



# Wheat plants invest more in mycorrhizae and receive more benefits from them under adverse than favorable soil conditions



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## ABSTRACT

Soil chemistry and biota heavily influence crop plant growth and mineral nutrition. The stress-severity and optimal resource allocation hypotheses predict mutualistic symbiotic benefits to increase with the degree of metabolic imbalance and environmental stress. Using two cross-factorial pot experiments with the same biologically active calcareous soil, one time highly saline and nutrient-deficient, and the other time partially desalinated and amended with mineral soil fertilizer, we explored whether these general predictions hold true for zinc (Zn) nutrition of bread wheat in mycorrhizal symbiosis. Increased arbuscular mycorrhizal (AM) fungal root colonization positively correlated with plant Zn nutrition, but only when plants were impaired in growth due to salinity and nutrient-deficiency; this was particularly so in a cultivar-responsive to application of mineral Zn fertilizer. Evidence for direct involvement of AM fungi were positive correlations between Zn uptake from soil and frequency of fungal symbiotic nutrient exchange organelles, as well as the quantitative abundance of AM fungi of the genera *Funneliformis* and *Rhizophagus*, but not *Claroideoglossum*. Combined partial soil desalination and fertilization swapped the dominance ranking from *Claroideoglossum* spp. to *Funneliformis* spp. Positive growth, nitrogen, and Zn uptake responses to mycorrhization were contingent on moderate soil fertilization with ZnSO<sub>4</sub>. In agreement with the predictions of the stress-severity and optimal resource allocation hypotheses, plants limited in growth due to chemically adverse soil conditions invested relatively more into AM fungi, as evident from heavier root colonization, and took up relatively more Zn and nitrogen in response to mycorrhization, than better growing and less mycorrhized plants. It thus appears that crop plant cultivar-dependent mycorrhization and Zn fertilizer-responsiveness may reinforce each other, provided that there is bioavailable Zn in soil and plant growth is impaired by suboptimal chemical soil conditions.

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## 1. Introduction

The strength of mutualism is predicted to increase among symbiotically associated organisms when habitat adversity increases for one or both symbiosis partners, according to the stress severity hypothesis (Bertness and Callaway, 1994; Brooker et al., 2005). This is because the symbiosis partners either relieve each other from environmental stress impacts and/or, because functional complementarity and thus mutual benefits are reinforced under extreme environmental conditions. This general idea is reflected in optimal resource allocation in

mycorrhizal metabolic functioning, where autotrophic plants allocate photosynthates to heterotrophic mycorrhizal fungi, which in return provide plants more extensive access to mineral soil nutrients (Johnson, 2010; Treseder, 2004). Optimal resource allocation in mycorrhizas is highly dynamic (Johnson et al., 1997) and context-dependent (Hoeksema et al., 2010), since the costs and benefits of the symbiosis depend on relative resource availability and imbalance among the symbiosis partners (Grman and Robinson, 2013).

The arbuscular mycorrhiza (AM), the most prevalent plant-fungal nutritional symbiosis on earth (Selosse and Le Tacon, 1998), is formed among fungi of the phylum *Glomeromycota* and the majority of crop and wild plants. Its agronomic importance is likely to increase in future as farmland will have to be extended onto unproductive land and external fertilizer inputs reduced

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(Menge, 1983; Tilman et al., 2011), leading to suboptimal growth conditions for many crop plants. Poor physicochemical soil conditions impair crop plant growth and in turn lead to carbohydrate (C) sink limitation, a situation not much dissimilar to the conditions under which the AM symbiosis is thought to have originally evolved (Field et al., 2012) and the conditions under which it still plays its most important role nowadays (Smith and Read, 2008). Poor growth of crop plants in soils of newly or re-used land may lead to production of a surplus of C that plants may try to invest into roots, AM fungi, and possibly other root symbionts, to get better access to soil mineral nutrients. Macro- and micronutrient deficiencies and soil salinity are two major limiting factors to crop plant production worldwide, whose impacts the AM symbiosis may alleviate (Bennett et al., 2013).

Arbuscular mycorrhizal fungi are primarily known as uptake facilitators of phosphorus (P), zinc (Zn), and some other plant nutrient elements in scarce supply from soil (Cavagnaro, 2008; Hart and Forsythe, 2012; Treseder, 2013). It is the small diameter of the fungal hyphae and hyphal growth beyond the rooting zone, which make AM fungi particularly effective in intercepting and taking up poorly mobile plant growth-limiting nutrients compared to the thicker and shorter roots and root hairs (Asghari and Cavagnaro, 2012; Jakobsen et al., 1992). Only recently, as an extension to the phenomenon of optimal macronutrient allocation in mycorrhizas (Johnson, 2010; Treseder, 2004), Fitter et al. (2011) suggested that the biotrophic AM fungi may invest any plant-growth limiting mineral nutrient, and not only P, for getting access to vital plant-derived C. This prediction complies well with the accumulated evidence that AM fungi also play a decisive role in plant Zn nutrition (Cavagnaro, 2008; Hart and Forsythe, 2012; Jansa et al., 2003).

In the present study we explored whether, indeed, sparingly available native soil Zn and fertilizer Zn is transferred by AM fungi to their wheat hosts when plant growth is impaired by additional adverse soil conditions beyond those of the strong Zn and other nutrient sorbing calcareous soil. We speculated that C sink limitation as a consequence of poor plant growth under adverse soil conditions (Marcelis, 1996; Munns and Tester, 2008) may stimulate AM fungi to deliver more Zn to their host plants. Plant C allocation was recently shown to drive the N and P delivery by AM fungi to their host plants (Fellbaum et al., 2012; Kiers et al., 2011).

Zinc binds to proteins and thereby contributes to the structural integrity of biomembranes, but it also plays a crucial role as cofactor in the transcription of genes and key enzymes alleviating oxidative stress (Hacisalihoglu and Kochian, 2003; Palmgren et al., 2008). As a consequence, normal growth development, health, and reproduction of all organisms, including crop plants, livestock animals, and humans, relies on an adequate supply with Zn (Graham et al., 2007; Welch and Graham, 2005). It is the low plant-availability and slow resupply of soil Zn, which limit crop plant growth, yield, and Zn concentration (=Zn density, in human nutritional terms) in the edible parts of crop plants (Alloway, 2008; Cakmak, 2008). Just as the AM symbiosis is known to be a key mediator of plant P nutrition (Bonfante and Genre, 2010; Smith et al., 2011; Treseder, 2013), the AM symbiosis is increasingly thought to be one of the major contributors to plant Zn nutrition (Jansa et al., 2003; Watts-Williams and Cavagnaro, 2012; Thompson et al., 2013). However, compared to the factors affecting AM involvement in plant P nutrition (Kaeppeler et al., 2000; Smith and Smith, 2011b), much less is known about the influence of plant genotypic, physiological and edaphic parameters on AM-mediated Zn uptake by plants (Gao et al., 2009; Hacisalihoglu and Kochian, 2003; Watts-Williams et al., 2014). In fact, looking at several determinants of tissue Zn levels in edible parts of crop plants at once and in plants produced in fully biologically active field soil seems a matter of urgency, given the need for more micronutrient-

rich cereal-based diets for the growing global human urban population (Kabir et al., 2014; Rawat et al., 2013). Scientific exploration of Zn mobilization and acquisition from soil targets the primary rate limiting step in plant Zn nutrition, given diffusion of Zn from bulk soil to roots is slow (Lindsay and Norvell, 1978). In fact, this slow Zn mobilisation from soil is the reason why solely improvements to germplasm and application of mineral Zn fertilizer will not solve the problem of low Zn levels in crop plants, but rather measures to increase the Zn resupply from soil. Nevertheless, it seems promising to combine agronomic means of soil nutrient management, such as mineral Zn fertilization (Cakmak, 2008) and manipulation of soil biology (Fester and Sawers, 2011), with a careful choice of crop plant cultivars (Gao et al., 2007; Kalayci et al., 1999; Newton et al., 2009). Plant breeding and genetic engineering are facing physiological limits (White and Broadley, 2011) and cultivars with an ability to accumulate Zn still depend on readily available and steady resupplies of Zn from the soil matrix that can only be improved by adequate agronomic soil fertility management practices (Frossard et al., 2009; Singh and Shivay, 2013).

Calcareous soils are renowned for causing problems in the supply of crop plants with sufficient amounts and balanced proportions of mineral nutrient elements, particularly P, iron (Fe), and Zn (Alloway, 2008; Chen and Barak, 1982). High soil salinity together with alkalinity impairs plant mineral nutrition and growth even further via root growth inhibition, ionic imbalance, and physiological drought (Bernstein, 1975; Mass and Hoffman, 1977; Munns and Tester, 2008). Two common strategies of plants to diminish the negative impacts of low mineral nutrient availability and soil salinity are: (1) Deployment of AM fungi for efficient and selective uptake of mineral nutrients, a strategy which may be chosen by plants, suffering from growth limitation and hence experiencing C sink limitation (Johnson et al., 2010; Marcelis, 1996). Arbuscular mycorrhizal fungi are known to act as selective filters, as well as support systems, for their host plants in mineral nutrient uptake from soil and as alleviators of salinity stress (Estrada et al., 2013; Joner et al., 2000; Mardukhi et al., 2011). (2) Release of chemical compounds, which act as chelating agents mobilizing soil Zn (Smolders et al., 2013), such as phytosiderophores, (Cakmak et al., 1996a; Daneshbakhsh et al., 2013; Kraemer et al., 2006), carboxylates (Ryan et al., 2012), and possibly plant- or microbe-derived proteinogenic amino acids (Ghasemi et al., 2013). Crop plant Zn nutrition could thus be promoted by combined reliance on efficient crop cultivars, mineral fertilizer application, and targeted utilization of soil biological services.

In the present study, we explored the role of naturally occurring AM fungi in mineral Zn fertilizer utilization by two bread wheat (*Triticum aestivum* L.) cultivars, known to show differential growth responses to application of mineral Zn fertilizer (Daneshbakhsh et al., 2013). The ecophysiological operation range of the AM symbiosis in Zn nutrition of wheat was further tested by carrying out one pot trial with saline, infertile arable soil (=‘plant growth-suppressive soil’) and a second pot trial which used the same soil, but after improving it via partial desalination and application of mineral fertilizer (=‘plant growth-supportive soil’).

We predicted the wheat plants grown in plant growth-suppressive soil (i) to become more heavily colonized by AM fungi and thus (ii) to utilize the applied mineral Zn fertilizer better than those raised in growth-supportive soil. Furthermore, we expected under no or moderate Zn fertilization (iii) the more Zn fertilization-responsive wheat cultivar to benefit more from support in Zn uptake from soil by AM fungi than the less Zn fertilization-responsive cultivar. Lastly, we anticipated (iv) AM fungi to complement Zn uptake by roots more in plant growth-suppressive soil than plant growth-supportive soil,

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