Nicotianamine Secretion for Zinc Excess Tolerance

Plants acquire micronutrients such as iron (Fe), zinc (Zn), manganese, or copper from soil. These micronutrients are often not readily available and they need to be mobilized to the proper free ionic form in order to be taken up by plant roots. Perhaps the only exception to this is the uptake of Fe by grasses, which have evolved a so-called strategy II uptake mechanism that involves the secretion of mugineic acid (MA)-family phytosiderophores to chelate Fe(III). These plants then take up the chelated Fe(III)-siderophore complexes. Most other plant species use strategy I for Fe uptake, which depends on the reduction of Fe(III) to Fe(II) and uptake through Fe^{2+} transporters. Because strategy II is less pH dependent than strategy I, it offers an evolutionary advance to grasses, especially when grown on calcareous soils (Römheld and Marschner, 1986).

Because micronutrients are generally poorly available, plants are not well adapted to situations in which micronutrient availability is high, as will be the case at certain metal-polluted sites such as Zn or copper smelter or mining sites. Only a few select flora of highly adapted metallophic species thrive at such sites. Some of these species evolved the ability not only to withstand the high metal exposure, but also use it to their benefit by hyperaccumulating some of these metals (generally nickel, Zn, or cadmium) as a defense to herbivores or pathogens (Boyd, 2007). How these metal hyperaccumulators manage to maintain mineral homeostasis of the same or similar elements to which they are highly exposed has been investigated primarily in two model species, Noccaea caerulescens and Arabidopsis halleri, both belonging to the Brassicaceae family (Krämer, 2010).

In this issue, Tsednee et al. (2014) add a new chapter to this investigation. They found that A. halleri roots secrete more nicotianamine (NA) than roots of its nonmetal-tolerant congeners Arabidopsis thaliana and that this secretion is increased for A. halleri when plants are exposed to excess Zn. It is already known that the root NA concentrations in A. halleri are higher than in A. thaliana (Weber et al., 2004), which is attributed to the elevated expression of the NICOTIANAMINE SYNTHASE2 gene (Deinlein et al., 2012). When secreted, NA forms a stable Zn(II)-NA complex in the root exudates, which is not taken up but instead reduces the uptake of Zn by A. halleri roots. If exogenous NA is added to the medium, it dramatically enhances tolerance of A. thaliana to excess Zn. Thus, it looks like A. halleri successfully evolved the secretion of NA as a way to control Zn influx under excess Zn supply conditions. Alternatively, NA secretion may have evolved to maintain Fe homeostasis under excess Zn, which is another characteristic difference between A. halleri and A. thaliana (Shanmugam et al., 2011).

The presence of NA in root exudates has not previously been reported. In pattern, it resembles the secretion of MA-like metal chelators of Graminaceae, but with a very different purpose. Rather than mobilizing a scarce micronutrient (Fe), the presence of NA prevents excessive uptake of an abundant one (Zn). It will be very interesting to see whether the NA secretion mechanism in A. halleri uses similar components as those needed for phytosiderophore secretion in grasses. The best candidate for an NA exporter is likely to be a member of the Major Facilitator Superfamily, which also hosts the rice (Oryza sativa) MA exporter TRANSPORTER OF MUGINEIC ACID1 (TOM1) and the NA exporters EFFLUX TRANSPORTER OF NA1 (ENA1) and ENA2 (Nozoye et al., 2011). However, the A. thaliana TOM1 ortholog ZINC-INDUCED FACILITATOR1 (ZIF1), and another recently described Major Facilitator Superfamily member involved in Zn excess tolerance, ZIF2, are both localized to the tonoplast rather than the plasma membrane (Haydon et al., 2012; Remy et al., 2014). A. thaliana expresses two other paralogues, ZIF1-LIKE1 (ZIFL1) and ZIFL2, which have not been studied to date. Intriguingly, both NICOTIANAMINE SYNTHASE and ZIF(L) genes are also (highly) expressed in the other metal hyperaccumulator, N. caerulescens (Halimaa et al., 2014; Lin et al., 2014), which may well have evolved the same mechanism as A. halleri to deal with excess Zn and continued demand for Fe.

Mark G.M. Aarts
Laboratory of Genetics, Wageningen University,
6708PB Wageningen, The Netherlands
ORCID ID: 0000-0001-5257-0740

LITERATURE CITED

efflux transporters are crucial for iron acquisition in graminaceous plants. J Biol Chem 286: 5446–5454


Commentary