Arbuscular mycorrhizal influence on zinc nutrition in crop plants — A meta-analysis

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ABSTRACT

The effects of soil Zinc (Zn) deficiency on human health and productivity of livestock and crops are severe and thus increasing the Zn concentration in plant tissue (and/or its bioavailability to humans, which we cannot explicitly consider here due to lack of data) has to be a goal of modern, sustainable agriculture. In this meta-analysis, we quantitatively analyzed the potential role of arbuscular mycorrhizal fungi (AMF) in improving Zn concentrations in plant tissues for a variety of crops and soils. We performed a random-effects meta-analysis on 104 articles comprising 263 trials to test the influence of 10 independent variables on AMF-mediated Zn concentration in comparison to non-mycorrhizal control plants for above-, belowground, fruit and seed tissue. AMF had a positive overall impact on Zn concentration in all tissue types and this positive effect was modulated primarily by soil texture. Soil pH and soil Zn concentration affected AMF-mediated shoot Zn concentration soil P concentration influenced fruit Zn concentration. For our dataset, we concluded that AMF positively affected Zn concentration in various crop plant tissues under distinct environmental conditions.

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1. Introduction

Zinc (Zn) is an essential micronutrient for plants, animals and humans and it is an integral component of hundreds of enzymes and thus obligate for metabolism (e.g. Coleman, 1992; Vallee and Falchuk, 1993; Alloway, 2009). Therefore, Zn is relevant for development, reproduction and signaling due to its structural, catalytic and activating functions (e.g. Bedwal and Bahuguna, 1994; Broadley et al., 2007; Cavagnaro, 2008; Roohani et al., 2013). Due to its vital role, Zn deficiency generally causes impairments in physical development and fertility (Abdelrahman et al., 1998; Cakmak, 2000; Alloway, 2009; Prasad, 2010). Zn deficiency usually appears simultaneously in humans, livestock and crops as a consequence of low soil Zn concentrations (White and Zasoski, 1999; Cakmak, 2008; Alloway, 2009; Prasad, 2010). Hence, any sustainable attempt to improve the nutritional quality of crops should include a focus on the plant—soil continuum as it represents the basis of the abovementioned food chain.

Zn has a low mobility in soil solution and its uptake is diffusion-limited. Reduced phytoavailability is a widespread problem especially in calcareous soils of arid and semiarid regions (Cakmak et al., 1999; Broadley et al., 2007) affecting about 50% of agricultural area used for cereal cropping world wide (Cakmak et al., 1999; Alloway, 2009). One solution for preventing Zn deficiencies in plants irrespective of soil Zn status is through biofortification; a technique that permits increasing bioavailable concentrations of essential minerals in the consumable portions of crops (White and Broadley, 2005). By this technique, food for humans and fodder for livestock can be improved in target crops. Additionally, not consumable plant portions (mostly shoots and roots) gain increased Zn concentrations and can be processed to green manure or compost and used as a sustainable and organic Zn fertilizer resource (Mishra et al., 2006).

Biofortification comprises two major approaches: genetic and agronomic biofortification (Cakmak, 2008). Genetically increased plant Zn tissue concentration is achieved by breeding and selection for improved Zn efficiency in plants; a plant trait comprising Zn acquisition, translocation and utilization (Hacisalihoglu and Kochian, 2003). However, this is a long-term process and can only be successful when focal soil is suitable for plant cropping (Hacisalihoglu and Kochian, 2003; Cakmak, 2008). By contrast, agronomical tools for enhanced Zn tissue concentration such as application of Zn fertilizers are readily usable and have been

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approved (Cakmak, 2008; Zhang et al., 2012). Zn fertilizer can be applied via soil and leaves (Rengel et al., 1999), but the resulting Zn concentration in edible tissues varies depending on factors such as soil properties (pH, organic matter content and cation exchange capacity) and fertilizer form (chemical or organic fertilizer) (Rashid and Fox, 1992; Phattarakul et al., 2012; Zou et al., 2012).

So far, these genetic and agronomic approaches have proven successful (Stein et al., 2007), but involve high investment costs for genetic engineering or fertilizer application. An additional, sustainable tool to improve micronutrient concentrations in crops could be arbuscular mycorrhizal fungi (AMF) (He and Nara, 2007; Cavagnaro, 2008); AMF are ubiquitous, symbiotic fungi from the phylum *Glomeromycota* (Schüßler et al., 2001). They are an integral root component (Smith and Smith, 2011) of crops capable of forming this symbiotic interaction; some crop species do not form mycorrhizae, such as members of the *Brassicaceae* (Wang and Qiu, 2006). The AMF-related services can result in better plant performance and soil quality (e.g. Newsham et al., 1995; Auge, 2001; Borowicz, 2001; Parniske, 2008; Smith and Read, 2008) but the most prominent facet of the range of services provided by AMF is the uptake of immobile nutrients such as P and Zn (e.g. Bolan, 1991; Bürkert and Robson, 1994; Marschner and Dell, 1994; Jansa et al., 2003).

Association with AMF allows an alternative nutrient assimilation pathway through extraradical and intraradical hyphae, arbuscules and the root apoplast interface (Parniske, 2008; Smith and Read, 2008). In *Glomus intraradices*, a Zn transporter has been identified (GintZnT1) (Gonzalez-Guerrero et al., 2005) and its putative function includes transport of Zn through hyphae or even Zn loading in the apoplastic space between fungi and plant plasma membrane (Palmiter and Findley, 1995; Anton et al., 1999; MacDiarmid et al., 2002; Cavagnaro, 2008). The connection of the plant root system with the AMF external hyphal network increases the surface area beyond the nutrient depletion zones of roots (Leake et al., 2004; Smith and Read, 2008) – a simple but effective step in the diffusion-limited process of Zn uptake. Additionally, AMF can acquire Zn in soil pores and nutrient patches not reachable for plant roots or root hairs (Bolan, 1991). Overall, the additional AMF-mediated pathway allows for an increased Zn uptake of 25% or higher in shoot and roots (Cooper and Tinker, 1978; Marschner and Dell, 1994).

However, the application of AMF as a sustainable management approach, primarily for improved plant growth, and also for improved Zn concentration in crops is not straightforward due to the high variability of plant responses to AMF; a vast amount of published literature testing the impact of different environmental and biological factors on AMF-mediated Zn concentration in plant tissues can be found. Soil texture not solely determines solubility and mobility of Zn in soil but simultaneously influences performance of AMF (Karagiannidis and Hadjisavva-Zinoviadi, 1998). Soils with high cation exchange capacity (CEC), pH, clay and organic matter content exhibit reduced Zn phytoavailability and allow for improved Zn acquisition by AMF (Armour et al., 1990; Alloway, 2009).

The identity of plant and AM fungi is one of the key sources of variability in AMF-mediated Zn tissue concentrations. Species-level and even intraspecific variation in Zn-efficiency exists in both AM fungi and associated plants (Graham and Rengel, 1993; Cakmak et al., 1997; Gao et al., 2007; Kafkas and Ortas, 2009; White and Broadley, 2009; Ciftci et al., 2010). For plants, variability in Zn efficiency can be mediated by morphological and physiological root traits. Cereals, for example, have fine, thin and highly branched root systems that can result in improved nutrient uptake but reduced AM fungal root colonization, and AM nutritive and growth responsiveness (Newsham et al., 1995; Tawaraya, 2003). For AMF, different species diverge functionally, i.e. AMF species or even isolates perform differently, for example in terms of hyphal growth,

nutrient uptake and root colonization (Allen et al., 1995; Mehravaran et al., 2000; Munkvold et al., 2004) due to their diverse functional traits and life strategies (Chagnon et al., 2013). In addition, the composition of AM fungal inoculum also determines plant responses. A more diverse assemblage of AMF species increases the probability of the presence of beneficial or complementary species being more effective in providing beneficial services to associated plants compared to single species inocula (Hart and Reader, 2002; Vogelsang et al., 2006; Maherali and Klironomos, 2007; Hoeksema et al., 2010; Hart and Forsythe, 2012).

Furthermore, the duration of an experiment may be of exceptional importance in determining AMF-mediated Zn tissue concentrations. Longer experiments can permit better development of the symbiosis (Vierheilig and Ocampo, 1991; Subramanian et al., 2008), while resources as rooting space and nutrients are decreasing (Daft, 1991; Schroeder and Janos, 2004). Additionally, the developmental stage of both AMF and associated plant is an influencing factor. In longer experiments, physiological changes resulting from the switch of vegetative to reproductive growth causes altered nutrient translocation, compartmentation and utilization (White and Broadley, 2009). So far, there has been no evidence that AMF can directly influence the xylem and phloem loading steps for Zn transport from root to shoot and grains; the major bottlenecks of Zn translocation occurring during the vegetative and reproductive phase (for a detailed review see Palmgren et al., 2008; Stomph et al., 2009).

Interpreting the impact of AMF on plant Zn nutrition can be complicated due to the simultaneous effects of AMF-mediated plant P nutrition (Cardoso and Kuyper, 2006). Enhanced P acquisition often results in plant growth promotion and hence potential dilution of Zn in plant tissue (Cavagnaro, 2008). Furthermore, an improved P nutrition can cause increased concentrations of phytate in seeds (Erdal et al., 2002); phytate is an anti-nutrient chelating essential nutrients like Zn and thus reduces their bioavailability for humans and livestock except for ruminants. On the other hand, AMF are able to reduce phytate concentration while enhancing Zn concentrations in maize seeds (Subramanian et al., 2013), although this effect might not be detectable in the field (Ryan et al., 2008).

As a consequence of this complex interaction framework of edaphic, environmental and biological factors affecting the AMF-mediated Zn nutrition, examples of positive, neutral and negative effects of mycorrhizal inoculation on crop tissue Zn concentrations are present in the literature (e.g. Mohandas, 1992; Bagayoko et al., 2000; Alloush and Clark, 2001; Karagiannidis et al., 2007; Cavagnaro et al., 2008; Rouphael et al., 2010). There have been a few qualitative syntheses (literature reviews) addressing this important issue (He and Nara, 2007; Cavagnaro, 2008; Impa and Johnson-Beebout, 2012; Rehman et al., 2012). However, to our knowledge, no meta-analysis has yet been conducted to quantitatively synthesize and evaluate the potential role of AMF for plant Zn nutrition across a range of crop species grown under various conditions. Therefore, we aimed at filling this gap by performing a meta-analysis to address the following hypotheses: (i) AMF increase Zn concentration for root, shoot and fruit tissue across different crops. (ii) The AMF-mediated Zn concentration in different crop tissues is influenced by edaphic factors (soil texture, soil pH and nutrient concentrations) limiting mobility of Zn in soil solution and thus plant and AM fungal bioavailability, respectively. (iii) Studies performed under controlled environmental conditions in pots result in higher AMF-mediated Zn tissue concentration than field studies due to exclusion of influential variables. This allows disentangling complex interaction frameworks but leads to overestimation of effects. (iv) Environmental factors optimizing plant growth conditions positively influence the AMF-mediated Zn tissue concentration; thus plants grown in adequate soil volume for