Opinion

Leaf manganese accumulation and phosphorus-acquisition efficiency

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Plants that deploy a phosphorus (P)-mobilising strategy based on the release of carboxylates tend to have high leaf manganese concentrations ([Mn]). This occurs because the carboxylates mobilise not only soil inorganic and organic P, but also a range of micronutrients, including Mn. Concentrations of most other micronutrients increase to a small extent, but Mn accumulates to significant levels, even when plants grow in soil with low concentrations of exchangeable Mn availability. Here, we propose that leaf [Mn] can be used to select for genotypes that are more efficient at acquiring P when soil P availability is low. Likewise, leaf [Mn] can be used to screen for belowground functional traits related to nutrient-acquisition strategies among species in low-P habitats.

Phosphorus-acquisition strategies

Here we explore the idea of using leaf [Mn] to indicate a carboxylate-releasing P-acquisition strategy. The rationale behind this contention is that the availability of both P and Mn are increased when roots release carboxylates into the rhizosphere [1] (Figure 1; see Glossary). The availability of some other micronutrients is also enhanced, but most of these do not lead to a signal as strong as that provided by Mn. The release of carboxylates into the rhizosphere is important for P acquisition, because they mobilise not only inorganic P, but also organic P, which can be a major fraction of soil P, especially when P availability is low [2].

Addressing this topic is timely, because there is a growing interest among plant ecologists in belowground functional traits, to complement the suite of 'easy-to-measure' aboveground traits [3]. Furthermore, because of the gradual decline in phosphate rock that is used to produce P fertilisers [4], there is an increasing need for more P-efficient cropping systems [5]. Therefore, a simple tool to screen for P-acquisition efficiency in crop species would be welcomed by agronomists and plant breeders.

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Keywords: carboxylates; exudation; manganese; phosphorus; phosphorus-acquisition efficiency.

1360-1385/

 http://dx.doi.org/10.1016/j.tplants.2014.10.007

Manganese as a plant nutrient

The significance of Mn as an essential plant nutrient was firmly established in 1922 [6]. More recent work has revealed the role of Mn in redox processes, as an activator of a large range of enzymes, and as a cofactor of a small number of enzymes, including proteins required for light-induced water oxidation in photosystem II [7,8]. Crop plants that contain 50 μg Mn g^{-1} dry weight (DW) in their

Glossary

Arbuscular mycorrhiza: a type of mycorrhizal association that forms arbuscules or coiled hyphae (highly branched exchange structures) within cortical cells of the root.
Carboxylate: an organic anion, which is the organic acid minus the proton(s). For example, citrate is the carboxylate released from the deprotonation of the organic acid, citric acid.
Chelate: a compound that combines reversibly, usually with high affinity, with a metal ion (e.g., iron, copper, or manganese).
Cluster roots: bottle brush-like or Christmas tree-like structures in roots with a dense packing of root hairs, releasing carboxylates into the rhizosphere, thus solubilising poorly available nutrients (e.g., P) in the soil.
Ectomycorrhiza: mycorrhizal association, mostly in woody species, in which a fungal mantle covers fine roots.
Heavy metal: a metal with a mass density exceeding 5 g ml^{-1}.
Hyperaccumulating plant species: plants that typically accumulate 100 times more of a specific heavy metal than the concentrations that occur in nonaccumulator plants growing in the same substrates. For most elements, including Mn, the threshold concentration is 1000 $\mu g\ g^{-1}$ DW, except for zinc (10 000 $\mu g\ g^{-1}$), gold (1 $\mu g\ g^{-1}$), and cadmium (100 $\mu g\ g^{-1}$).
Iron-regulated transporter (IRT): associated with the uptake of iron from the rhizosphere into root cells. It is not highly specific and transports other micronutrients.
Micronutrient: inorganic nutrients that a plant requires in relatively small quantities, such as copper, iron, Mn, molybdenum, and zinc.
Mycorrhiza: a structure arising from a symbiotic association between a mycorrhizal fungus and the root of a higher plant [from the Greek words for fungus and root, respectively; the Greek plural would be mycorrhizas, but the Latin plural (mycorrhizae) is also used].
Natural resistance associated macrophage protein (NRAMP): a divalent cation transporter associated with the uptake of transition metals, such as copper, iron, Mn, and zinc.
Nonmycorrhizal plant family: a plant family whose members predominantly are unable to establish a symbiotic association with a mycorrhizal fungus.
Rhizosphere: the zone of soil influenced by the presence of a root.
Scleromorphic: containing a relatively large amount of tough structures (sclerenchyma).
Sorption: the process referring to the binding of, for example, phosphate onto the surface of (i.e., adsorption) and inside (i.e., absorption) soil particles. The term was coined by McBain in 1909 [79]. In soil science, the noncommittal term 'sorption' is used to indicate all processes that result in the transfer of material from the soil solution to the solid phase.
Transition metal: any metal in the d-block of the periodic table, which includes groups 3–12 of the periodic table; the f-block lanthanide and actinide series are also considered transition metals and are referred to as 'inner transition metals'.

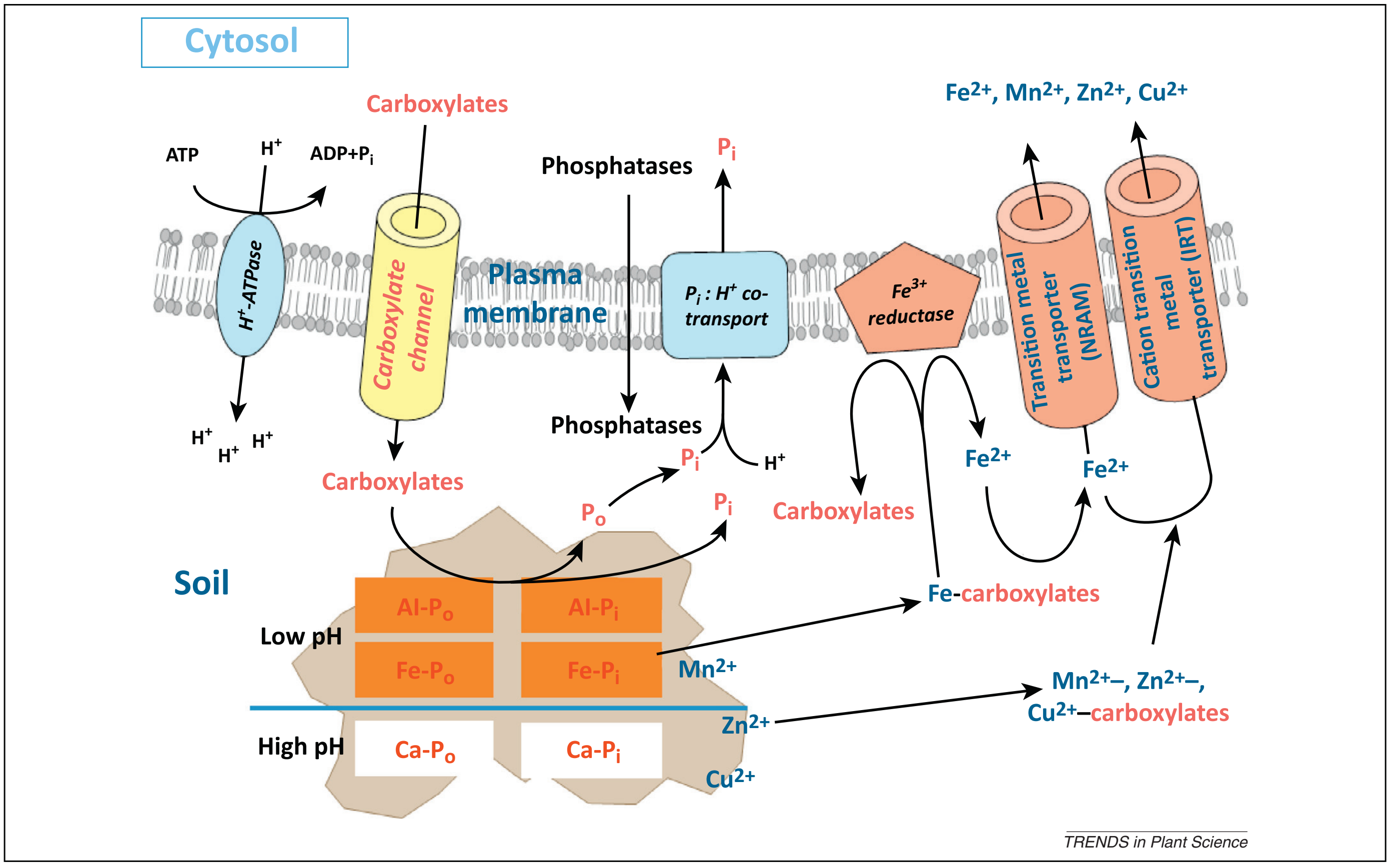

Figure 1. Effects of carboxylates (and other exudates with similar effects, e.g., polygalacturonate [80]) on mobilisation of phosphorus (P) and transition metals. Carboxylates (organic anions) are released via a carboxylate channel. The manner in which phosphatases are released is unknown. Carboxylates mobilise both inorganic (Pi) and organic (Po) P, which are both sorbed onto soil particles. At acid pH, Pi and Po bind to oxides and hydroxides of iron (Fe) and aluminium (Al); at alkaline pH, these compounds are precipitated by calcium (Ca). The carboxylates effectively take the place of Pi or Po, thus pushing this into solution. The released phosphatase enzymes hydrolyse Po compounds after they have been mobilised by carboxylates. Carboxylates also mobilise some of the transition metal cations, especially Fe, manganese (Mn), zinc (Zn), and copper (Cu). Chelated Fe moves to the root surface, where it is reduced, followed by uptake via a Fe^{2+} transporter [iron-regulated transporter (IRT)]. This transporter is not specific and also transports other micronutrients, such as Mn, Cu, and Zn, which have been mobilised by carboxylates in soil. Alternatively, these transition metals can be taken up by a transporter referred to as natural resistance associated macrophage protein (NRAMP). For further explanation, see the main text. Modified from [13].

leaves are considered to have sufficient Mn for maximum growth and yield [9]. Conversely, Mn toxicity can occur when plants are grown at moderately low soil pH or in flooded soils, when Mn availability is increased [10–13] and its uptake is not tightly regulated. Critical toxicity concentrations in leaves range from 200 to 3500 μg Mn g^{-1} DW [14], but some hyperaccumulators, such as Proteaceae species in New Caledonia, may contain >10 000 μg Mn g^{-1} DW without harmful effects [14,15]. Mechanisms that counter Mn toxicity in plants involve Mn export from the cytoplasm, across the tonoplast for sequestration into the vacuole, or across the plasma membrane out of the cell [16]. The *Arabidopsis AtMTP* family of genes encode proteins of the cation diffusion facilitator family, some of which have a role in metal tolerance [17]. Expression of cation diffusion facilitators in a Mn-hypersensitive yeast mutant restored Mn tolerance to wild type levels, showing the importance of this transport system for Mn tolerance [18].

High leaf [Mn] in nonmycorrhizal species with cluster roots

Relatively high leaf [Mn] are typically found in species that produce cluster roots, particularly Proteaceae species, which are almost all nonmycorrhizal and occur on soils with very low P availability [19–22]. Cluster roots also occur in actinorhizal species and in many Fabaceae [1,23]. These specialised roots release large amounts of carboxylates in an ‘exudative burst’ to mobilise P, and this also mobilises Mn [23,24]. For a large number of Proteaceae, the range of [Mn] is 126–10 000 μg Mn g^{-1} DW [20,25–29]. In New Caledonia, no Proteaceae species exhibit leaf [Mn] <100 μg Mn g^{-1} DW [20]. Likewise, in Fabaceae species with cluster roots, relatively high leaf [Mn] have been observed: 7370 μg Mn g^{-1} DW in *Lupinus albus*, which is also nonmycorrhizal [30], and 120 μg Mn g^{-1} DW in *Aspalathus linearis* [31]. These high concentrations can be explained by the ability of cluster roots to mobilise Mn as well as P [24,32,33]. For example, in a glasshouse experiment with *Hakea prostrata* (Proteaceae), variation in leaf [Mn] was positively correlated with investment in cluster roots [34], and similar results were found for *L. albus* [35]. Given that a concentration of 50 μg Mn g^{-1} DW is considered sufficient for maximum growth of crop plants [9], concentrations >100 μg Mn g^{-1} DW are considered ‘high’, especially for species with scleromorphic leaves (e.g., many Proteaceae). However, the exact concentrations will also depend on Mn availability in the soil