

## FOCUSED REVIEW

# 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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## SUMMARY

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. Although 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 because of the low availability of other soil nutrients such as the metals potassium (K), calcium (Ca), magnesium (Mg), and iron (Fe), which 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 the 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<sub>2</sub>) and other greenhouse gases; elevated CO<sub>2</sub> 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 (Peñuelas, Janssens, et al., 2020). 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 (Paseka et al., 2019; Peñuelas et al., 2013; Peñuelas, Fernández-Martínez, et al., 2020). 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<sub>2</sub> concentrations, and atmospheric N deposition (Brouder & Volenec, 2008; Elbassiouny et al., 2022). For example, the impacts of some global change drivers such as acid rain, N deposition, drought, and species invasion on soil pH (Ouyang et al., 2022; Tipping et al., 2003; Wei et al., 2020; Zia et al., 2020) enhance soil mineral leaching and thus soil nutrient mobilization (Cui et al., 2019; Wei et al., 2020), with different effects on specific nutrients (Cui et al., 2019; Sharpley, 1991). 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 (Nicholson et al., 2021; Paseka et al., 2019; Peñuelas, Fernández-Martínez, et al., 2020).

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. Although 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.

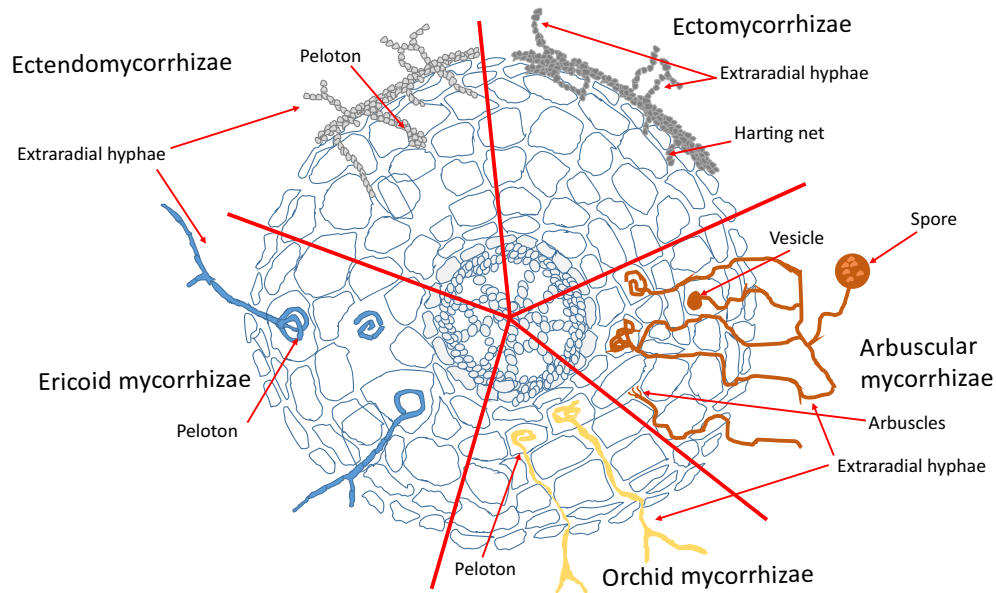
## METHODOLOGY

We have reviewed 'Web of Science', 'Google Scholar', and 'Scopus' using combinations of keywords, such as 'root & exudate & nitrogen', 'root & exudate & phosphorus', 'root & exudate & calcium', 'root & exudate & magnesium', 'root & exudate & potassium', 'root & exudate & mycorrhiza', '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', and 'root & ectomycorrhizas & 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 (Chiu & Paszkowski, 2019; Smith & Read, 2008). 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, which extends into the root, penetrating between the epidermis and cortex of ectomycorrhizal plants, but they do not penetrate the root cell plasma membrane, whereas arbuscular mycorrhizal fungi (AMF) penetrate the cell wall but not the plasma membrane/cytosol (Peay et al., 2015; Smith & Read, 2008) (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 (Doity 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; Hou 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 (Albornoz et al., 2021; Smith & Read, 2008). 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 approximately 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<sub>4</sub><sup>+</sup>) (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, although 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



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

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 energized by  $H^+$ -ATPases (Krajinski et al., 2014; Walder et al., 2015; Wang, Li, et al., 2014; Wang, Yu, et al., 2014). 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 (Ai et al., 2009; Chiou et al., 2001). The mycorrhiza-specific Pi transporters all belong to the family of *Pht1* transporters, but cluster in two different subgroups, named subfamilies I and III, respectively (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 (Glassop et al., 2005; Güimil et al., 2005; Karandashov et al., 2004; Maeda et al., 2006; Nagy et al., 2005; Nagy et al., 2006; Paszkowski et al., 2002; Rausch et al., 2001; Tamura et al., 2012). 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 (Javot et al., 2007; Maeda et al., 2006; Yang et al., 2012).

In ectomycorrhizal (EM) 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 that the 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 is 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, Li, et al., 2014; Wang, Yu, 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 non-photosynthetic host tissues, the fungus is assumed 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 non-photosynthetic orchid host (Cameron et al., 2006; Dearnaley & Cameron, 2016). Ericaceous plants rely on ericoid mycorrhizal (ERM) fungi for nutrient acquisition (Leopold et al., 2021; Vohnik, 2020) (Figure 1), particularly for uptake of P (Leopold et al., 2021; Mitchell & Gibson, 2006) and N (Mitchell & 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 not only present many of the same characteristics as 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. Cavendishoid 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, such as the described association between the ascomycete *Leotia lubrica* and the Ericaceae species *Comarostaphylis arbutoides* (Kühndorf et al., 2015). Monotropoid ectendomycorrhizas occur in species of *Monotropa*, non-chlorophyllous plants growing under forest trees, such as *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 (El Maaloum et al., 2020; Minaxi et al., 2013; Ordoñez et al., 2016). 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 solubilization/desorption of P from Fe oxides and hydroxides and Ca salts using exuded organic acids (Browne et al., 2009; El Maaloum et al., 2020; Marschner et al., 2001; Ordoñez et al., 2016; Rodriguez & Fraga, 1999; Toljander et al., 2007). 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, Hoffland, et al., 2017; Wang, Shi, et al., 2017). Phosphatase release has been commonly observed in AM and EM (Araujo Costa et al., 2016; Hirano et al., 2022; Joner & Johanson, 2000; Meeds et al., 2021; Qi et al., 2022).

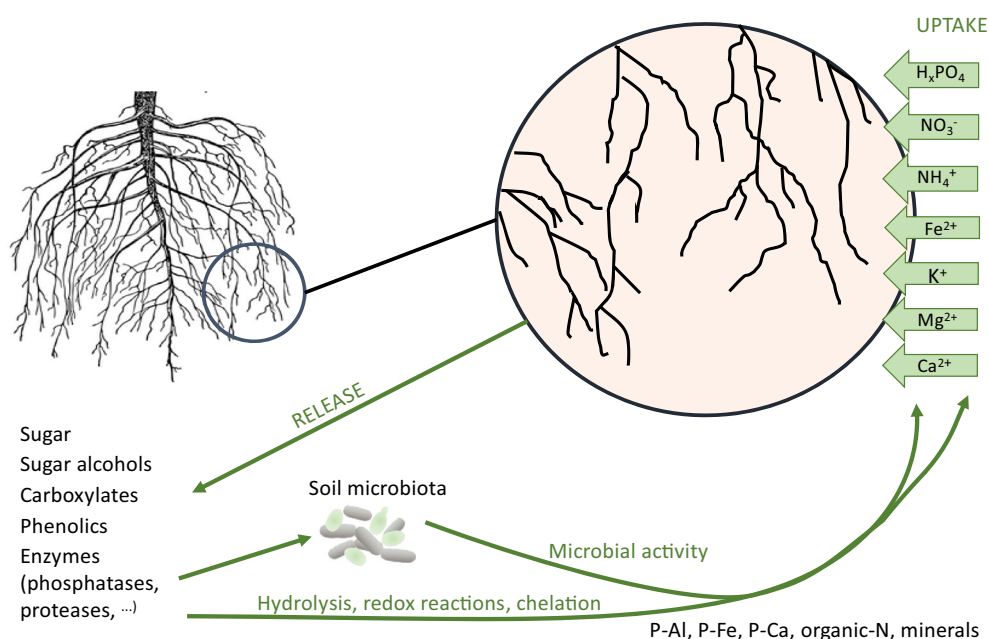
There is growing knowledge of the effects of root exudates on the availability of soil P for use by plants. Exudates comprise a range of substances, including carboxylates, sugars, mucilage, protons, water, phenolics, amino acids, and enzymes, such as phosphatases and phytases (Lambers et al., 2006; Tarafdar & Claassen, 2005). The direct exudation of acid phosphatase has been observed in several species (Aslam et al., 2022; Playsted et al., 2006). 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, which 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 by the 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 & 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). The 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., 2017), whereas 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 non-mycorrhizal 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 (Shen et al., 2001; Subbarao et al., 1997), such as in calcareous (Hinsinger, 2001; Vance et al., 2003; Zohlen &

Tyler, 2004) and siliceous soils (Dakora & 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, such as cluster roots, dauciform roots or capillaroid roots (Lambers, 2022), and are 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 (Güsewell, 2016) and increase P availability through the release of carboxylates and phosphatases (Güsewell, 2016; Playsted et al., 2006; Shane et al., 2006). However, Güsewell 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 compared to non-cluster 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 & Lambers, 2005).

There is evidence that root exudates from non-mycorrhizal plants inhibit mycorrhization in mycorrhizal plant species, through the release of allelopathic compounds, especially in nutrient-rich habitats (Lambers & Teste, 2013). This suggests that non-mycorrhizal species may have developed a greater capacity to release exudates than mycorrhizal species; this possibility warrants future research. Species-level comparisons of 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 rhizosphere (Wen et al., 2019).

Several studies have considered the use and manipulation of mycorrhizas to improve P-uptake capacity (Deguchi et al., 2012; Rahou et al., 2021; Schneider et al., 2019) and root exudates to improve P-uptake efficiency in crop



**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 that mobilize nutrients from minerals and enable its water transport to roots and uptake. These exudates also contribute to maintaining heterotrophic microbes that in turn contribute to mobilizing nutrients.

species as a strategy to ensure global food security (Hajjar & Hodgkin, 2007; Preece & Peñuelas, 2020; Verma & Verma, 2021). Further research is required to fully understand the roles of mycorrhizas and root exudates in P uptake (Albornoz et al., 2021; Honvault et al., 2021; Raven et al., 2018; Wang & Lambers, 2020).

### PLANT STRATEGIES FOR NITROGEN UPTAKE

The role of mycorrhizas in N uptake is assumed 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 & Tamai, 2012; Wang et al., 2018). Thus, studies of the 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). Although plant N uptake increases with AM fungi (Jentschke et al., 2001; Labidi et al., 2012; Mardukhi et al., 2011; Sales et al., 2018; Verzeaux et al., 2017; Zhu et al., 2016) and N is absorbed mainly as  $\text{NH}_4^+$  (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 & Read, 2008). ERM and EM fungi release hydrolytic enzymes that hydrolyze soil organic N, releasing  $\text{NH}_4^+$  and amino acids, which 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). By 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 & Smith, 2011), current understanding of the effects of mycorrhizas on N uptake allows for the statement of some general concepts (Makarov, 2019). Rapid  $\text{NH}_4^+$  transfer occurs around arbuscular branches by recruiting  $\text{NH}_4^+$  in the acidic periarbuscular space and releasing the uncharged  $\text{NH}_3$  into the cytoplasm of the arbusculated cells (Guether et al., 2009; Kobae et al., 2010; Koegel et al., 2013). Some of the plant NRT (i.e. nitrate transporters) are induced not only by the presence of the fungus in both AM- and EM-colonized roots (Guether et al., 2009; Hildebrandt et al., 2002; Willmann et al., 2014), but also in response to high-phosphate or low-nitrate concentrations (Hohnjec et al., 2005; Willmann et al., 2014). This complex gene expression modulation suggests a mechanism of  $\text{NO}_3$  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 (Coskun et al., 2017; Li et al., 2021). 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  $\text{N}_2$ -fixing bacteria (Chai & Schachtman, 2021; Coskun et al., 2017) 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 (Coskun et al., 2017; Sun et al., 2016). 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, thus generating more sources of N for plant uptake (Kohli et al., 2012; Paungfoo-Lonhienne et al., 2008). 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, which are the preferred nutrient forms for plants (Jacoby et al., 2017; van der Heijden et al., 2008).

### 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 (Ahonen-Jonnarth et al., 2003; Artega-Leon et al., 2018; Finlay, 1995; Jarosz et al., 2021; Jentschke et al., 2001; Jourand et al., 2014) and AM (Balsam et al., 2013; Caris et al., 1998; Chorianopoulou et al., 2015; Jarosz et al., 2021; Mardukhi et al., 2011; Prity et al., 2020; Zhang et al., 2015); however, the underlying mechanisms of these positive effects remain to be resolved.

Although 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 (Dominguez-Nuñez et al., 2016; Garcia & Zimmermann, 2014; Pallon et al., 2007; Smith & Read, 2008), the contribution of mycorrhization to plant K nutrition is not well understood

and scarcely studied (Garcia & 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<sup>+</sup> transporters and channels (Benito & González-Guerrero, 2014; Corrátege et al., 2007; Frank & Garcia, 2021; Garcia et al., 2014; Guerrero-Galán, Delteil, et al., 2018; Guerrero-Galán, Garcia, et al., 2018; Guerrero-Galán, Houdinert, et al., 2018). Strong associations between mycorrhizal P and K uptake have been observed in both AM (Olsson et al., 2011) and EM symbioses (Garcia et al., 2014; Jung & Tamai, 2013). The EM fungus *Pisolithus microcarpus* colonizing *Eucalyptus globulus* seedling was able to mobilize K from clay minerals using EM exudates (Dominguez-Nuñez et al., 2016; Yuan et al., 2004). Plant uptake of Mg was positively associated with AM colonization (Chen, Koide, et al., 2017; Chen, Li, et al., 2017; Giri & Mukerji, 2004; Zare-Maivan et al., 2017), including in Mg-limited soils (Xiao et al., 2014; Zhang et al., 2015). 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. Although the presence of EM fungi reduced root K and Mg concentrations (Zhang & George, 2010), it enhanced K and Mg uptake in *Pinus sylvestris* (Christophe et al., 2010), and also increased tree Mg concentrations, although the exact mechanisms were not studied (Arteaga-Leon et al., 2018). In this regard, Rosenstock et al. (2016) observed not only that ectomycorrhizal communities may respond to increased host-tree P demand by increased mobilization of P-containing minerals, but also 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; Khabou et al., 2014; Kosuta et al., 2008; Liu, et al., 2013b; Navazio & Mariani, 2008; Piao et al., 2016) including being involved in AM fungal signaling pathways to facilitate fungal penetration of root tissues (Chabaud et al., 2011). The 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 as a result of its release from apatite (Blum et al., 2002; Pylro et al., 2013), and AM also increase K and Ca uptake as a result of the greater volume of soil explored (Ruan et al., 2013). Although studies of the effects of mycorrhization on plant Fe uptake are limited, mobilization of Fe and Si is 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 & Garbaye, 2010). Although 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, and schist by AM fungi (Burghelea et al., 2015), as well as 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 mediated 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, Smits, & Hoffland, 2006). Uptake of nutrients varies with species of mycorrhizal fungus (Seven & Polle, 2014). 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 (Souza et al., 2010) or K (Frank & Garcia, 2021; Yuan et al., 2004). 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; Yu & Matsiu, 1997), more recent studies have reported that root exudates enhance plant uptake of K (Benito et al., 2011; Ruan et al., 2013; Wang et al., 2011), Ca (Ohta & Hiura, 2016), Mg (Ohta & Hiura, 2016), and Fe (Chai & Schachtman, 2021; Marastoni et al., 2020). 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., 2021a,b). Indeed, release of root exudates mobilizes K in the rhizosphere, leading to subsequent increases in plant K uptake (Li et al., 2020; Xu et al., 2021a,b; Yang et al., 2020), likely as a result of 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 improve plant uptake of water and nutrients (Xu et al., 2021a,b), which is consistent with the role of K in plant adaptations to drought stress (Sardans & Peñuelas, 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 (Ohta & Hiura, 2016; Tauson & Arocena, 2009). Higher oxalate concentrations are associated with greater soil Mg availability and root Mg uptake in *P. sylvestris* (Van Scholl, Hoffand, & van Breemen, 2006). 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 acid (Kochian et al., 2015; Ma et al., 2014; Silva et al., 2001). 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. By contrast, they readily desorb P from Fe and Al oxides and hydroxides (Bhadoria et al., 2002). Moreover, root exudates are not able to increase rhizosphere P availability to mobilize P from calcium phosphates (Bhadoria et al., 2002).

Root exudates mobilize Fe as a result of ligand exchange and chelation and the release of Fe<sup>3+</sup>-reducing compounds (Marastoni et al., 2020). Fe-binding phenolic compounds are released in root exudates (Aggrawal et al., 1999). 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<sup>3+</sup>, triggering the mobilization of Fe (Chen, Wang, & Yeh, 2017; Kobayashi & Nishizawa, 2012), as well as P (Zhou et al., 2022). Vempati et al. (1995) observed that *Glycine max* root exudates reduce Fe<sup>3+</sup> in soil to Fe<sup>2+</sup>, 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 a result of Fe precipitation with carbonates (Awad et al., 1998). Secondary metabolites such as coumarins (Awad et al., 1998; 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, Wang, & Yeh, 2017). 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  $\gamma$ -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 (Carvalho 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 pre-dawn 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 reinitiation 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

Although 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, whereas 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 that 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 non-mycorrhizal plants have evolved to enable a greater release of exudates compared to mycorrhizal plants, such that further research is warranted to confirm this.

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, our understanding of 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, is the investigation of the effects of root exudates and mycorrhization, as well as the associated underlying mechanisms, 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, aiming to reduce the use of nutrients/fertilizers.

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## AUTHOR CONTRIBUTIONS

JS write the first draft of the manuscript, CP, HL, AFA and JP checked, improved, corrected and enriched the references in all the 5 posterior drafts.

## CONFLICT OF INTEREST

All the coauthors declare no conflict of interest.

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