Possible consequences of an inability of plants to control manganese uptake

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Abstract

Background This commentary presents several thoughts elicited by the observation of Lambers et al. (Plant Soil, 2021) in this Special Issue that the release of carboxylates by roots increases manganese (Mn) uptake by plants. Manganese is a plant nutrient, but is toxic in excess. Root cells take up Mn from the rhizosphere solution through non-specific transporters, whose activities are regulated by elements other than Mn, and Mn phytoavailability in soil is also impacted by plant nutritional status of elements other than Mn. These complications could result in a plant being unable to respond appropriately to vagaries in Mn phytoavailability.

Scope The release of carboxylates by roots increases Mn phytoavailability and Mn uptake by plants. Lambers et al. (Plant Soil, 2021) suggest that this phenomenon might be used to identify plant species that release carboxylates into the rhizosphere in response to P deficiency. We suggest that, for the approach of Lambers and colleagues to be successful, it is necessary for all plants being compared (1) to be capable of increasing root Mn uptake and leaf Mn concentration should carboxylates be released, and increase these to a similar extent for the approach to be quantitative, and (2) to tolerate the greater tissue Mn concentrations resulting from increased Mn phytoavailability.

Conclusions We observe (1) that the leaf Mn requirement, critical leaf Mn concentration for toxicity and capacity for Mn accumulation when grown hydroponically in a nutrient-replete solution are all positively correlated among plant species, which suggests that they might have evolved in parallel, and (2) that, although some orders containing species accumulating large shoot Mn concentrations are typically non-mycorrhizal and release carboxylates into the rhizosphere, such as the Proteales, many orders containing species with this trait are characterised by conventional mycorrhizal associations.

Keywords Carboxylates · Hyperaccumulator · Leaf manganese concentration · Mycorrhiza · Phosphorus acquisition · Phylogeny

Commentary

This commentary presents several thoughts elicited by the observation of Lambers et al. (2021) in this Special Issue that the release of carboxylates by roots increases manganese (Mn) uptake by plants. Manganese (Mn) is an essential plant micronutrient. It is required for the oxygen-evolving complex of photosystem II and for the activities of enzymes involved in photosynthesis, carbon and nitrogen metabolism, synthesis of RNA, and detoxification of reactive oxygen species (Alejandro et al. 2020; Schmidt and Husted 2019; White and Pongrac 2017). Tissue Mn concentrations greater than 10–20 mg kg⁻¹ dry matter (DM) are generally considered adequate for optimal growth, development and

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fecundity of crop species (White and Pongrac 2017). However, Mn requirements differ greatly between crop species, ranging from 5 mg kg⁻¹ DM for *Nandina domestica* Thunb. (Berberidaceae, Ranunculales) to 1400 mg kg⁻¹ DM for *Ilex pernyi* Franch. (Aquifoliaceae; Aquifoliales) (Fig. 1b; Mills and Jones 1996). Although tissue Mn concentrations greater than about 100–200 mg kg⁻¹ DM can be toxic to many crop species, there is considerable variation among plant species in their tolerance of larger tissue Mn concentrations (Fig. 1b; Mills and Jones 1996) and some species have evolved an ability to hyperaccumulate Mn at concentrations above 10 g kg⁻¹ DM in their tissues (Reeves et al. 2017; White and Pongrac 2017). There appears to be a positive correlation between the leaf Mn concentration required by a crop species and the leaf Mn concentration that is toxic to it (Fig. 1b; $R = 0.71$, $n = 355$ taxa, $P < 0.001$). More than 270 taxa (species) are known to hyperaccumulate Mn in their shoots (Fig. 1a; Gei et al. 2020; McLay et al. 2018; Reeves et al. 2017; van der Ent et al. 2018, 2019; White and Pongrac 2017). Angiosperm orders (and families) with a large number of known Mn hyperaccumulators include: Malpighiales (Phyllanthaceae, Cunoniaceae, Salicaceae, Euphorbiaceae), Myrtales (Myrtaceae), Ericales (Sapotaceae, Ericaceae), Gentianales (Rubiaceae, Apocynaceae), and Proteales (Proteaceae) (Fig. 1a; Gei et al. 2020; McLay et al. 2018; Reeves et al. 2017; van der Ent et al. 2018, 2019; White and Pongrac 2017).

Manganese is acquired from the rhizosphere solution as Mn²⁺ by roots of all plant species and also as Mn-phytosiderophore complexes by roots of graminaceous species (Alejandro et al. 2020; Curie et al. 2009; White and Pongrac 2017). In aerated soils Mn is present in the soil solution as Mn²⁺, although a significant amount can be present as organic complexes (Alejandro et al. 2020; White and Pongrac 2017). The Mn²⁺ concentration in the soil solution generally increases as pH falls and also increases as soils become anaerobic (Alejandro et al. 2020; Rengel 2015; White and Pongrac 2017). Thus, Mn toxicity often reduces plant growth and survival on acidic and waterlogged soils (Alejandro et al. 2020; Rengel 2015; White and Greenwood 2013). When plants have insufficient Mn to meet their physiological requirements, their roots often acidify the rhizosphere and release organic acids and enzymes capable of degrading organic compounds into the soil to increase Mn phytoavailability (Alejandro et al. 2020; George et al. 2014; Gherardi and Rengel 2004; Rengel 2015).

Fig. 1 **a** Phylogenetic relationship between angiosperm orders according to APGIV (2016) and (i) the average (arithmetic mean) manganese (Mn) concentration in leaves considered to be sufficient for optimal growth of taxa (species) in an order (termed “requirement” here) calculated from data on 355 taxa presented by Mills and Jones (1996), (ii) the average (arithmetic mean) lowest Mn concentration in leaves considered to be toxic to taxa in an order (termed “tolerance” here) calculated from data on 355 taxa presented by Mills and Jones (1996), (iii) the average (arithmetic mean) Mn concentrations in leaves of species grown hydroponically in a nutrient-replete medium in an order (termed “capacity” here) calculated using data from 247 species grown in the experiments described by White et al. (2017) and tabulated by Neugebauer et al. (2018), and (iv) the number of taxa known to hyperaccumulate Mn in leaves to concentrations above 10 g kg⁻¹ DM in their natural environment (Gei et al. 2020; McLay et al. 2018; Reeves et al. 2017; van der Ent et al. 2018; Ent et al. 2019; White and Pongrac 2017). Eleven Mn hyperaccumulators (three taxa in the Canellales, one taxon in the Paracryphiales, and seven taxa in the Santalales) are not shown. The colour coding is scaled from the smallest to the largest Mn concentrations of the orders (yellow = smallest, orange = intermediate, red = largest). **b** The relationship between the leaf Mn concentrations required by crop taxa ([Mn]_{leaf} “requirement”) and the leaf Mn concentrations that are toxic to them ([Mn]_{leaf} “tolerance”) based on data for 355 taxa presented by Mills and Jones (1996). Statistics for the regression line are $R = 0.71$, $n = 355$ taxa, $P < 0.001$. **c** The relationship between the leaf Mn concentrations in species grown hydroponically in a nutrient-replete medium ([Mn]_{leaf} “capacity”) and the leaf Mn concentrations that are toxic to them ([Mn]_{leaf} “tolerance”) based on data for 31 taxa presented by both Mills and Jones (1996) and Neugebauer et al. (2018). Statistics for the regression line are $R = 0.61$, $n = 31$, $P < 0.001$

However, the expression of these acclimatory responses can differ within and among plant species (George et al. 2014; Rengel 2015). Furthermore, the acidification of the rhizosphere by roots and the release of organic acids, phytosiderophores and enzymes that degrade organic material is also induced in response to deficiencies of both macronutrients, such as P, and micronutrients, such as Fe, Zn and Cu (Rengel 2015; Wang et al. 2019; White and Pongrac 2017). Thus, the phytoavailability of Mn in the rhizosphere is often determined by the plant nutritional status of elements other than Mn.

The uptake of Mn²⁺ by root cells of all plant species is facilitated by members of the Zinc Regulated Transporter/Iron-Regulated Transporter (ZRT/IRT)-related Protein (ZIP) family, principally AtIRT1 in *Arabidopsis thaliana*, and members of the Natural Resistance Associated Macrophage Protein (NRAMP) family, principally NRAMP1 in *Arabidopsis thaliana* and OsNRAMP5 in rice (Alejandro et al. 2020; White and Pongrac 2017). Root cells of graminaceous species can

(a)

Order	Requirement	Tolerance	Capacity	Hyper-accumulators
Garrryales	191	325		
Boraginiales	105	122	97.5	
Gentianales	134.1	329.6		20
Lamiales	82.2	244.1	152.9	
Solanales	38.7	281.5	198	
Dipsacales	114.5	321.1	167.5	
Apiales	83	401.3	134.2	9
Asterales	86.6	282.7	174.4	3
Aquifoliales	645.5	1785.1		2
Ericales	206.1	734.3	315.1	27
Cornales	56.9	222.9		
Caryophyllales	73.6	371.3	217.6	7
Saxifragales	125.8	175.3	131.6	
Vitales	93.8	193.8		
Sapindales	97.7	398.4		13
Brassicales	38.9	179.3	143	
Malvales	60.6	247.8	163.1	1
Myrtales	65	369.3	278.9	31
Geraniales			161.9	
Celastrales	51.5	260.7		5
Malpighiales	37.9	230.8	93.3	109
Oxalidales			90.8	9
Cucurbitales	50	270	193	
Fagales	220.4	746.4	1052.2	3
Rosales	141.1	312.3	829.9	
Fabales	36.6	152.1	159.7	
Buxales	17	67		
Proteales	75.5	589.5	461.6	19
Ranunculales	175.2	341.7	170.5	
Alismatales	46.7	508.3	230.5	
Dioscoreales			330.4	
Liliales	42.5	200	110.4	
Asparagales	53.8	253.7	171.6	
Zingiberales	93	504.4	399.6	
Commelinales	142	251	65.8	
Poales	41	166.9	149.9	
Arecales	40.8	144.4	147.8	
Piperiales	140	256.7	88.2	
Laurales	63.7	308.7	147.2	5
Magnoliales	147.5	473.1	230.9	1
Austrobaileyales	195.5	525		

(b) Tolerance vs. Requirement **(c)** Tolerance vs. Capacity

also take up Mn^{2+} as phytosiderophore complexes, catalysed by members of the Yellow Stripe-Like (YSL) protein family, principally OsYSL6 in rice (Alejandro et al. 2020; White and Pongrac 2017). It is noteworthy that these transporters are all non-selective and that the genes encoding them are regulated in response to plant nutritional status. For example, AtIRT1 is permeable to Mn, Fe, Zn, Cu, Co and Ni and the expression of *AtIRT1* is upregulated by Fe deficiency; AtNRAMP1 and OsNRAMP5 are permeable to Mn, Fe and Cd and the expression of *AtNRAMP1* is upregulated by Mn and Fe deficiencies whereas that of *OsNRAMP5* is upregulated by Fe and Zn deficiencies but unaffected by Mn deficiency; and OsYSL6 likely transports a variety of transition-metal / phytosiderophore chelates (Alejandro et al. 2020; White and Pongrac 2017). It is possible that Mn^{2+} also enters root cells through non-selective cation channels (White and Pongrac 2017). Thus, the capacity for Mn uptake by root cells is often determined by the plant nutritional status of other elements. In particular, Mn uptake capacity is increased by Fe, Zn and S deficiencies (Neugebauer et al. 2018; Pii et al. 2015; Stich et al. 2020) and also by Fe deficiencies induced by excess divalent cations. The lack of specificity of transporters catalysing Mn uptake is often cited as a possible reason for correlations among Mn, Zn, Fe and Cu in their accumulation by plants (Neugebauer et al. 2018) and it is perhaps noteworthy that genotypes of, for example, barley, with greater ability to tolerate soil Mn limitation not only have greater leaf Mn concentrations, but also greater leaf Zn and Cu concentrations than other genotypes when grown hydroponically (Schmidt et al. 2019).

Manganese is loaded into the xylem by H^+ -coupled antiporters, such as OsMTP9 in rice (Alejandro et al. 2020). The expression of *OsMTP9* is unaffected by Mn deficiency, although its orthologs in other plant species are often down-regulated by Mn or Zn deficiency (Alejandro et al. 2020). In the xylem sap Mn is present as Mn^{2+} and as Mn-complexes with organic acid anions, such as citrate and malate, or nicotianamine (Curie et al. 2009; Welch 1995). Manganese follows the transpiration stream and is thought to be taken up by shoot cells as Mn^{2+} by members of the ZIP family (Alejandro et al. 2020; White and Pongrac 2017). Manganese is relatively immobile in the phloem (White 2012) and shoot Mn concentrations are generally larger than root Mn concentrations in most plants (Neugebauer et al. 2020). Thus, Mn deficiencies often originate in developing shoot tissues and Mn toxicities occur in older leaves where Mn is accumulated

(Alejandro et al. 2020; White and Pongrac 2017). Shoot Mn concentration, as a proxy for the capacity of a plant to take up Mn and translocate it to the shoot in the xylem, appears to differ among plant species growing in nutrient-replete media, as exemplified in studies using hydroponics systems (Fig. 1c; Neugebauer et al. 2018). There appears to be a positive correlation between the shoot Mn concentrations of plant species grown hydroponically in a nutrient-replete medium and both the Mn concentration required by these plant species ($R = 0.51$, $n = 31$, $P = 0.004$) and the leaf Mn concentration that would be toxic to them (Fig. 1c; $R = 0.61$, $n = 31$, $P < 0.001$).

An inability to respond effectively to vagaries in the Mn concentration in the soil solution might result from (1) the phytoavailability of Mn in the soil solution being regulated by the plant nutritional status of elements other than Mn, (2) the lack of specificity of transporters facilitating Mn uptake by root cells, and (3) the regulation of Mn-uptake capacity by the plant nutritional status of elements other than Mn. This could result in a greater susceptibility to both Mn deficiency and Mn toxicity, depending on soil properties and environmental conditions. In particular, should either Mn phytoavailability or the Mn uptake capacity be increased in response to nutrient deficiencies of elements other than Mn, this might necessitate greater tissue Mn tolerance of species growing on soils where these deficiencies occur to allow them to survive.

In this Special Issue of *Plant and Soil*, Lambers et al. (2021) discuss whether leaf Mn concentrations can be used as a tool to assess belowground functioning in phosphorus-impooverished environments. The rationale for this suggestion is founded on the observation that the release of carboxylates into the rhizosphere in response to P deficiency can increase Mn uptake by plants (Lambers et al. 2015). The authors combined data for leaf Mn concentration, root functional type and environmental variables from 727 species collected at 66 sites in Australia and New Zealand. They observed (1) that, in general, non-mycorrhizal plants that released carboxylates had larger (site-adjusted) leaf Mn concentrations than mycorrhizal plants when grown in soils with low P availability, but (2) that leaf Mn concentration did not provide information about root functional types under seasonally-waterlogged conditions, when Fe phytoavailability is high. The first observation is consistent with the hypothesis that Mn phytoavailability is increased by the release of carboxylates upon P deficiency, which results in greater root Mn uptake and leaf Mn concentration. The second observation is consistent with the hypothesis that high Fe phytoavailability greatly

reduces the capacity for Mn uptake by root cells and, therefore, any increase in Mn phytoavailability produced by the release of carboxylates upon P deficiency has negligible effect on root Mn uptake and leaf Mn concentration. Nevertheless, it would appear that several assumptions must be fulfilled for the use of leaf Mn concentration as a proxy for root functional type to work. One assumption is that all plant species circumscribed in a comparative study are capable of increasing root Mn uptake and leaf Mn concentration should carboxylates be released by roots, and increase these to a similar extent for the approach to be quantitative. A second assumption is that all plant species must be able to tolerate (survive) the greater tissue Mn concentration resulting from the increased Mn phytoavailability, although it should be noted that, on severely P-impoorished soils, Mn is often limiting and leaf Mn concentrations would not reach toxic concentrations. These assumptions might be tested in future experiments. It is noteworthy that the carboxylate concentration in the rhizosheath of chickpea genotypes is directly correlated with foliar Mn concentrations under low phosphorus supply (Pang et al. 2018).

If the ability of plants to control Mn uptake and shoot Mn concentration is compromised when they are subject to common environmental challenges (e.g., low P soils, alkaline soils with low micronutrient phytoavailability, flooded soils), then it might be anticipated that plants from such environments would have evolved low Mn requirements and greater tissue Mn tolerance. The significant positive correlation between the shoot Mn concentration of plants grown hydroponically in a nutrient-replete medium and the tissue Mn concentration that would be toxic to these species, suggests that Mn uptake capacity and tissue Mn tolerance evolved together. This is consistent with the evolution of Mn hyperaccumulation through allelopathy to competitors and protection against pests and pathogens (Boyd 2007). Interestingly, the known Mn-hyperaccumulators exhibit a variety of root functional types. Although the Proteales that hyperaccumulate Mn form typical cluster-roots that release carboxylates in soils with low P availability (Lambers et al. 2021), members of other orders that include species that hyperaccumulate Mn, such as Malpighiales, Myrtales, Ericales and Gentianales, typically form mycorrhizal associations (Brundrett 2009). The large Mn uptake of some members of these orders could result from the high phytoavailability of Mn in the soils on which they grow, either because of their low pH or because of the underlying (serpentine) geology, but

many species that hyperaccumulate Mn grow on soils without abnormally large Mn concentrations (van der Ent et al. 2019). It is noteworthy, therefore, that some species from these orders are mycorrhizal but also release carboxylates, such as species in the genera *Phytolacca* (Malpighiales) and *Vaccinium* (Ericales) (DeGroote et al. 2018; Lambers et al. 2015; Millaleo et al. 2020).

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Data availability All data can be found in the sources cited.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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