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Role of mycorrhizas and root exudates in plant uptake of soil nutrients (calcium, iron, magnesium, and potassium): has the puzzle been completely solved?

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Abstract

Anthropogenic global change is driving an increase in the frequency and intensity of drought and flood events, along with associated imbalances and limitation of several soil nutrients. In the context of an increasing human population, these impacts represent a global-scale challenge for biodiversity conservation and sustainable crop production to ensure food security. Plants have evolved strategies to enhance uptake of soil nutrients under environmental stress conditions; for example, symbioses with fungi (mycorrhization) in the rhizosphere and the release of exudates from roots. While crop cultivation is managed for the effects of limited availability of nitrogen (N) and phosphorus (P), there is increasing evidence for limitation of plant growth and fitness due to low availability of other soil nutrients such as the metals potassium (K), calcium (Ca), magnesium (Mg), and iron (Fe) that may become increasingly limiting for plant productivity under global change. The roles of mycorrhizas and plant exudates on N and P uptake have been studied intensively; however, our understanding of effects on metal nutrients is less clear and still inconsistent. Here, we review the literature on the role of mycorrhizas and root exudates in plant uptake of key nutrients (N, P, K, Ca, Mg, and Fe) in the context of potential nutrient deficiencies in crop and non-crop terrestrial ecosystems, and identify knowledge gaps for future research to improve nutrient- uptake capacity in food crop plants.

Keywords: Bacteria; drought; fertility; fungi; nitrogen; phosphorus; soil

Introduction

Anthropogenic global climate change is caused by ongoing increases in atmospheric concentrations of carbon dioxide (CO_2) and other greenhouse gases; elevated CO_2 enhances the availability of carbon (C) for photosynthesis, which may enhance plant growth. As a result, the plant demand for nutrients increases as does the content of these nutrients in plant biomass. This may lead to a decrease in the concentration of nutrients, such as phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and iron (Fe). However, in some heavily fertilized croplands, soil concentrations of N, and particularly P, are increasing, especially, in the case of P, because of immobilization in the soil (Penuelas et al., 2020a). This leads to a scenario of higher ratios of C and frequently of N and P to elements such as K, Ca, Mg, and Fe (Paseka et al., 2019). However, in natural terrestrial ecosystems, higher ratios of C and N to elements such as P, K, Ca, Mg and Fe are generally observed (Penuelas et al., 2013,2020b; Paseka et al., 2019). These changes in C:element ratios indicate reductions in plant element concentrations (dilution effects) that have implications for nutrient element concentrations of food crops (Paseka et al., 2019). Plant nutrient-acquisition capacities can be affected by global changes in temperature, water availability, atmospheric CO_2 concentrations, and atmospheric N deposition (Brouder and Volenec, 2008; Elbasiouny et al., 2022). For instance, the impacts of some global change drivers such as acid rain, N deposition, drought, and species invasion on soil pH (Wei et al., 2020; Zia et al., 2020; Tipping et al., 2003; Ouyang et al., 2022) enhance soil mineral leaching and thus soil nutrient mobilization (Cui et al., 2019; Wei et al., 2020), with different effects on specific nutrients (Sharpley, 1991; Cui et al., 2019). Given that elemental ratios are a key driver of ecosystem structure and crop production, with associated implications for human health, continuing global nutrient imbalances and dilution effects under global change are of great concern for sustainable crop production and food security (Paseka et al., 2019; Penuelas et al., 2020b; Nicholson et al., 2021).

Plants have evolved a wide array of strategies to enhance the soil nutrient-acquisition capacity by roots, including symbiotic mycorrhizal associations and release of exudates into the rhizosphere. While the role of these strategies in the uptake of N and P has been widely studied and reported, their contribution to plant absorption of the principal metal nutrients, K, Ca, Mg, and Fe, is less clear, with studies reporting contrasting findings for some nutrients (Gryndler et al., 1991; Rosenstock et al., 2016). Therefore, the aim of our review is to synthesize the literature on the role of mycorrhizas and root exudates in plant uptake of key nutrients (N and P) and metals (K, Ca, Mg, and Fe) in the context of potential nutrient deficiencies in crop and non-crop terrestrial ecosystems and identify knowledge gaps for the focus of future research.

Methodology

We have reviewed "Web of Science", "Google Scholar" and "Scopus" using combinations of keywords, such as: "root & exudate & nitrorgen", "root & exudate & phosphorus", "root & exudate & calcium", "root & exudate & magnesium", "root & exudate & potassium", "root & exudate & mycorrizha", "root & arbuscular & nitrogen", "root & arbuscular & phosphorus", "root & arbuscular & calcium", "root & arbuscular & magnesium", "root & arbuscular & iron", "root & exudate & nitrogen", "root & arbuscular & potassium", "root & ectomycorrhiza & nitrogen", "root & ectomycorrhiza & phosphorus", "root & ectomycorrhiza & calcium", "root & Ectomycorrhiza & magnesium", "root & Ectomycorrhiza & potassium", "root & ectomycorrhiza & iron", "root & ectendomycorrhizas & nitrogen".

Consistent role of mycorrhizas and root exudates in phosphorus uptake

Although plants directly take up P via the root system, this is dependent on mycorrhizas in most plant species (Smith and Read, 2008; Chiu and Paszkowski, 2019). Two main types of fungi establish symbioses with plant roots. Ectomycorrhizal fungi produce a sheath around the roots of host plants and a Hartig net, a network of inward-growing hyphae, that extends into the root, penetrating between the epidermis and cortex of ectomycorrhizal plants, but they do not penetrate the root cell plasma membrane, while arbuscular mycorrhizal fungi (AMF) penetrate the cell wall but not the plasma membrane/cytosol (Smith and Read, 2008; Peay et al., 2016) (Figure 1). Several studies suggest that in mycorrhizal associations the fungus is primarily fed by soluble sugars and lipids originating from sucrose transported towards the roots (Gutjahr et al. 2011; Rich et al., 2017). The sugar fluxes are coordinated by transport systems, comprising sucrose (SUTs), monosaccharide (MST), and the SWEET sugars transporter family (Doidy et al. 2012). However, once sucrose reaches the arbuscular mycorrhized (AM) root, some specific type II transporters seem to return sugars back towards the plant cells (Bitterlich et al. 2014), thus suggesting that there can be a mechanism of reverse transport to influence symbiotic fungal growth. Experimental studies have reported the key roles of arbuscular mycorrhizas (AM) and ectomycorrhizas (EM) in increasing plant P uptake (Caris et al., 1998; Etesami et al., 2021), and it has been suggested that most plant species can improve their ability to take up highly immobile soil P by symbiosis with mycorrhizal fungi (Smith and Read, 2008; Albornoz et al., 2021). Mycorrhizas are less important for more mobile macronutrients such as N that are readily taken up by roots (Lambers et al., 2008). Symbioses between types of Glomeromycota fungi, which can form AM fungi, and vascular plants are common, occurring in about 80% of terrestrial plant species, and are predominantly involved in the enhancement of P uptake, as well as greater acquisition of additional nutrients, such as ammonium (NH_4+) (Brundrett, 2002; Lambers et al., 2008). AM fungi (AMF) frequently produce numerous vesicles that serve as storage structures for the accumulation of P and other nutrients, such as K, Ca and Fe, in colonized nutrient- deficient plants (Olsson et al., 2011). The uptake mechanisms of different minerals by mycorrhizas vary depending on the nutrient. For example, while Ca released from apatite is deposited as Ca oxalate crystals on the surface of rhizomorphs, phosphate P that is released from apatite, the primary mineral containing P (Pallon et al., 2007), is transported by EM mycorrhizas, increasing P availability and plant uptake (Wallander et al., 2002;2003). In AM fungi H+/Na+ coupled transporters have been described that enable orthophosphate (Pi) uptake over a wide soil pH range (Johri et al., 2015). Uptake of negatively charged orthophosphate requires an energy-driven transport process mediated by phosphate transporters and energised by H+-ATPases (Krajinski et al., 2014; Wang et al., 2014; Walder et al., 2015). Some of these transporters are specifically involved in transport of phosphate released by mycorrhizal fungi. In AM associations, the fungi release phosphate from their arbuscules within cortical cells, and the plant uses these transporters to take up phosphate across the periarbuscular membrane into cortical cells (Harrison et al., 2002). Most *Pht1* genes are strongly expressed in root epidermal cells under P deficiency, including root hairs and cortical cells, suggesting a role in Pi uptake (Chiou et al., 2001; Ai et al., 2009). The mycorrhiza-specific Pi transporters all belong to the family of Pht1 transporters, but cluster in two different subgroups, respectively named subfamilies I and III (Bucher, 2007). Most members of subfamily I are only expressed in arbuscule-containing cortical cells during AM symbiosis (Harrison et al., 2002; Javot et al., 2007). AM-induced *Pht1* genes of subfamily III are more broadly expressed in plant roots but specifically induced in cortical cells during AM symbiosis (Rausch et al., 2001; Maeda et al., 2006; Nagy et al., 2005; Karandashov et al., 2004; Tamura et al., 2012; Paszkowski et al., 2002; Guimi et al., 2005; Glassop et al., 2005; Nagy et al., 2006). Interestingly, mycorrhiza-specific induction of *Pht1* transporter genes is conserved between perennial woody and herbaceous plant species (Loth-Pereda et al., 2011). Remarkably, several studies have found that these Pi transporters are crucial for AM mycorrhization and their maintenance (Maeda. et al., 2006; Javot et al., 2007; Yang et al., 2012).

In ECM fungi, several genes putatively encoding Pi transporters have been identified (Casieri et al., 2013; Kohler et al., 2015). Most of these transporters are H+/Pi transporters, suggesting thatthe efficiency of fungal Pi uptake strongly relies on external pH values. Two H+/Pi transporters (HcPT1.1, HcPT2) found in extra-radical hyphae of *Hebeloma cylindrosporum,* could mediate Pi uptake when soil P availability was low (Garcia et al., 2013; Tatry et al., 2009). Similarly to HcPT1.1, upregulation by low Pi has been found for other H+/Pi transporters in *Tricholoma* spp. (Kothe et al., 2002), *Boletus edulis* (Wang et al., 2014), *Rhizopogon luteolus* (Zheng et al., 2016), and *Leucocortinarius bulbiger* (Zheng et al., 2016).

Other mycorrhizal types that are more specialized in specific plant taxa or environmental conditions also enhance a plant's capacity to take up soil nutrients (Figure 1). In orchid mycorrhizas, comprising fungi and orchid nonphotosynthetic host tissues, the fungus is thought to provide both inorganic and organic nutrition to the plant and apparently does not receive anything in return. However, recent research has shown a flow of nutrients back to the fungal partner from the nonphotosynthetic orchid host (Cameron et al., 2006;

Dearnaley and Cameron, 2016). Ericaceous plants rely on ericoid mycorrhizal (ERM) fungi for nutrient acquisition (Vohnik, 2020; Leopold et al., 2021) (Figure 1), particularly for uptake of P (Mitchell and Gibson, 2006; Leopold et al., 2021) and N (Mitchell and Gibson, 2006) under limiting conditions. Ectendomycorrhizas are restricted mostly to the plant genera *Pinus* (pine), *Picea* (spruce) and to a lesser extent *Larix* (larch) (Mikola, 1988; Turgeman et al., 2016) (Figure 1), but their establishment has also been observed in other plant taxa such as in *Helianthemum sessiliflorum* (Turgeman et al., 2016). These ectendomycorrhizas present many of the same characteristics as ectomycorrhizas (EM), but also show extensive root tissue penetration (Mikola, 1988; Yu et al., 2001). The formation of ectendomycorrhizas begins with the formation of a Hartig net, which grows behind the apical meristem of the growing root tip. Following this, in the older parts of the root, intracellular penetration increases, with the oldest cells being filled with coils of septate hyphae (Yu et al., 2001). Some variants of ectendomycorrhizas have been described with some slight morphological differences, but with the fundamental structure of ectendomycorrhizas. Cavendishioid ectendomycorrhizas have been described in the Andean clade of Ericaceae (Setaro et al., 2006). In this case, the formation of a hyphal sheath is observed with intercellular penetration of fine hyphae and colonization of the cortical cells by swollen hyphae of the same fungus. Another type of ectendomycorrhiza is arbutoid mycorrhiza, which is a symbiosis between fungi and some plant species of the Ericaceae family as for example the described association between the ascomycete *Leotia lubrica* and the Ericacea species *Comarostaphylis arbutoides* (Kuhdorf et al., 2015). Monotropoid ectendomycorrhizas occur in species of Monotropa, nonchlorophyllous plants growing under forest trees like *Fagus, Pinus, Quercus,* and *Salix* as epiparasites depending on the fungal partner, and in this case the hyphae are restricted to epidermal cells and do not penetrate the host cell (Manoharachary et al., 2002). Feremycorrhiza (FM) is a recently discovered plant-fungus symbiosis, which enhances plant growth and nutrition without the development of interface structures; the range of plant species that establish FM relationships is currently unknown (Kariman et al., 2020).

Mycorrhizas also allow plants to take advantage of phosphate-solubilizing bacteria. Certain bacteria can indirectly improve P mobilization and its uptake by plants. Some phosphate-solubilizing bacteria do not only mobilize P into forms that AM fungi can absorb but they can interact mutually favoring the growth of each other (Minaxi et al., 2013; Ordonez et al., 2016; El Maaloum et al., 2020). In this regard, many bacterial species belonging to *Pseudomonas, Azotobacter, Bacillus, Burkholderia* and *Rhizobium* genera have the capacity to mobilize poorly-available P, including organic and inorganic forms to soluble orthophosphate by lowering soil pH and/or solubilizing/desroption P from Fe oxides and hydroxides and Ca salts using exuded organic acids (Rodriguez and Fraga, 1999; Marschner et al., 2001; Toljander et al., 2007; Browne et al., 2009; Ordonez et al., 2016; El Maaloum et al., 2020). Moreover, bacteria associated with extraradical AM hyphae can also secrete phosphatases (Sato et al., 2015, 2019) and phytase secretion has also been associated with extraradical AM hyphae (Wang et al., 2017). Phosphatase release has been commonly observed in AM and ECM (Araujo et al., 2016; Meeds et al., 2021: Hirano et al., 2022; Qi et al., 2022).

There is growing knowledge of the effects of root exudates on the availability of soil P for use by plants. Exudates comprise a range of substances, such as carboxylates, sugars, mucilage, protons, water, phenolics, amino acids, and enzymes, such as phosphatases and phytases (Tarafdar and Claassen, 2005; Lambers et al., 2006). The direct exudation of acid phosphatase has been observed in several species (Playsted et al., 2006; Aslam et al., 2022). High activities of alkaline phosphatase have been observed in the rhizosphere in some studies (Song et al., 2012; Touhami et al., 2020), and root exudates promote the growth of Saccharimonadales that then improve the alkaline phosphatase activity in the maize rhizosphere (Wang et al., 2022). The composition and release of root exudates are dynamic and vary in response to soil P availability; for example, release of compounds, such as strigolactones (Yoneyama et al., 2008), carboxylates (Zhou et al., 2021), and flavonoids (Tomasi et al., 2008), is stimulated by P deficiency in the rhizosphere, where the strigolactones (sesquiterpene lactones) stimulate AM fungal spore germination and hyphal branching (Bouwmeester et al., 2007). Stimulation by root exudates of mycorrhizal establishment is more common, through inhibition of root pathogens, and stimulation of germination of mycorrhizal spores and hyphal branching that extend the root zone and density required for greater uptake of less-mobile nutrients (Hassan and Mathesius, 2012; Tian et al., 2021).

However, there are also studies that have shown that root exudates can inhibit the development of AM fungi (Vierheilig et al., 2003). Effects of mycorrhizas on root exudation vary with type, but this requires further study; for example, greater fluxes in exudates have been observed in *Pinus* species colonized by EM under drought and N- limiting conditions (Liese et al., 2018), while no changes have been observed for AM- colonized tomato *(Solanum lycopersicum)* roots (Lioussanne et al., 2009). Similarly, the role and impacts of climate change on root exudation are yet to be fully understood; however, Zhou et al. (2021) recently reported that prolonged warming increases root exudation and Ca-P mobilization, by nonmycorrhizal Cyperaceae, indicating that plants may rely increasingly on inorganic P mobilization under high P demand to sustain increased growth under warmer conditions. Plant uptake of P is problematic when it is strongly bound to soil particles and precipitated in minerals, such as in calcareous soils (Lambers et al., 2009). However, root exudates mobilize P by desorbing from Fe-and Al- phosphates oxydes and hydroxides in different soil types (Subbarao et al., 1997; Shen et al., 2001), such as in calcareous (Hinsinger, 2001, Vance et al., 2003; Zohlen and Tyler, 2004) and siliceous soils (Dakora and Phillips, 2002; Louw-Gaume, et al., 2017) (Figure 2). In particular, exuded carboxylates mobilize phosphates (Lambers, 2022). This capacity to mobilize P from minerals also depends on the nature of root exudates, and their relative proportions (Pearse et al., 2007; Shi et al., 2020). However, non- mycorrhizal plant species tend to be characterized by specialized root systems, for example cluster roots, dauciform roots or capillaroid roots (Lambers, 2022), and associated with a high level of production of root exudates as an evolved nutrient- mining strategy, particularly in environments with limited P availability (Lambers et al., 2009). The presence of specialized roots associated with P acquisition does not invariably imply faster P uptake than in plants that release carboxylates without specialized structures. For example, dauciform roots, which are found in some Cyperaceae and are functionally similar to cluster roots, are formed under low-P conditions (Gusewell, 2016), and increase P availability through the release of carboxylates and phosphatases (Gusewell, 2016, Playsted et al., 2006, Shane et al., 2006). However, Gusewell and Schroth (2017) found no differences in the acquisition of various inorganic and organic P compounds in Cyperaceae with and without dauciform roots, because Cyperaceae without dauciform roots also release carboxylates and phosphatases. In the case of species with cluster roots, there is significant variability in root architecture and exudation and different species have a distinct capacity to mobilize P from specific chemical forms in soil (Pang et al., 2021). These plants exude huge amounts of protons, carboxylates, and phosphatases, particularly in comparison with noncluster rooted plants (Skene, 2000; Uhde-Stone, 2017). Furthermore, cluster roots also release large amounts of flavonoids (e.g., genistein), possibly to prevent microbial degradation of exuded carboxylates (Tomasi et al., 2008). The array of exudates in terms of composition and concentration changes depending on the environment and plants, such as soil P- availability, root age and species (Shane and Lambers, 2005).

There is evidence that root exudates from nonmycorrhizal plants inhibit mycorrhization in mycorrhizal plant species, through the release of allelopathic compounds, especially in nutrient-rich habitats (Lambers and Teste, 2013). This suggests that nonmycorrhizal species may have developed a greater capacity to release exudates than mycorrhizal species; this possibility warrants future research. Species-level comparisons of the P uptake show that root diameter is a good predictor of dominant mechanism (root morphology-growth, exudates, and mycorrhizas); for example, P- uptake in species with thinner roots is positively correlated with root branching and length and negatively correlated with colonization by AMF and exudate production, whereas P uptake in species with thicker roots is positively correlated with AMF colonization and/or P-mobilizing exudates in the rhizosheath (Wen et al., 2019).

Several studies have considered the use and manipulation of mycorrhizas to improve P-uptake capacity (Deguchi et al., 2012; Schneider et al., 2019; Rahou et al., 2021) and root exudates to improve P-uptake efficiency in crop species as a strategy to ensure global food security (Haijar and Hodgkin 2007; Devempewolf, 2017; Preece and Penuelas, 2020; Verma and Verma, 2021). Further research is required to fully understand the roles of mycorrhizas and root exudates in P uptake (Raven et al., 2018; Wang and Lambers, 2020; Albornoz et al., 2021; Honvault et al., 2021).

Plant strategies for nitrogen uptake

The role of mycorrhizas in N uptake is thought to be less determinant than that in P uptake, because N is more mobile and, therefore, the availability of N is frequently much greater (Jung and Tamai, 2012; Wang et al., 2018). Thus, studies of effects of mycorrhizas on N uptake tend to be restricted to N-limited soils, including young soils, such as in central- north Europe and North America (Lambers et al., 2008; Makarov, 2019). While plant N uptake increases with AM fungi (Jentschke et al., 2001; Labidi et al., 2011; Mardukhi et al., 2011; Zhu et al., 2016; Verzeaux et al., 2017; Sales et al., 2018) and N is absorbed mainly as NH4+ (Lopez-Pedrosa et al., 2006), it may be more related to the absorption of inorganic N or organic forms released by the hydrolytic action of saprotrophic microorganisms, rather than to the direct release by AM fungi of hydrolytic enzymes (Makarov, 2019). In boreal regions, where plant growth is limited by N, rather than P, EM fungi mobilize polymeric N compounds and acquire amino acids (Plassard et al., 2002; Smith and Read, 2008). ERM and EM fungi release hydrolytic enzymes that hydrolyze soil organic N, releasing NH4+ and amino acids that are then taken up directly by roots or in sites where the fine roots are covered by the fungal sheath/mantle the nutrient uptake and transfer to the plant are mediated by fungal hyphae and transfer via the Hartig net (Makarov, 2019). In contrast, some studies have reported that AM fungi decrease plant N acquisition (Wang et al., 2018). Thus, despite there being fewer studies on N than on P (Smith and Smith, 2011), current understanding of effects of mycorrhizas on N uptake allows for the statement of some general concepts (Makarov, 2019). Rapid NH4+ transfer occurs around arbuscular branches by recruiting NH4+ in the acidic periarbuscular space and releasing the uncharged NH_3 into the cytoplasm of the arbusculated cells (Guether et al., 2009; Kobae et al., 2010; Koegel et al., 2013). Some of the plant NRT (nitrate transporters) are induced by the presence of the fungus in both AM- and ECM-colonized roots (Guether et al., 2009; Hildebrandt et al., 2002; Willmann et al., 2014), but also induced in response to high-phosphate or low-nitrate concentrations (Willmann et al., 2014; Hohnjec et al., 2005). This complex gene expression modulation suggests a mechanism of NO_3 acquisition depending on the plant and fungal nutritional status as well as competition with other nutrients that are taken up with other nutrients.

Plant roots exude metabolites that enhance N mobilization, allowing plant uptake of N from the rhizosphere (Li et al., 2021; Tawaraya et al., 2018). Several studies have shown that root exudates are positively associated with mobilization and plant uptake of N (Li et al., 2021; Coskun et al., 2017). Moreover, exudate composition varies among plants, in response to P or N demand even in the same plant species (Tawaraya et al., 2018). Under N-limiting conditions, root exudates released by legumes enhance plant associations with N_2-fixing bacteria (Coskun et al., 2017; Chai and Schachman, 2021) and flavonoids in exudates may stimulate or inhibit expression of rhizobial nodulation genes, affecting chemoattraction of rhizobia to the root (Li et al., 2016). Positive impacts of root exudates on mobilization and plant uptake of N have been attributed, at least in part, to direct effects of exudates on the soil microbial community (Li et al., 2021; Mastny et al., 2021). Root exudates can inhibit the rates of soil nitrification and other microbially-based N transformations (Sun et al., 2016; Coskun et al., 2017). Root exudates may increase N availability and plant uptake in the rhizosphere through mobilization of organic N and N-monomers bound to mineral surfaces (Jilling et al., 2018), and also through the release of proteases catalyzing protein mineralization and thus generating more sources of N for plant uptake (Paungfoo-Lonhienne et al., 2008; Kohli et al., 2012). Certainly, all these rhizosphere bacteria possess the metabolic machinery to hydrolyze and mineralize organic forms of N, P, and S. The contents of these microbial cells are subsequently released, either through cell lysis, or following protozoic predation (Bonkowski, 2004; Richardson et al., 2009). This liberates inorganic N, P, and S forms into the soil, including ammonium, nitrate, organic-N, phosphate, and sulfate that are the preferred nutrient forms for plants (van der Heijden et al., 2008; Jacoby et al., 2017).

Uncertainty of mycorrhizal effects on plant metal nutrient uptake: an incomplete puzzle

Experimental studies have demonstrated greater soil mobilization and plant content of Ca, K, Mg, and Fe when plants are associated with EM fungi (Finlay, 1995; Jentschke et al., 2001; Ahonen-Jonnarth et al., 2003; Jourand et al., 2014; Artega-Leon et al., 2018; Jarosz et al., 2021) and AM (Caris et al., 1998; Mardukhi et al., 2011; Balsam et al., 2013; Chorianopolou et al., 2015; Zhang et al., 2015; Prity et al., 2020; Jarosz et al., 2021); however, the underlying mechanisms of these positive effects remain to be resolved.

While it has long been known that K is essential for plant function and yield, and AM and EM fungi have been shown to improve its uptake in plants (Pallon et al., 2007; Smith and Read, 2008; Garcia and Zimmermann, 2014; Dominguez-Nunez et al., 2016), the contribution of mycorrhization to plant K nutrition is not well understood and scarcely studied (Garcia and Zimmermann, 2014). AM lead to the over-expression of several K- (Benedito et al., 2010; Liu et al., 2019) and Fe-transporter genes (Kabir et al., 2020). Similarly, EM also increase plant K+ transporters and channels (Benito and Gonzalez- Guerrero, 2014; Garcia et al., 2014; Guerrero-Galan et al., 2018a,b,c; Frank and Garcia, 2021). Strong associations between mycorrhizal P and K uptake have been observed in both AM (Olsson et al., 2011) and EM symbioses (Jung and Tamai, 2013; Garcia et al., 2014). The EMfungus *Pisolithus microcarpus* colonizing *Eucalyptus globulus* seedling was able to mobilize K from clay minerals using EM exudates (Yuan et al., 2004; Dominguez- Nunez et al., 2016). Plant uptake of Mg was positively associated with AM colonization (Giri and Mukerji, 2004; Chen et al., 2017; Zare-Maivan et al., 2017), including in Mg- limited soils (Zhang et al., 2015; Xiao et al., 2014). However, the increase in nutrient uptake as a result of AM colonization may depend on the specific nutrient investigated. Zare-Maivan et al. (2017) observed that mycorrhizal colonization increased Mg uptake but decreased K uptake of maize plants colonized by *Glomus* sp. While the presence of EM fungi reduced root K and Mg concentrations (Zhang and George, 2010), it enhanced K and Mg uptake in *Pinus sylvestris* (Christophe et al., 2010), and increased tree Mg concentrations, although the exact mechanisms were not studied (Artega-Leon et al., 2018). In this regard, Rosenstock et al. (2016) observed that ectomycorrhizal communities may respond to increased host-tree P demand by increased mobilization of P-containing minerals, but also observed that this response to nutrient demand does not appear to exist for K or Mg limitation. Empirical studies have shown that Ca is important in the formation, maintenance, and function of AM fungi (Jarstfer et al., 1998; Navazio and Mariani, 2008; Kosuta et al., 2008; Liu et al., 2013; Khabou et al., 2014; Piao et al., 2016) including being involved in AM fungal signaling pathways to facilitate fungal penetration of root tissues (Chabaud et al., 2011). Presence of EM fungi improves availability of metal elements, as indicated by greater Ca uptake in temperate forests, in which there is strong leaching of Ca from silicate minerals, due to its release from apatite (Blum et al., 2002; Pyrlo et al., 2013), and AM also increase K and Ca uptake due to the greater volume of soil explored (Ruan et al., 2013; Flores et al., 2019). Although studies of effects of mycorrhization on plant Fe uptake are limited, mobilization of Fe and Si are positively correlated with hyphal length (van Hees et al., 2004) and mycorrhization is positively associated with plant Fe concentrations (Ibiang, et al., 2017), indicating that mycorrhizas enhance plant Fe uptake. AM-mediated plant Fe uptake is mostly based on enhancing the availability of Fe, rather than on up-regulation of Fe transporters in *Medicago sativa* under low-Fe conditions (Awad et al., 1994; Rahman et al., 2020). EM-mediated plant Fe uptake has been linked to the release of siderophores and/or organic acids EM (Rineau and Garbaye, 2010). While there is evidence for mobilization of K, Ca, Mg, and Fe, in addition to P, from minerals of widespread types of soil parent material, such as basalt, rhyolite, granite, schist by AM fungi (Burghelea et al., 2015) and from perlite by EM fungi (Hobbie et al., 2009), a clear understanding of the variation and key underlying mechanisms among plant taxa and types of mycorrhizas is lacking. For example, leaching of K and Mg meditated by EM fungi has been reported for a range of minerals, whereas mobilization mediated by fungi varies with type of mineral and species of fungus (Van Scholl et al., 2006a). Uptake of nutrients varies with species of mycorrhizal fungus (Seven and Polle, 2014; Chen et al., 2018). Some studies have shown that the same plant species colonized by different species mixtures of EM fungi have a distinct capacity for plant uptake of different nutrients such as N (Sousa et al., 2010) or K (Yuan et al., 2004; Frank and Garcia, 2021). Thus, future studies are required to test effects and drivers of mycorrhizal fungal species on K, Ca, Mg and K plant uptake.

Do root exudates contribute to uptake of metal nutrients?

Despite some initial studies reporting negative correlations between the amount of root exudates and uptake of K, Ca, Mg, and Fe (Jones et al., 1994; Matsiu, 1997), more recent studies have reported that root exudates enhance plant uptake of K (Wang et al., 2011; Ruan et al., 2013), Ca (Ohta and Hiura, 2016), Mg (Ohta and Hiura, 2016), and Fe (Marastoni et al., 2020; Chai and Schachtman, 2021). Supply of K and Ca is positively associated with plant root length and density and with exudation of organic acids (Lijun et al., 2011; Xu et al., 2021). Indeed, releases of root exudates mobilize K in the rhizosphere, leading to subsequent increases in plant K uptake (Xu et al., 2021; Li et al., 2020; Yang et al., 2020), likely due to carboxylates in exudates that are positively correlated with K uptake across a range of plant species (Suriyagoda et al., 2012). This release of root exudates that mobilize K which depends on soil K availability (Li et al., 2020; Yang et al., 2020), varies with genotype within a species, such as observed in *Camelia sinensis* and *Nicotiana tabacum* (Li et al., 2020; Yang et al., 2019), with K-stress- tolerant genotypes releasing greater amounts of organic acids in root exudates (Yang et al., 2020). Metabolomic studies have revealed that greater amounts of organic acids in root exudates improves plant uptake of water and nutrients (Xu et al., 2021), consistent with the role of K in plant adaptations to drought stress (Sardans and Penuelas, 2015; 2021).

Despite the key roles of Ca and Mg in plant nutrition, there are only very few studies on the role of root exudates on the mobilization and availability of Ca and Mg in the rhizosphere. These studies report a positive effect of root exudates on soil Ca and Mg availability (Tauson and Arocena, 2009; Ohta and Hiura, 2016). Higher oxalate concentrations are associated with greater soil Mg availability and root Mg uptake in *Pinus sylvestris* (van Scholl et al., 2006b). The presence of Ca and Mg in the rhizosphere can promote the alleviation of Al toxicity by promoting the exudation of organic acids such as citric and malic (Silva et al., 2001; Ma et al., 2014; Kochian et al., 2015). Moreover, Mg enhances the citrate concentration at the root tip and stimulates citrate secretion by roots. An increased Al tolerance in the presence of low Mg levels could, thus, result from detoxification of Al in the rhizosphere through formation of non-toxic Al-citrate complexes (Silva et al., 2001). Khorassani et al. (2011) observed that root exudates of *Beta vulgaris* contain abundant salicylic and citramalic acid that bind with Ca and thus reduce the formation of insoluble complexes of Ca with P. In contrast, they readily desorb P from Fe and Al oxides and hydroxides (Bhadoria et al., 2002). Moreoves, have been shown that root exudates are not able to increase rhizosphere P availability to mobilize P from calcium phjosphates (Bhadoria et al., 2002).

Root exudates mobilize Fe, due to ligand exchange and chelation and the release of Fe^3+-reducing compounds (Marastoni et al., 2020). Fe-binding phenolic compounds are released in root exudates (Aggarwal et al., 1998). Phenolic compounds in microbial siderophores are also involved in the mobilization and plant uptake of Fe in the rhizosphere (Nuzzo et al., 2018). In addition, grasses secrete phytosiderophores that act as strong chelators of Fe^3+, triggering the mobilization of Fe (Kobeyashi and Nishizawa, 2012; Chen et al., 2017c) as well as P (Zhou et al., 2022). Vempati et al. (1995) observed that *Glycine max* root exudates reduce Fe^3+ in soil to Fe^2+, thus increasing Fe availability in the rhizosphere; this reduction was likely caused by phenolics in root exudates which were oxidized to diquinones. This role of exudates in Fe uptake is particularly important in calcareous soils, where Fe deficiency is due to Fe precipitation with carbonates (Rahman et al., 2008). Secondary metabolites, such as coumarins (Rajniak et al., 2018; Rosenkranz et al., 2021; Sarashgi et al., 2021) and diverse structurally diverse redox- active molecules (Rajniak et al., 2018) in plant root exudates have been linked to greater rhizosphere Fe availability. Conversely, greater exudate concentrations of dehydroascorbic acid, galactonic acid, sucrose, and thymidine (Valentinuzzi et al., 2015) have been linked to Fe deficiency. The role of riboflavin in exudates in Fe uptake varies, including the facilitation of reductase activity and dissolution of Fe(III), which has low solubility, and modification of the rhizosphere microbiome (Chen et al., 2017c).

Increases in root exudates linked to Ca and/or Fe deficiency solubilize metals and increase uptake of toxic metals, such as cadmium (He et al., 2017). Finally, the composition of root exudates can vary in the same plant species depending on the most limiting nutrient (Astolfi et al., 2020; Dietz et al., 2020). For example, *Zea mays* root exudates contain higher concentrations of glutamate, glucose, ribitol, and citrate under Fe-deficient conditions, higher concentrations of y-aminobutyric acid and carbohydrates under P-limited conditions, lower concentrations of sugar alcohols and sugars, particularly glycerol, ribitol, fructose, and maltose under K-limited conditions, and lower concentrations of amino acids under N deficiency (Carvalhais et al., 2011) (Figure 2).

One key aspect to consider is the impact that increasing incidences of drought may have on root exudates. Under increasingly severe drought, root organic C increases concurrently with declining predawn leaf water potential and photosynthesis, and root exudate composition mirrors the physiological gradient of drought severity (Ulrich et al., 2022). Despite reducing C uptake, plants may increase release of C in root exudates with increasing drought severity (Ulrich et al., 2022). In a metabolomic study Gargallo-Garriga et al. (2018) observed that root exudates of *Quercus ilex* seedlings under drought consisted mainly of secondary metabolites (71% of total metabolites) associated with plant responses to drought stress. Conversely, the metabolite composition under recovery shifted towards a dominance of primary metabolites (81% of total metabolites). These results indicate that roots exude a wide range of root metabolites. The maintenance of root exudates under drought has also been related to a fast re- initiation of soil microbial activity after rewetting, allowing fast nutrient mobilization and uptake that should favor plant recovery (Karlowsky et al., 2018). However, when drought is intense, a threshold is reached and plant exudate production recovery cannot be achieved (Gargallo-Garriga et al., 2018) reducing the nutrient-uptake capacity.

Conclusions and future directions

While some effects of mycorrhizas and exudates on nutrient uptake are common across plant taxa, such as the universal presence of carboxylates in root exudates, the type and structure of mycorrhizal associations and composition of exudates vary with species and level and type of nutrient limitation. Correlations between root exudates and mycorrhization in enhanced P uptake are consistent in the literature, while contemporary studies continue to identify and disentangle those involved in N uptake, N-use efficiency, and soil N cycling. Root exudates contribute to increased nutrient uptake through reduction, chelation, and solubilization of nutrients in soil which facilitate their mobilization and availability. The effects of root exudates may also involve impacts on the rhizosphere microbiome. In summary, the studies of N and P absorption by plants, taken together, strongly suggest that nonmycorrhizal plants have evolved the release of exudates more than mycorrhizal plants, so further research is warranted to confirm it.

In general, specific root exudates tend to enhance mycorrhization, although there is some evidence for inhibition of other exudates, and little is known about the mechanisms underlying mycorrhizal mediation of root exudate release. Crop cultivation is managed to address the effects of limited availability of N and P, but less so for the effects of other soil nutrients, such as the metals K, Ca, Mg and Fe that may become increasingly limiting under global change. The roles of mycorrhizas and plant exudates on N and P uptake have been studied intensively; however, understanding the effects on metal nutrients is less clear and more inconsistent. A key area for future research, in the context of managing food security and human health, should thus be the study of these effects, and associated underlying mechanisms, of root exudates and mycorrhization on the uptake and balance of K and important other metal nutrients, such as Ca, Mg, and Fe, in cultivated soils for food crops. For example, it may be possible to improve mycorrhization of crop plants through breeding, as has been achieved for P- absorption capacity, to reduce the use of nutrients/fertilizers.

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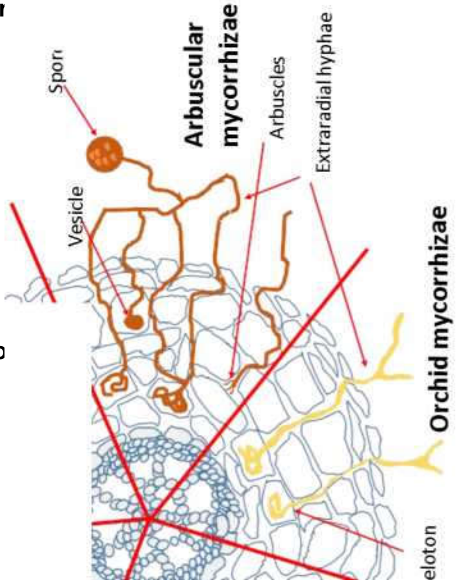
Figure captions

Figure 1. Structure, form and type of anatomical structures of different types of mycorrhizal Associations.

Figure 2. Root exudate function. Root exudates comprise several compounds that change the physico-chemical properties of soil close to the fine roots (rhizosphere) favoring several chemical processes able to mobilize nutrients from minerals and make possible its water transport to roots and uptake. These exudates also contribute to maintain heterotrophic microbes that also contribute with their activities to mobilize nutrients.

Ectendomycorr

Extraradial hyphae



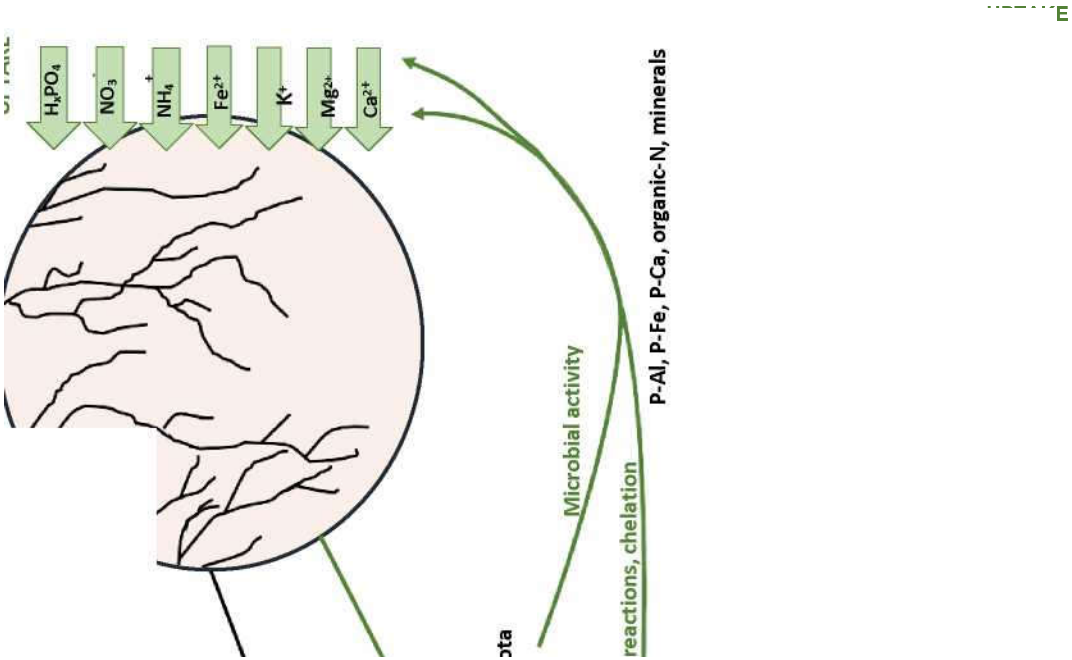
Ericoid myco

Arbuscular mycorrhizae

Arbuscles

Extraradial hyphae

Figure 1



Sugar

Sugar alcohols

Carboxylates

Phenolics

Enzymes (phosphatases,

P-Al, P-Fe, P-Ca, organic-N, minerals

proteases,

Figure 2