into the chloroplast and participates in the formation of different structural proteins in oxygen involving complexes of PS II (multiprotein pigment complex embedded in the thylakoid membranes), which participate in H_2O photolysis, electron transport, and also as an antioxidant (Goussias *et al*., 2002). Kiato *et al*. (1997) studied the effects of Mn toxicity on photosynthesis in white birch (*Betula platyphylla* var. *japonica*) by measuring gas exchange and chlorophyll fluorescence. It was observed that the net photosynthetic rate at saturating light and ambient CO_2 decreased with increasing leaf Mn concentration, while the maximum quantum yield of O_2 evolution at saturating CO_2 was not affected. These results suggested that excess Mn in leaves affected the

activities of the CO_2 reduction cycle, leading to an increase in the QA reduction state, thermal energy dissipation, and a decrease in the quantum yield of PSII in the steady state. Mn toxicity on broad beans also resulted in an increased concentration of Mn in the root and shoot progressively in response to increasing concentration, where the Mn level in the roots increased by 13-fold over the shoots, where an 8-fold increase was observed (Arya & Roy, 2011). A similar observation was reported in rice beans and white birch, where excess Mn concentrations inhibited photosynthesis (Subrahmanyam & Rathore, 2000). Mn accumulation is associated with inhibition of net photosynthesis and

carboxylation efficiency in various plant species. The decline in photosynthesis rate is considered one of the major mechanisms constituting the toxic effects of excess Mn in rice and wheat (Lidon *et al*., 2004; Macfie & Taylor, 1992). Moreover, in the hyperaccumulator species *Phytolacca acinosa,* Mn affects photosynthetic activity, attributing the hyperaccumulator capacity of the species to efficient Mn complexing and not to abruptly modifying the chloroplast structures (Weng *et al*., 2013). Thus, in a comprehensive way, it can be assumed that Mn toxicity hampers the photosynthesis process in plants, thereby restricting the growth of the plant in a concerted manner (Figure 2).
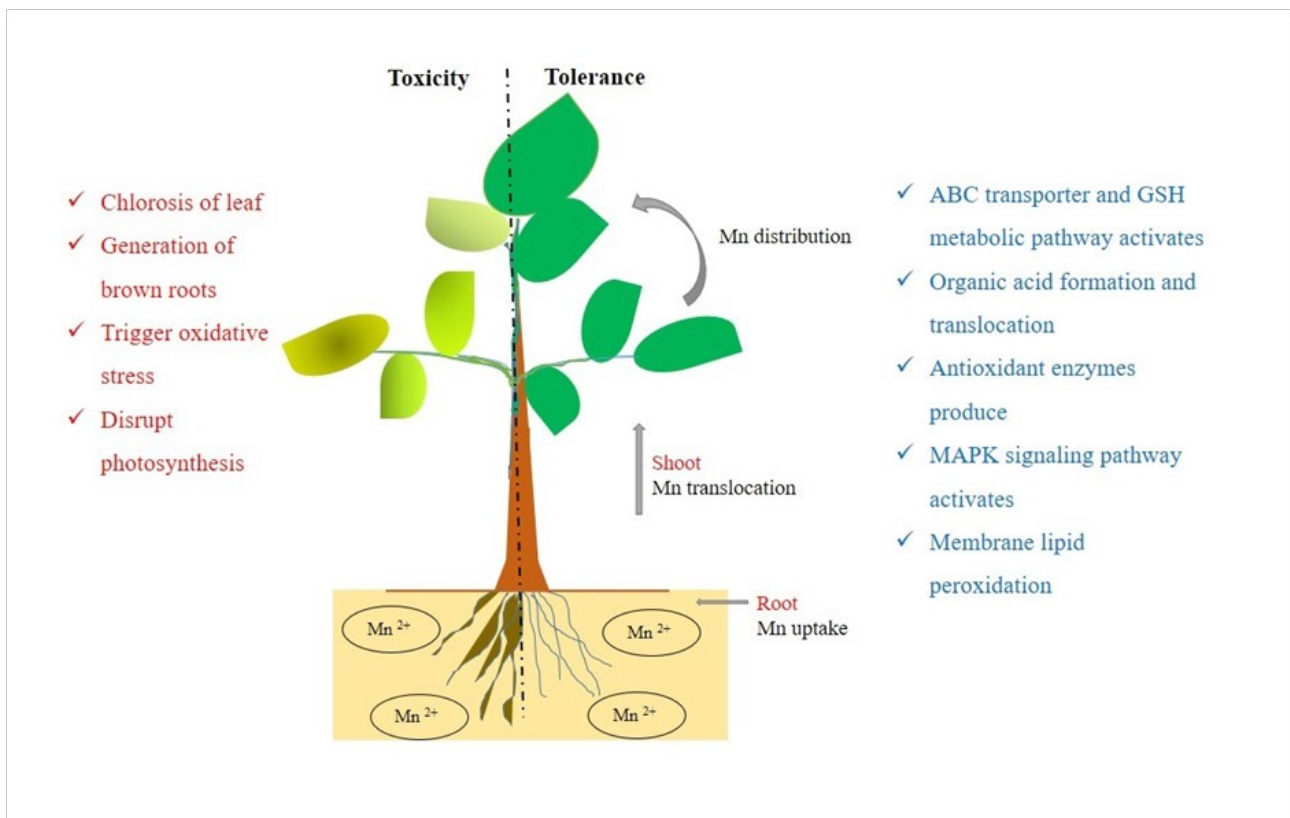

Figure 1. Schematic representation of toxicity and strategies of tolerance adopted by plants towards Mn. Uptake of Mn from soil and thereby translocation and distribution of Mn towards aerial parts.
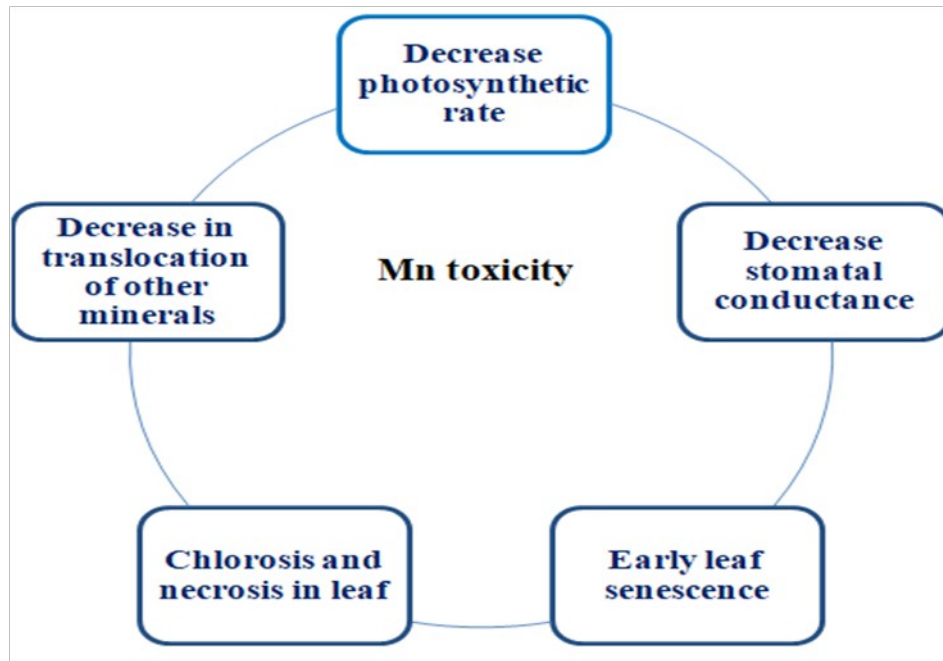
Figure 2. Effect of Mn toxicity in photosynthesis leading to decline plant growth.

Table 1: Tolerance mechanism adopted by Mn hyperaccumulator plant species.

Plants/family	Mechanism	References
Celosia argentea (Amarantheaceae)	Plant transport Mn from root to shoot, where ABC transporter and GSH metabolic pathway help in the detoxification.	Yu *et al*. (2023), Liang *et al*. (2024)
Chengiopanax sciadopylloide (Araliaceae)	Carboxylic acids, *viz.,* malate or citrate, play an important role in the hyperaccumulation of Mn.	Fernando *et al*. (2010)
Eucalyptus grandis × Eucalyptus urophylla (Myrtaceae)	Plants detoxify Mn by forming complexes with high-molecular-weight proteins and low-molecular-weight organic acids.	Xie *et al*. (2015)
Phytolacca americana (Phytolaccaceae)	Mn is removed from the root surface by precipitation of the phosphate to form Mn phosphate crystals in rhizosphere.	Dou & Qi (2023)
Polygonum hydropiper (Polygonacceae)	Enzymes like sulfhydryl group (-SH) and glutathion (GSH) play a major role in detoxification.	Yang *et al*. (2016)
Polygonum lapathifolium (Polygonacceae)	Sulphate regulates Mn uptake and translocation in this plant.	Liu *et al*. (2021a)
Polygonum perfoliatum (Polygonacceae)	This plant tolerates Mn stress through the production and transportation of organic acids and membrane lipid peroxidation.	Xue *et al*. (2018)
Polygonum pubescens (Polygonacceae)	Antioxidant enzymes play a vital role in alleviating Mn stress.	Liu *et al*. (2021b)
Schima superba (Theaceae)	Under stress condition, mitogen-activated protein kinase (MAPK) signalling regulates Mn stress.	Liaquat *et al*. (2022)

Interaction of Mn with other elements

Al may have an antagonistic effect on Mn uptake by plant roots. Previous reports have indicated that Al can reduce Mn accumulation in barley, atriplex, corn, wheat, cowpea, and soyabean (Rees & Sidak, 1961; Blair & Taylor, 1997; Taylor *et al*., 1998; Yang *et al*., 2009). Additionally, P could also reduce Mn toxicity in *G. max*, *S. tuberosum*, *L. perenne,* and *T. repens* (Nogueira *et*

al., 2004; Sarkar *et al*., 2004; Rosas *et al*., 2007). In agreement, in *Pseudotsuga menziesii*, low P supply partly alleviated the negative Mn effect on biomass production (Ducic & Polle, 2007). Plant tolerance to soluble Mn was affected by the concentration of other nutrient elements in the medium. An element present in excess can interfere with metabolism through competition for absorption, inactivation of enzymes, or displacement of essential elements from functional sites. Mn toxicity induces deficiencies in other elements due to competition for transporter proteins (Huang *et al*., 2019). Higher concentrations of Mn promote a higher level of competition for active sites of divalent ions, like Mg^{2+} or Ca^{2+}, resulting in an antagonistic effect and preventing them from performing their functional roles (Fernando & Lynch, 2015). Additionally, surplus levels of Mn in the nutrient solution decreased shoot concentrations of Si, K, Ca, Mg, Zn, Cu and root concentrations of K and Mg (Galvez *et al*., 1989). Moreover, the addition of Si, Fe, Ca, or Mg alleviates Mn toxicity (Osawa & Ikeda, 1976). Ca deficiency is a well-known symptom (called "crinkle leaf") induced by Mn toxicity in dicotyledons such as cotton (Foy *et al*., 1995) and beans (Horst & Marschner, 1978). The translocation of Ca into the shoot apex is inhibited due to Mn toxicity (Horst & Marschner, 1990). This inhibition might be related to the fact that high Mn levels decrease the cation exchange capacity of the leaf tissue (Horst & Marschner, 1978) and decrease the IAA levels in the areas of new growth (Morgan *et al*., 1976). It was reported that increased Ca levels in the growth medium often decreased Mn absorption and toxicity (Shuman & Anderson, 1976). Increasing the Ca level in the solution culture reduced the adverse effects of a high Mn level on suppressing the number of root nodules on white clover (*Trifolium repens* L.) (Vose & Jones, 1963). Excess Mn may reduce Mg uptake by up to 50% (Kazda & Znacek, 1989) due to competition between Mg and Mn for binding sites in the roots during absorption (Horst & Marschner, 1990). It was reported that Mn toxicity can often be counteracted by a large Mg supply (Elamin & Wilcox, 1986). On the other hand, in some cases, Mg application is not a practical method for the avoidance of Mn toxicity (Davis, 1996). In addition, using Mg to prevent Mn toxicity would require large Mg applications, which could lead to serious nutritional imbalance because Mg also interferes with Ca uptake. As compared to other nutrient elements, the absorption of K is slightly affected by increasing Mn concentrations (Heenan & Campbell, 1981). High K levels in the shoots of Mn-tolerant 'Lee' soybean alleviated the harmful effects of high internal Mn concentrations (Brown & Jones, 1977). Abundant evidence shows that a soluble source of Si in the growth medium can protect plants against Mn toxicity (Bowen, 1972). The higher absorption of Si by monocots than by dicots may help explain the higher tolerance of monocots to Mn toxicity (Foy *et al*., 1978). Si reduced or prevented Mn toxicity in barley, rice, rye, ryegrass, and sorghum (Vlamis & Williams, 1967; Galvez *et al*., 1989). Plant tolerance to soluble Mn may also be affected by the concentration of S, Al, Zn and Cu in the medium. Additional S may lower the pH of the growth medium and increase the availability of Mn to plants. Thus, all the elements behave diversely to increase the internal concentration of Mn in plants.

Mn detoxification mechanisms

For normal plant growth maintenance, ionic homeostasis is necessary for adaptation to toxic metal ions. Excess uptake of redox-active elements causes oxidative destruction of diverse cellular components. Metal ions make complexes with different ligand molecules, including chelators and chaperones. Chelators contribute to metal detoxification by buffering cytosolic metal concentrations, while chaperones specifically deliver metal ions to organelles and metal-requiring proteins (Clements, 2001). Horst *et al*. (1999) suggested the tolerance to excess Mn in *Vigna unguiculata* to be a consequence of a reduction in Mn activity in the apoplast through the formation of insoluble complexes by organic acids. Due to the exposure to high Mn levels (130 μM), an increase in phenolic compounds was found in the hydrophyte *Trapa natans* leaves (Baldisserotto *et al*., 2007). These compounds chelate Mn within the vacuole, segregating the metal ion in the protoplasm and thus reducing the damage (Davis *et al*., 2001). Recently, a role of oxalic acid in Mn internal sequestration has been demonstrated by

chelating specifically the Mn excess in the hyperaccumulator plant *Phytolacca americana* (Dou *et al*., 2008). The accumulation and secretion of Mn in and around the trichomes of sunflower plants is looked upon as a Mn tolerance strategy (Blarney *et al*., 1986). Horiguchi (1987) reported that rice retains less Mn in its roots than other species, and the shoots were also able to tolerate a high Mn concentration. On the other hand, the shoots of alfalfa were sensitive to a high Mn concentration in the tissues, although the roots oxidised Mn and retained it in high concentrations. Thus, there are species-specific variations as well as organ-specific variations observed in response to Mn toxicity. Foy *et al*. (1995) reported the differential Mn tolerance in cotton genotypes to be associated with differential internal tolerance to excess Mn. Rice may tolerate 5 to 10 times as much Mn as many other grasses, such as oats, barley, wheat, etc. A possible explanation for the internal tolerance of some plants to high levels of Mn in the shoots is the oxidation of excess Mn (Horiguchi, 1987). Another strategy that plants use to prevent the toxic effects of heavy metals is the efflux from the cell, where the cellular Mn is delivered into the golgi apparatus and finally exported from the cell via secretory pathway vesicles that carry the metal to the cell surface (Ducic & Polle, 2005).

Hyperaccumulator of Mn

Some rare plants accumulate trace elements in extreme concentrations and are known as hyperaccumulator plants. Cuba, an island country, has the highest number of plant hyperaccumulators, accounting for 128 species (Reeves *et al*., 1999). Several Mn hyperaccumulator plant species, along with their specific tolerance strategies, have been enlisted in Table 1. In an experiment with Mn hyperaccumulators (*Phytolacca americana*, *P. perfoliatum, and P. hydropiper),* it was found that *P. perfoliatum* has superior Mn accumulation and tolerance abilities (Liu *et al*., 2010). However, *P. americana* is a common weedy species and has no specific association with high Mn soils. It was suggested that *P. americana* secretes acids into the rhizosphere as a means of acquiring P, which might coincidentally increase Mn uptake.

Conclusion and future prospects

Mn toxicity hampers plant growth and yield worldwide, particularly in acidic soils. Mn, however, is necessary for plant growth in trace amounts, but the surplus availability of this metal ion consequently leads to phtotoxicity. Thus, in the global scenario, it is imperative to study the response of diverse agroecosystems to surplus Mn concentrations. Furthermore, a clearer understanding of the mechanisms of Mn toxicity and tolerance among different plants is of the utmost necessity for future sustainable agriculture. In this context, the Mn hyperaccumulator species are likely to serve as an important genotype for understanding the tolerance strategies adopted by those plants to survive the Mn surplus condition. In addition, the interactive influence of Mn with other co-occurring factors in the acidic soils, such as other heavy metals as well as Al stress and surplus Fe concentrations, needs to be appropriately addressed. Moreover, cereal crops must be genetically engineered in order to develop Mn-tolerant crops that can be grown in soil with low pH conditions to maintain the production of food grains with low yield losses.

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CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

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