Plant Soil
https://doi.org/10.1007/s11104-021-04957-2

REGULAR ARTICLE

Arbuscular mycorrhizae increase biomass and nutrient uptake of tomato fertilized with struvite compared to monoammonium phosphate

Isako Di Tomassi · Neha Chatterjee · Felipe H. Barrios-Masias · Qiuhong Zhou · Chunhao Gu · Andrew J. Margenot

Received: 11 December 2020 / Accepted: 11 April 2021

Abstract
Purpose Struvite is a wastewater-derived P mineral that offers a means to redirect wastestream P flows to agroecosystems. The low water solubility of struvite (< 3%) has been reported to limit early-season crop P uptake. Arbuscular mycorrhizae (AM) could enhance dissolution of struvite and thereby increase crop utilization of struvite-P. We tested the hypothesis that AM would increase struvite dissolution and thereby enhance plant P uptake and biomass in a P-deficient soil.
Methods We employed a tomato (*Solanum lycopersicum* L.) genotype model with a wild-type mycorrhizal tomato (MYC) and a reduced mycorrhizal mutant (*rmc*). Monoammonium phosphate (MAP) was used as a highly water soluble P fertilizer for comparison with struvite.
Results Struvite granules underwent 4-fold less dissolution (% mass remaining) than MAP granules, and apparent struvite dissolution was similar under MYC and *rmc*. However, scanning electron microscopy revealed qualitative differences in surface morphology of residual struvite between MYC and *rmc*. Under struvite fertilization, biomass of MYC was 22% greater than *rmc,* and P and N shoot uptake (mg plant^{-1}) were 32% and 34% greater than *rmc*. Shoot biomass was 24% greater for MYC fertilized with struvite than with MAP, and shoot P and N uptake were 26% and 34% greater, respectively.
Conclusion Increased N and P uptake by AM-associated tomato plants fertilized with struvite suggests AM as a strategy to surmount solubility constraints to the use of struvite as a fertilizer.

Keywords *Solanum lycopersicum* L · Magnesium ammonium phosphate · Monoammonium phosphate · Mycorrhizal fungi · Phosphorus

Responsible Editor: Peter Christie.

I. Di Tomassi
Community College of Philadelphia, Philadelphia, PA 19141, USA

N. Chatterjee · C. Gu · A. J. Margenot (✉)
Department of Crop Sciences, University of Illinois Urbana-Champaign, Urbana, IL 61801, USA
e-mail: margenot@illinois.edu

F. H. Barrios-Masias
Department of Agriculture, Veterinary and Rangeland Sciences, University of Nevada, Reno, NV 89557, USA

Q. Zhou
Changjiang Institute of Survey, Planning, Design and Research, Wuhan 430074, Republic of China

C. Gu
Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19716, USA

Published online: 22 April 2021

Introduction

Phosphorus (P) application is essential for agricultural production, yet current strategies to supply P to meet crop needs entail agronomic inefficiencies that encumber high environmental costs. The high water solubility of acidulated P fertilizers such as ammonium phosphates or superphosphates results in high crop availability but also P loss risk (Sharpley et al. 1996) and fixation by soil minerals (Roy et al. 2016). Additionally, the cost of acidulated P fertilizers manufactured from mined phosphate rock is projected to increase and is vulnerable to market volatility (Ulrich and Frossard 2014; Vaccari and Strigul 2011). In contrast, struvite ($NH_4MgPO_4{\cdot}6H_2O$) is a low water solubility (<3%) P mineral recovered from wastestreams with potential as a fertilizer (Talboys et al. 2016). Struvite generated from P-rich wastestreams offers recircularization of P otherwise lost in the largely linear human trophic chain (Margenot et al. 2019; Trimmer and Guest 2018) and its low water solubility may decrease dissolved reactive P loss risk from soils following fertilization (Hertzberger et al. 2020). However, the low water solubility of struvite can also limit its ability to meet early crop P demand and thus constrain growth (Talboys et al. 2016). Though soil acidity can facilitate struvite dissolution abiotically, the magnitude of soil pH-driven dissolution appears limited (Hertzberger et al. 2020) and is not applicable in alkaline soils. To facilitate agricultural use of struvite as a P fertilizer, strategies relying on biological solubilization developed for other P minerals with low water solubility (e.g., apatite or phosphate rock) may offer improved struvite-P crop availability across diverse soil contexts.

Arbuscular mycorrhizae (AM) have been proposed as a means to enhance host plant P uptake from low solubility P forms (Bolan 1991). Facilitating greater host plant uptake of P is one of the most well characterized and common benefits of AM (Ruzicka et al. 2012; Smith et al. 2011). Arbuscular mycorrhizae can enhance host plant uptake of inorganic P from soil by (i) exploring a greater volume of soil and thus accessing more distal P resources than the plant root system alone, and (ii) enhancing dissolution of low solubility P, presumably through hyphal exudation of organic acids or depressing the pH of the mycosphere (Bolan 1991). Though soil exploration and hyphal interception of soil P is a well-established mechanism by which AM can facilitate greater host plant P uptake (George et al. 1995; Smith et al. 2011), less understood is the contribution of AM to dissolution of low solubility P forms (Plassard and Dell 2010). Depending on crop species, AM species, and/or phosphate rock quality, AM have been found to increase crop uptake of P from phosphate rock (e.g., Ramirez et al. 2009), which is generally less water soluble (< 1%) than struvite (Chien 1977). Arbuscular mycorrhizae exudates have been implicated in enhanced phosphate rock dissolution by AM (Tawaraya et al. 2006), and in particular organic acids (Duponnois et al. 2005). Enhanced P uptake by crop species from calcium phosphate compounds, which serve as a model mineral for phosphate rock (Chien 1977), have been interpreted as increased dissolution via organic acid exudates (Chien 1977; Wang et al. 2019; Yao et al. 2001).

Increasing dissolution of struvite by AM stands to help mitigate P limitation of early crop growth by struvite relative to more water soluble P fertilizers (Talboys et al. 2016). Though previous work has not evaluated AM impacts on crop uptake of struvite-P, the P-solubilizing bacterium *Bacillus megaterium* was found to increase P uptake by oat (*Avena sativa*) by nearly one-third (Hernández Jiménez et al. 2020). The potential of AM to increase plant utilization of low water solubility phosphate rock (Blal et al. 1990; Powell 1979; Powell and Daniel 1978) raises the possibility of similar benefits of AM for struvite dissolution. As for phosphate rock (Szilas et al. 2007), organic acids (e.g., acetic, citric, malic) have been found to increase dissolution rates of struvite (Talboys et al. 2016). The greater citrate solubility of struvite (18–29%) (Hertzberger et al. 2020) compared to most phosphate rocks (< 4%) (Chien and Menon 1995; Szilas et al. 2007) suggests that AM may offer relatively greater enhancement of dissolution of struvite. Moreover, the higher solubility of Mg-organic acid complexes (e.g., 155-fold for oxalate) than for Ca-organic acid complexes suggests that Mg^{2+} solubilized from struvite will less strongly inhibit dissolution of remaining struvite, in contrast to a strong negative feedback effect of Ca^{2+} released during dissolution of calcium phosphates (Qiu and Lian 2012).

This study tested the hypothesized enhancement of struvite dissolution by AM and thus increased struvite-P utilization by the host plant. To this end, a well-characterized genotypic model of AM-plant associations was used to furnish contrasting scenarios of root colonization in a tomato cultivar and its

AM-deficient mutant (referred to as MYC and *rmc*, respectively) (Cavagnaro et al. 2008; Watts-Williams and Cavagnaro 2014, 2015). To test the two mechanisms by which AM may improve P acquisition from low water solubility forms – physical access vs dissolution – struvite granules were placed directly in the root zone (5 cm) or at a soil depth below the seedlings (16 cm) of MYC and *rmc*. Specific objectives were to evaluate the effect of AM associations and placement on (1) struvite dissolution (% of granule mass remaining) and (2) nutrient uptake and tomato biomass relative to highly water soluble monoammonium phosphate (MAP). Struvite shallow placed in the root zone of MYC was hypothesized to undergo greater dissolution than for *rmc*. Less dissolution was expected for more deeply placed struvite, and dissolution was expected to be similar for MYC and *rmc*. It was further hypothesized that greater dissolution of shallow-placed struvite for MYC would entail greater P uptake, thereby yielding greater biomass compared to *rmc*. In contrast, it was hypothesized that MYC and *rmc* fertilized with MAP would have similar nutrient uptake and biomass, which would be greater compared to plants fertilized with struvite.

Methods

Plants and soil

A tomato mutant with reduced mycorrhizal colonization (*rmc*) and its wild type progenitor *Solanum lycopersicum* L. cv. 76R (MYC) were used to furnish differences in AM colonization (Barker et al. 1998). The 0–25 cm depth of the A horizon of a fine, smectitic, mesic Aquic Argiudoll (Flanagan series) was harvested from the University of Illinois Crop Sciences Research and Education Center in Urbana, IL. The soil was collected from secondary forest (>25 y) to ensure presence of AM spores and to avoid a high available P concentration, which generally disincentivizes AM colonization (Richardson and Simpson 2011). The soil used for the experiment had a clay loam texture (22% sand, 28% clay, 50% silt) with pH 6.9 (1:2 m/v in water). Soil Mehlich-3 P (colorimetric) was 19.4 mg kg^{-1}, below the threshold of 25 mg kg^{-1} considered optimum for annual crop production in this region (Mallarino et al. 2013).

Phosphorus source and placement treatments

Two P sources of contrasting water solubility but similar size were used at the same P rate, in the form of MAP (95% soluble) and struvite (<3% soluble) in the form of Crystal Green® (Ostara Nutrient Recovery Technologies, Inc.) (Gu et al. 2020). To enable comparison of P source, particle size effects were controlled by sieving both struvite and MAP granules to be 2.8–3.0 mm diameter using 2.8 and 3.0 mm sieves. In order to raise soil Mehlich-3 P concentrations to a sufficiency target of 30 mg kg^{-1} based on regional agronomic recommendations (Fernández and Hoeft 2009; Mallarino et al. 2013), a field-equivalent rate of 19.8 kg P ha^{-1} was added, either in the form of MAP (316 mg pot^{-1}) or struvite (587 mg pot^{-1}). To ensure similar amounts of and forms of N were added across treatments, differences in NH_4^+-N content between struvite and MAP were accounted for by adding 25.5 mg ammonium sulfate (5.4 mg total N) to soils treated with struvite. Thus, struvite and MAP treatments had the same P rate and N application rates, enabling their comparison to test hypothesized differences in mycorrhizal and plant response between P sources. To remove N limitations to plant growth, a field-equivalent rate of 80 kg N ha^{-1} as urea (563 mg pot^{-1}) was thoroughly incorporated into the soil before potting. To enable placement treatments and the recovery of undissolved struvite and MAP granules at the end of the experiment, granules were contained in nylon mesh pouches (12.0 × 7.5 cm) mixed with 30 mL of soil to ensure soil contact. Nylon mesh pouches had 400 μm diameter openings, which does not restrict plant root or hyphal exploration of soil within the mesh bag (Bearden and Petersen 2000; Wu et al. 2014; Zou et al. 2015) since this diameter size is (i) larger than the median root diameter of this specific genotypic tomato model (Müller et al. 2017), (ii) larger than tomato fine root diameter (<150 μm) (Müller et al. 2017) and (iii) larger than AM hyphae diameter by two orders of magnitude (2–5 μm) (Wu et al. 2014). One pouch per pot was situated 5 cm laterally from the seedling, at one of two placement depths: 5 cm or 16 cm below the soil surface. Six replicates for each of the 2 × 2 treatment of P source and placement ($n = 24$) were used, for a total of 60 pots.

Seeds were surface sterilized with ethanol prior to planting in a mix of 25% soil (< 4.0 mm sieved) combined with 25% fine silica and 50% peat moss-based potting mixture (BM2, Berger Inc.). At four

weeks post-sowing, seedlings were transferred to 6.52 L pots containing 6.60 kg of soil sieved to <4.0 mm. Pots were watered daily with distilled water to maintain 30–35% of the soil's water holding capacity, determined gravimetrically. No leachate was observed during or after watering. The greenhouse was maintained at a daytime (14 h) temperature of 23.9–26.7 °C and a nighttime (10 h) temperature of 21.1–23.9 °C. No supplemental lighting was used. Tomato plants were grown for 35 days after transplanting.

Soil and plant harvest and analysis

Plants were harvested at 35 days post-transplant by separating into aboveground and belowground biomass fractions. Shoot (aboveground) biomass consisted of leaves and stems, cut at 1 cm above the soil surface. Root (belowground) biomass was first sampled for fine, live roots to assess AM colonization and stored in 50% ethanol prior to root colonization counts. To quantify root colonization, roots were stained with Trypan Blue solution, placed on slides and examined for presence of intraradical structures: hyphae coils, vesicles and arbuscules (McGonigle et al. 1990). AM colonization rates were assessed by counting presence or absence of intraradical structures in the intersection of roots with an eyepiece crosshair arranged perpendicular to the root axis. A total of 10–0 intersections were assessed per slide. Though other methods exist to estimate AM biomass (e.g., quantitative polymerase chain reaction), for the specific tomato-AM genotype model that we used, multiple studies have demonstrated the value of root colonization rates as a proxy of high vs low/no AM associations (e.g., Bowles et al. 2016, 2018; Cavagnaro et al. 2008; Lazcano et al. 2014; Ruzicka et al. 2010, 2012).

Remaining roots were washed and oven-dried at 50° C for 72 h to determine dry biomass. Total concentrations of P, Mg, zinc (Zn), copper (Cu), and calcium (Ca) in aboveground and belowground biomass were determined by digesting finely ground biomass (<0.5 mm) in nitric acid (10% *v*/v) at 95 °C with quantification using inductively coupled optical emission spectroscopy (ICP OES) (Havlin and Soltanpour 1980). Total N of biomass samples was determined by dry combustion (Campbell and Plank 1992). Shoot (stems + leaves), root and total plant uptake (mg plant^{-1}) were calculated by normalizing concentrations to biomass.

Struvite dissolution

Nylon pouches containing struvite or MAP were harvested from pots and remaining granules were manually extracted using tweezers. Clinging soil particles were gently removed by tweezers, and the recovered granules were air-dried (25 °C) and weighed. Apparent dissolution of struvite or MAP was calculated as the difference (%) in total mass of granules initially added to each pouch compared to the mass of granules recovered at the end of the experiment. As very fine granules could not be fully recovered (estimated <0.2 mm), this approach may have slightly overestimated dissolution. However, orders of magnitude higher dissolution and plant availability of fine (<0.5 mm) struvite compared to 1–2 mm granule sizes (Degryse et al. 2017; Hertzberger et al. 2020) suggests that particles of struvite too fine to be manually recovered by this approach are effectively plant available.

To complement mass-based calculation of dissolution, qualitative visual evaluation of residual struvite granule surfaces were evaluated using scanning electron microscopy (SEM). Scanning electron microscopy images were collected and elemental chemical analysis were conducted for struvite using an Inspect JSM-7800F (JEOL, Japan) SEM at an acceleration voltage of 3.0 kV. Struvite granules subjected to three treatments were evaluated: pure struvite, struvite after being subjected to Mehlich-3 extraction (Mehlich 1984) as a chemical weathering control, and residual struvite recovered from the greenhouse experiment. Struvite granules were oven dried at 65 °C for 48 h prior to SEM analysis. Though qualitative, SEM imaging has been successfully used to diagnose non-mass based differences in biologically-driven dissolution of low water solubility P minerals such as apatite (e.g., Calvaruso et al. 2013; Koele et al. 2014), thereby complementing quantitative dissolution data.

Data analysis

Dissolution of struvite and MAP granules and the response of tomato biomass and nutrient uptake were evaluated for genotype, P source and placement of P source using analysis of variance (ANOVA) with PROC GLM in SAS version 9.4 (SAS Institute, Cary,

NC). Assumptions of normality of residuals and heteroscedasticity of variance were confirmed. First, a global model was used to test for all possible interactions ($p < 0.05$), including the three-way interaction of genotype × P source × P placement. Then, nonsignificant interactions were removed from the initial model to increase sensitivity to remaining interactions and factors (Martınez 2015). Six replicate plants were used to test treatment effects, with the exception of MYC with struvite shallow placement, and *rmc* with MAP shallow placement, for which five replicates were used due to outliers in plant biomass (>3-fold lower total biomass than the treatment mean). Finally, Tukey's HSD were performed to test significant difference of the four treatment combinations result from the factorial of genotype × P source (2 × 2) with $\alpha = 0.05$.

Results

Mycorrhizal colonization and plant growth

Root colonization by AM at harvest was 19.1 ± 3.2% for MYC and 0.45 ± 0.40% for *rmc*, confirming differences in AM associations furnished by the genotype model ($p < 0.0001$). There was no effect of P source on root colonization ($p = 0.42$), though deeper placement – regardless of P source – compared to shallow placement entailed a tendency towards greater mean colonization of MYC roots ($p = 0.064$). Though root biomass was similar for MYC and *rmc* regardless of P source (genotype × P source, $p = 0.46$), shoot biomass depended on the combination of genotype and P source (genotype × P source, $p = 0.012$) and thus drove differences in total biomass (genotype × P source, $p = 0.013$) (Fig. 1). Shoot biomass of MYC was 23.1% greater when fertilized with struvite compared to MAP ($p = 0.029$).

P source dissolution

Dissolution of struvite granules was approximately 4-fold less than MAP granules regardless of depth placement and tomato genotype. Struvite dissolution was similar for MYC between shallow placement (25.4%) and deep placement (22.2%) ($F = 3.1$, $p = 0.11$). Likewise, no differences in struvite dissolution by depth placement were observed for *rmc* ($F = 0.6$, $p = 0.45$). MAP dissolution averaged 87.8% and was similar across genotype and placement.

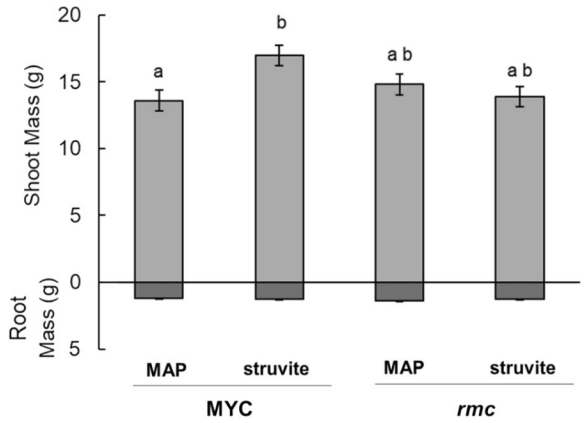

Fig. 1 Dry biomass of a mycorrhizal wildtype (MYC) and the reduced mycorrhizal colonization mutant (*rmc*) tomato fertilized with struvite or monoammonium phosphate (MAP) in a soil with low P availability. Columns marked with the same letter do not significantly differ in shoot biomass ($p < 0.05$) determined by Tukey's HSD test

However, surface morphology of residual struvite granules were distinct for MYC and *rmc* depending on placement (representative images in Fig. 2c-f; all images in Fig. S1–6), and exhibited signs of surface weathering not evident in fresh struvite (Fig. 2a). Differences in struvite surface morphology between MYC and *rmc* were most pronounced for struvite placed at the shallow depth of 5 cm in the root zone (Fig. 2c, d). The smoother surface of the residual struvite granules were distinct from the surface of struvite granules that were chemically weathered by exposing to acidic Mehlich-3 solution (Fig. 2b) despite Mehlich-3 treated struvite granules undergoing similar dissolution (24.0%) as struvite granules buried in soils over the 35-day experiment. Residual struvite placed at depth showed greatest similarities in surface morphology between MYC and *rmc* (Fig. 2e, f) in addition to similar total dissolution (Table 1) and exhibited a textured surface of lacunae and tesserae that most closely resembled fresh struvite.

Tomato nutrient uptake

Total tomato uptake of P (mg plant^{-1}) was significantly elevated for MYC-struvite relative to *rmc*-struvite, *rmc*-MAP and MYC-MAP (Fig. 3). However, shoot N uptake ($F = 10.1$, $p = 0.003$) differed more by genotype and by P source than shoot P uptake ($F = 6.0$, $p = 0.019$), with greater uptake of N by MYC-struvite than MYC-MAP but not *rmc*-MAP. Compared to *rmc*-struvite, MYC-struvite had 31.6% more shoot P and

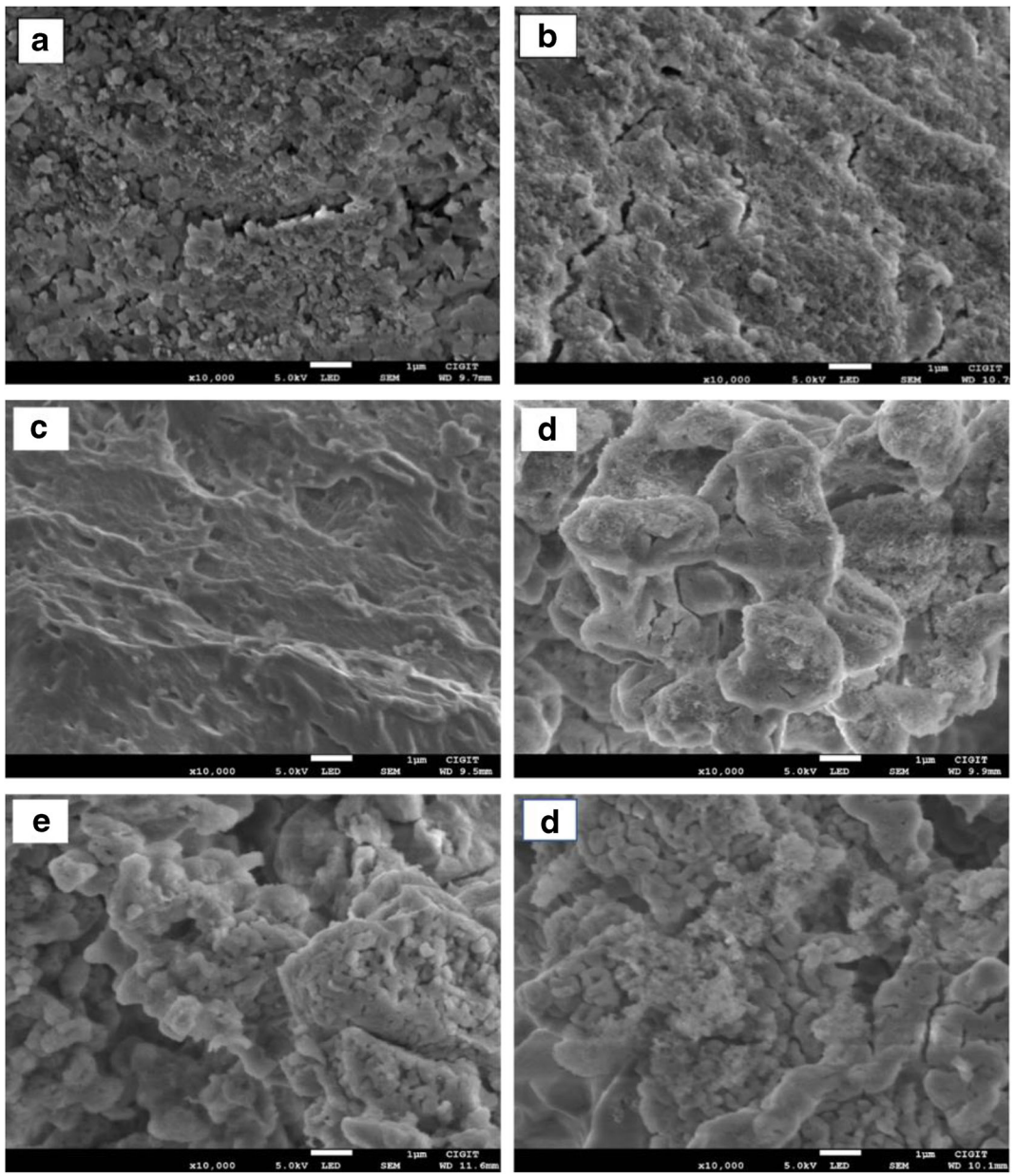

Fig. 2 Scanning electron microscope (SEM) images of (**a**) pure struvite, and (**b**) struvite following 5 min extraction in Mehlich-3 solution. These two struvite treatments serve as soil- and plant-free controls of surface weathering for residual struvite recovered from soils used for a 35-day greenhouse tomato growth experiment under the following treatments: (**c**) MYC-struvite shallow placement, (**d**) *rmc*-struvite shallow placement, (**e**) MYC-struvite deep placement, and (**f**) *rmc*-struvite deep placement. Dissolution of struvite in Mehlich-3 solution was 24.0 ± 2.0%. Additional images of replicate granules and at varying magnifications are provided in the Supporting Information

34.1% more shoot N. When fertilized with struvite instead of MAP, MYC had 26.1% more shoot P, and 33.6% more shoot N. Shoot and total N uptake of MYC-struvite was similar to *rmc*-MAP. As the majority of total biomass was shoot biomass, total N and P uptake were driven by shoot N and P uptake (92% and 90% of total uptake). To a lesser extent than P and N, shoot Mg uptake also depended on genotype and P source ($F = 4.5$, $p = 0.041$), and was 28.1% greater for MYC-struvite relative to other treatments (i.e., genotype ×

Table 1 Dissolution of monoammonium phosphate (MAP) vs struvite across genotypes and soil placement, determined by mass of fertilizer granule recovered. Values are mean ± s.e

Genotype	Placement	Dissolution (%) MAP	Struvite
MYC	shallow	88.8±1.76	25.4±1.57
MYC	deep	87.8±1.57	22.2±0.82
rmc	shallow	88.8±1.75	20.6±2.26
rmc	deep	85.8±1.67	22.7±1.14

fertilizer). In contrast to total uptake (mg plant^{-1}), shoot and root P concentrations differed by genotype only, and were higher for MYC compared to *rmc* (p_{shoot} = 0.020, p_{root} = 0.024) regardless of P source (Table S1). Unlike P uptake, shoot and root N concentrations were similar across all treatments, indicating genotype and P source influenced both biomass and foliar nutrient concentrations (Table S1).

As MYC-struvite exhibited significantly higher N uptake compared to *rmc*-struvite and to MYC-MAP, we additionally analyzed nutrient elements known to be influenced by AM and specifically for MYC and *rmc* (Watts-Williams and Cavagnaro 2014). Similar patterns in total shoot uptake of divalent metal nutrients were observed as for N and P, including Zn (F = 9.5, p = 0.0037), Cu (F = 4.5, p = 0.041), and Ca (F = 5.5, p = 0.023) (Table S2). Compared to *rmc*-struvite, MYC-struvite shoot uptake was greater by 36.2% for Ca, 39.3% for Cu, and 35.9% for Zn. When fertilized with

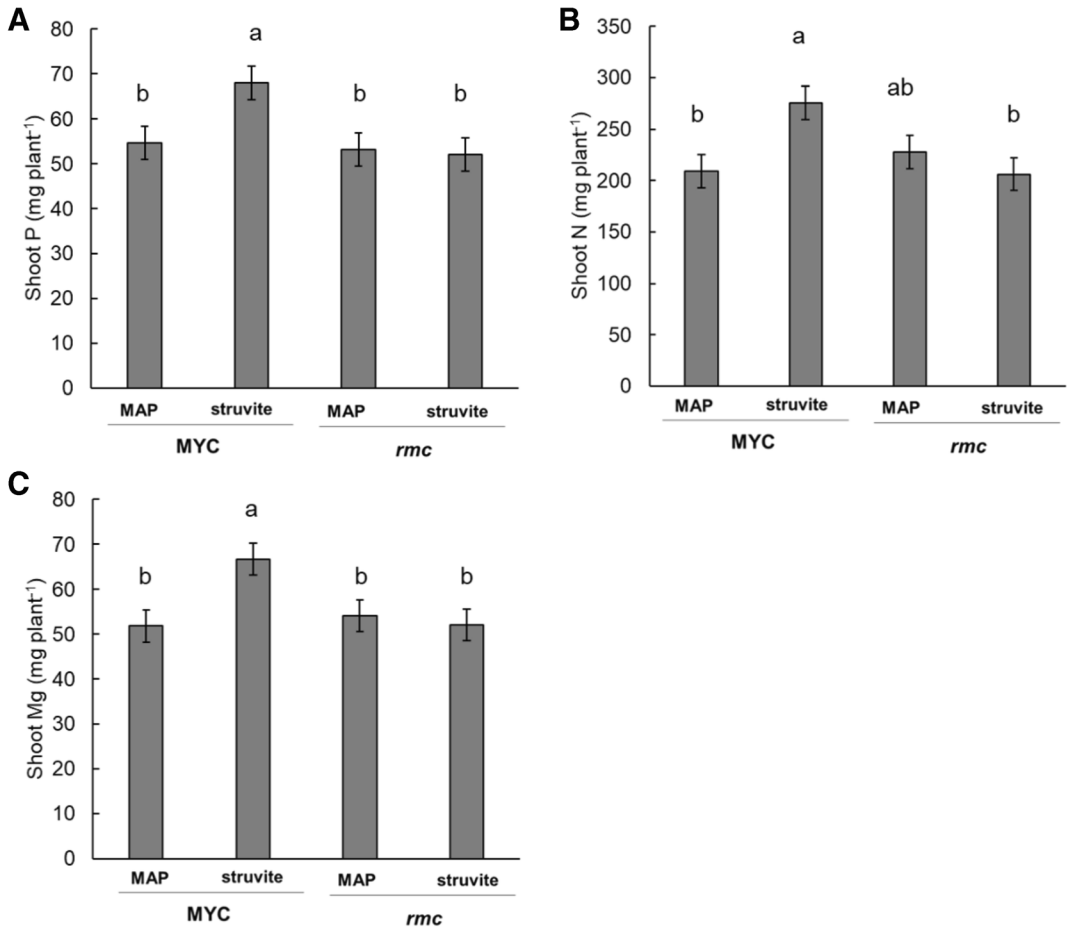

Fig. 3 Tomato shoot uptake of (**a**) phosphorus (P), (**b**) nitrogen (N), and (**c**) magnesium (Mg) for the mycorrhizal wildtype (MYC) and the reduced mycorrhizal colonization mutant (*rmc*) using struvite or monoammonium phosphate (MAP) as a P source. Tomato plants were grown for 35 days in a low P availability soil in a greenhouse. Columns marked with the same letter do not significantly differ (genotype × P source, $p < 0.05$) for nutrient uptake, determined by Tukey's honest significant difference test

struvite instead of MAP, MYC shoot uptake was greater for Ca by 42.6%, Cu by 39.0%, and Zn by 32.3%.

Discussion

AM do not influence magnitude of apparent dissolution of particulate struvite

Similar residual mass of struvite granules between MYC and *rmc* does not support the hypothesized enhanced dissolution of struvite by AM. This is further supported by similar root biomass between MYC and *rmc*, but two orders of magnitude greater AM colonization of MYC roots. Similar apparent dissolution of struvite placed at shallow and deep depths, despite the high root density qualitatively observed at the soil surface during plant harvest, indicates a minor role of roots and dominant effects of abiotic processes in dissolution. However, the circumneutral pH of the soil used in this study (pH 6.9) would be expected to account for only a minor proportion of the observed dissolution of struvite over the 35 day experimental period given that a previous evaluation found that struvite dissolution over 60 days was <5% in a pH 8.5 soil (Degryse et al. 2017). On the other hand, nitrification can drive struvite dissolution (Bridger et al. 1962; Lunt et al. 1964), consistent with soil-applied nitrification inhibitors retarding struvite dissolution (Watson et al. 2019). This could also explain why the relative dissolution of struvite compared to MAP (1:4) after 35 days in soil was 8-fold greater than the relative difference in water solubility of struvite and MAP (1:32), and is consistent with previous findings that extractions (e.g., sequential fractionation) underestimate the bioavailability of struvite-P in soil (Meyer et al. 2018). However, the amount of struvite dissolved by Mehlich-3 extraction in 5 min was the same as 35 days in the soil, suggesting that commonly employed acidic extractants with organic acids may offer a more realistic metric of struvite bioavailability than its water solubility.

Qualitative differences in the surface morphology of residual struvite between MYC and *rmc* identified by SEM are suggestive of an AM effect on dissolution at the granule surface, even though there were no differences in the (measurable) mass of struvite dissolved. Greater surface area contact of granules by AM hyphae may have altered the surface morphology of struvite granules and increased the amount of P available to the plant. Similar surface scarring and residual tesserae or needle-like structures have been observed for apatite exposed to roots (*Pinus sylvestris*) (Calvaruso et al. 2013) or after long-term soil incubations (4 y) (Uroz et al. 2012). In our study, hyphae may have provided access to P from struvite particles smaller than 0.2 mm, the approximate diameter limit of manual recovery in our study, that roots would otherwise not have access to, which could explain apparent similar dissolution of struvite calculated from >0.2 mm residual particles. The qualitative visual similarity of struvite granule surfaces subjected to AM-associated roots (MYC) and chemical weathering by organic acid solution (Mehlich-3) is consistent with the hypothesis that AM hyphal exudates may contain organic acids (Tawaraya et al. 2006; Toljander et al. 2006) known to increase struvite dissolution (Talboys et al. 2016). However, deliberate quantification and characterization of hyphal exudates is needed to explicitly test this potential mechanism. In vitro, ectomycorrhizae (*P. involutus*) have been found to preferentially invest in hyphae in close proximity to P minerals (Smits et al. 2008), consistent with selective colonization of minerals depending on nutrient element content, including P, in soil-free (e.g., peat moss, agar) greenhouse experiments (Bonneville et al. 2011; Rosling et al. 2004). In situ, however, mycorrhizal abundance appears to be inversely related to soil weathering and thus apatite abundance (Smits et al. 2014), indicating that AM dissolution mechanisms observed in controlled but simplified ex situ experiments may not necessarily manifest in the more complex environment of soil.

AM and P fertilizer interactions

As struvite dissolution was not substantially influenced by AM, the observed AM advantage (i.e., greater P uptake by MYC relative to *rmc* plants) was likely mediated by a non-solubilization mechanism(s). Hyphal exploration could explain differences in P uptake between MYC and *rmc* fertilized with struvite (Sharif and Claassen 2011). In some cases, AM associations confer greater P uptake by the host crop from highly water soluble P sources (e.g., triple superphosphate) but not phosphate rock (Saia et al. 2020; Satter et al. 2006), suggesting that the scavenging mechanism may outstrip solubilization by AM in relative importance. However, this does not explain why MYC fertilized with MAP had less P uptake than when fertilized with struvite, as

AM would be expected to similarly scavenge orthophosphate once dissolved, regardless of its origin. It is possible that the higher availability of soil P, directly to roots, from MAP reduced the benefits of AM colonization even as plant P demands increased overtime (Grant et al. 2005; Menge et al. 1978). The 'slow-release' nature of struvite implied by its low water solubility and moderate citrate solubility (Talboys et al. 2016) raises the possibility of greater synchronization of P availability from struvite than rapidly-solubilized MAP. Rapid flushes of orthophosphate susceptible to binding to mineral surfaces has been proposed to explain why highly soluble P fertilizers such as TSP do not necessarily outperform phosphate rock (Szilas et al. 2007), though this is largely limited to highly weathered soils with high P fixation capacity and sufficient acidity to drive phosphate rock dissolution (Margenot et al. 2016) and is unlikely to operate in the soil (an Endoaquoll) used here.

Despite using a P-deficient soil and 4-fold lower (apparent) dissolution of struvite compared to MAP and reports of lower early-stage crop growth for struvite-fertilized plants (e.g., Talboys et al. 2016), we did not observe lower shoot, root, or total biomass of tomato fertilized with struvite compared to ammonium phosphate. The mean difference in total P uptake of 12 mg plant^{-1} between MYC with struvite compared to *rmc* and/or MAP is equivalent in magnitude to ~17% of P added as struvite, which is comparable to but lower than the 23% dissolution of struvite granules. On the other hand, crop P uptake is not necessarily an accurate measure of fertilizer P use efficiency because it is confounded by uptake of soil P not derived from fertilizer. Our use of a soil with low available P minimized, but does not rule out, this potential artifact. As radiolabeling of P in struvite and triple superphosphate have revealed, non-fertilizer soil P can contribute the majority (>60%) of plant P uptake regardless of P source (Achat et al. 2014b), consistent with estimates of 15–30% fertilizer P use efficiency by annual crops in the first season following application (Syers et al. 2008). The high organic carbon (7.5%) content of the soil used for this experiment entailed a high concentration of organic P (1,247 mg kg^{-1}), which can undergo mineralization by extracellular phosphatases to yield plant-available orthophosphate. Given the potential of AM to secrete phosphatases and reports of elevated phosphomonoesterase activities in rhizospheres of AM-inoculated roots of perennial (Wang et al. 2019) and annual (Tarafdar and Marschner 1994) crop species, enhanced P uptake observed for AM-associated tomatoes may have been partly mediated by greater contributions from mineralized P. Quantifying P uptake from P sources and its discrimination from soil-derived P is not possible without isotopically labeling P (i.e., ^{32}P or ^{33}P). Future work with radioisotopically labeled struvite and reference P fertilizers (e.g., Achat et al. 2014a; b) is needed to further test the hypothesis, supported but not fully confirmed by the results of this study, that AM increase crop P uptake under struvite fertilization. Similarly, labeling struvite-N with ^{15}N can identify the source of the observed high N uptake of MYC fertilized with struvite.

MYC had similar root colonization rates under struvite and MAP fertilization, ruling out the possibility that lower soil solution P with struvite fertilization observed by others (Hertzberger et al. 2021) stimulated colonization. Initial colonization of roots by AM has been shown to not be affected by soil P if root P concentrations are low (Grant et al. 2005; Menge et al. 1978). Moreover, greater AM colonization of MYC when P sources – regardless of water solubility – were placed at depth ($p = 0.064$) compared to shallow placement is consistent with P limitation of early crop growth incentivizing AM associations (Yoneyama et al. 2007) and greater soil solution P disincentivizing root colonization (Grant et al. 2001; Thomson et al. 1992). Though AM species were not evaluated in our study, greater diversity of AM colonizing roots of apple (*Malus domestica*) fertilized with struvite compared to high water solubility P sources (Van Geel et al. 2016) could also explain observed differences in P uptake by MYC fertilized with struvite vs MAP. On the other hand, the low species-specificity of AM colonization of tomato roots has led to the proposition that AM species diversity may not necessarily translate to differences in host crop P uptake for a given degree of colonization (Kahiluoto et al. 2012).

Since P, but not N was limiting, increased tomato P uptake afforded by AM-associations (MYC) under struvite fertilization entailed growth-driven demand and higher uptake of N. This is consistent with greater uptake of divalent metals (Ca, Zn, Cu) for MYC with struvite relative to MAP or to *rmc* with either P source. When fertilized with struvite and inoculated with P-solubilizing bacteria, oat (*Avena sativa*) had greater

uptake of N compared to TSP at the same N rate, which the authors attributed to P limitation of crop biomass and thus N uptake (Hernández Jiménez et al. 2020).

Implications for struvite as a P fertilizer

Greater plant growth and nutrient uptake with struvite compared to MAP facilitated by AM suggests these belowground relationships can be employed to promote struvite as an agronomically viable alternative to highly water-soluble P fertilizers. Beyond increase recycling of P from wastestreams, the low water solubility of struvite entails lower P loss risk and thus ameliorated impacts on water quality (Gu et al. 2020; Margenot et al. 2019). Greater P uptake and thus greater growth of AM-associated tomato plants fertilized with struvite relative to MAP challenges the notion that AM is limited to mitigating a P uptake deficit imposed by low water solubility, as has been found for phosphate rock (e.g., Satter et al. 2006). Benefits of AM for increasing crop P uptake in agroecosystems have been historically considered in low P-input systems (Hoeksema et al. 2010), notably in resource-limited smallholder agriculture reliant on less expensive phosphate rock inputs (Margenot et al. 2016; Nziguheba et al. 2015). Though AM can increase host plant P uptake from phosphate rock, plant P uptake from highly water soluble P forms is often still higher and/or is also enhanced by AM. For example, even with AM inoculation, biomass and P uptake by tomato and black wattle (*Acacia mangium*) were significantly lower for phosphate rock compared to TSP fertilization (Saia et al. 2020; Satter et al. 2006). This could be explained by AM-mediated uptake of P incurring a greater photosynthate cost to the host plant for low solubility P forms such as calcium phosphate (Andrino et al. 2020). In contrast, this study identifies an 'overyield' (vegetative biomass) effect of AM for tomato fertilized with struvite relative to MAP. Notably, this AM effect appear to be facilitated by means other than dissolution.

By relying on native or indigenous soil AM, our study provides a realistic evaluation of how AM can influence struvite dissolution and uptake in the early growth stages of a broad-field crop. In addition to avoiding biases in the use of potting mixtures or coarse-textured soils commonly used in greenhouse evaluations of struvite, the low soil P availability and realistic application rates used in this study avoids overestimating crop availability of struvite-P (Hertzberger et al. 2020). Furthermore, reliance on indigenous soil AM for colonization of plant roots has the benefit of emulating realistic field conditions (van der Heijden et al. 1998) and avoids inoculant-driven effects at the greenhouse scale not necessarily observed in the field (Thirkell et al. 2017). Though it is not known which AM species colonized MYC in our study, potential variation in AM species colonizing MYC vs *rmc* is secondary to total root colonization driving differences between the two genotypes in acquisition of P and other nutrients (Watts-Williams and Cavagnaro 2014, 2015). Nonetheless, given AM species-specific effects on tomato P uptake from low solubility P forms such as phosphate rock (Saia et al. 2020), future experiments should evaluate the effect of AM species on struvite dissolution, either by characterizing the indigenous species that colonizes host plants and/or by inoculation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-04957-2.

Funding Financial support was in part provide by the National Science Foundation under grant #NSF REU 1559908/1559929, as part of the Phenotypic Plasticity Research Experience for Community College Students, through the University of Illinois at Urbana-Champaign Institute for Genomic Biology and Parkland College. Additional support was provided by Illinois Nutrient Research and Education Council (NREC) award #2018–4–360731-385 (A.J.M.).

Availability of data and material Data will be made available upon request.Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-04957-2.

Declarations

Conflict of interest The authors have no competing interests to declare.

References

Achat DL, Daumer M-L, Sperandio M, Santellani A-C, Morel C (2014a) Solubility and mobility of phosphorus recycled from dairy effluents and pig manures in incubated soils with different characteristics. Nutr Cycl Agroecosyst 99:1–15. https://doi.org/10.1007/s10705-014-9614-0

Achat DL, Sperandio M, Daumer M-L, Santellani A-C, Prud'Homme L, Akhtar M, Morel C (2014b) Plant-availability of phosphorus recycled from pig manures and

dairy effluents as assessed by isotopic labeling techniques. Geoderma 232:24–33. https://doi.org/10.1016/j.geoderma.2014.04.028

Andrino A, Guggenberger G, Sauheitl L, Burkart S, Boy J (2020) Carbon investment into mobilization of mineral and organic phosphorus by arbuscular mycorrhiza. Biol Fertil Soils 57:47–64. https://doi.org/10.1007/s00374-020-01505-5

Barker SJ, Stummer B, Gao L, Dispain I, O'Connor PJ, Smith SE (1998) A mutant in *Lycopersicon esculentum* Mill with highly reduced VA mycorrhizal colonization: Isolation and preliminary characterisation. Plant J 15:15–797. https://doi.org/10.1046/j.1365-313X.1998.00252.x

Bearden BN, Petersen L (2000) Influence of arbuscular mycorrhizal fungi on soil structure and aggregate stability of a vertisol. Plant Soil 218:173–183

Blal B, Morel C, Gianinazzi-Pearson V, Fardeau JC, Gianinazzi S (1990) Influence of vesicular-arbuscular mycorrhizae on phosphate fertilizer efficiency in two tropical acid soils planted with micropropagated oil palm (Elaeis guineensis jacq.). Biol Fertil Soils 9:43–48. https://doi.org/10.1007/BF00335860

Bolan NS (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant Soil 134:189–207. https://doi.org/10.1007/BF00012037

Bonneville S, Morgan DJ, Schmalenberger A, Bray A, Brown A, Banwart SA, Benning LG (2011) Tree-mycorrhiza symbiosis accelerate mineral weathering: evidences from nanometer-scale elemental fluxes at the hypha–mineral interface. Geochim Cosmochim Acta 75:6988–7005. https://doi.org/10.1016/j.gca.2011.08.041

Bowles TM, Jackson LE, Cavagnaro TR (2018) Mycorrhizal fungi enhance plant nutrient acquisition and modulate nitrogen loss with variable water regimes. Glob Chang Biol 24(1):e171–e182

Bowles TM, Barrios-Masias FH, Carlisle EA, Cavagnaro TR, Jackson LE (2016) Effects of arbuscular mycorrhizae on tomato yield, nutrient uptake, water relations, and soil carbon dynamics under deficit irrigation in field conditions. Sci Total Environ 566:1223–1234

Bridger G, Salutsky ML, Starostka R (1962) Micronutrient sources, metal ammonium phosphates as fertilizers. J Agric Food Chem 10:181–188

Calvaruso C, Turpault M-P, Frey-Klett P, Uroz S, Pierret M-C, Tosheva Z, Kies A (2013) Increase of apatite dissolution rate by scots pine roots associated or not with Burkholderia glathei PML1(12)Rp in open-system flow microcosms. Geochim Cosmochim Acta 106:287–306. https://doi.org/10.1016/j.gca.2012.12.014

Campbell C, Plank CO (1992) Determination of total nitrogen in plant tissue by combustion. Plant analysis reference procedures for the southern US Southern Coop Ser Bull 368:20–22

Cavagnaro TR, Langley AJ, Jackson LE, Smukler SM, Koch GW (2008) Growth, nutrition, and soil respiration of a mycorrhiza-defective tomato mutant and its mycorrhizal wild-type progenitor. Funct Plant Biol 35:228–235. https://doi.org/10.1071/FP07281

Chien SH (1977) Thermodynamic considerations on the solubility of phosphate rock. Soil Sci 123:117–121

Chien SH, Menon RG (1995) Factors affecting the agronomic effectiveness of phosphate rock for direct application. Fertil Res 41:227–234. https://doi.org/10.1007/BF00748312

Degryse F, Baird R, da Silva RC, McLaughlin MJ (2017) Dissolution rate and agronomic effectiveness of struvite fertilizers – effect of soil pH, granulation and base excess. Plant Soil 410:139–152. https://doi.org/10.1007/s11104-016-2990-2

Duponnois R, Colombet A, Hien V, Thioulouse J (2005) The mycorrhizal fungus Glomus intraradices and rock phosphate amendment influence plant growth and microbial activity in the rhizosphere of Acacia holosericea. Soil Biol Biochem 37:1460–1468

Fernández FG, Hoeft RG (2009) Managing soil pH and crop nutrients. Illinois Agronomy Handbook 24:91–112

George E, Marschner H, Jakobsen I (1995) Role of Arbuscular Mycorrhizal Fungi in uptake of phosphorus and nitrogen from soil. Crit Rev Biotechnol 15:257–270. https://doi.org/10.3109/07388559509147412

Grant CA, Flaten DN, Tomasiewicz DJ, Sheppard SC (2001) The importance of early season phosphorus nutrition. Can J Plant Sci 81:211–224. https://doi.org/10.4141/P00-093

Grant C, Bittman S, Montreal M, Plenchette C, Morel C (2005) Soil and fertilizer phosphorus: effects on plant P supply and mycorrhizal development. Can J Plant Sci 85:3–14. https://doi.org/10.4141/p03-182

Gu C, Gates BA, Margenot AJ (2020) Phosphate recycled as struvite immobilizes bioaccessible soil lead while minimizing environmental risk. J Clean Prod 276:122635. https://doi.org/10.1016/j.jclepro.2020.122635

Havlin JL, Soltanpour PN (1980) A nitric acid plant tissue digest method for use with inductively coupled plasma spectrometry. Commun Soil Sci Plant Anal 11:969–980. https://doi.org/10.1080/00103628009367096

Hernández Jiménez JE, Nyiraneza J, Fraser TD, Peach Brown HC, Lopez-Sanchez IJ, Botero-Botero LR (2020) Enhancing phosphorus release from struvite with biostimulants. Can J Soil Sci 101:1–11. https://doi.org/10.1139/cjss-2019-0147

Hertzberger AJ, Cusick RD, Margenot AJ (2020) A review and meta-analysis of the agricultural potential of struvite as a phosphorus fertilizer. Soil Sci Soc Am J 84:653–671. https://doi.org/10.1002/saj2.20065

Hertzberger AJ, Cusick RD, Margenot AJ (2021) Maize and soybean response to phosphorus fertilization with blends of struvite and monoammonium phosphate. Plant and Soil. https://doi.org/10.1007/s11104-021-04830-2

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407. https://doi.org/10.1111/j.1461-0248.2009.01430.x

Kahiluoto H, Ketoja E, Vestberg M (2012) Plant-available P supply is not the main factor determining the benefit from arbuscular mycorrhiza to crop P nutrition and growth in contrasting cropping systems. Plant Soil 350:85–98. https://doi.org/10.1007/s11104-011-0884-x

Koele N, Dickie IA, Blum JD, Gleason JD, de Graaf L (2014) Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. Soil Biol Biochem 69:63–70

Lazcano C, Barrios-Masias FH, Jackson LE (2014) Arbuscular mycorrhizal effects on plant water relations and soil

greenhouse gas emissions under changing moisture regimes. Soil Biol Biochem 74:184–192

Lunt O, Kofranek A, Clark S (1964) Nutrient availability in soil, availability of minerals from magnesium ammonium phosphates. J Agric Food Chem 12:497–504

Mallarino AP, Sawyer JE, Barnhart SK (2013) A general guide for crop nutrient and limestone recommendations in Iowa. Iowa State University Extension and Outreach

Margenot AJ, Singh BR, Rao IM, Sommer R (2016) Phosphorus fertilization and Management in Soils of sub-Saharan Africa. In: Lal R (ed) Soil phosphorus. CRC Press, New York

Margenot AJ, Kitt D, Gramig BM, Berkshire TB, Chatterjee N, Hertzberger AJ, Aguiar S, Furneaux A, Sharma N, Cusick RD (2019) Toward a regional phosphorus (re)cycle in the US Midwest. J Environ Qual 48:1397–1413. https://doi.org/10.2134/jeq2019.02.0068

Martınez HDR (2015) Analysing interactions of fitted models. CRAN-R Project

McGonigle TP, Miller MH, Evans DG, Fairchid GL, Swan JA (1990) A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytol 115:495–501. https://doi.org/10.1111/j.1469-8137.1990.tb00476.x

Mehlich A (1984) Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun Soil Sci Plant Anal 15:1409–1416. https://doi.org/10.1080/00103628409367568

Menge JA, Steirle D, Bagyaraj DJ, Johnson ELV, Leonard RT (1978) Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. New Phytol 80:575–578. https://doi.org/10.1111/j.1469-8137.1978.tb01589.x

Meyer G, Frossard E, Mäder P, Nanzer S, Randall DG, Udert KM, Oberson A (2018) Water soluble phosphate fertilizers for crops grown in calcareous soils – an outdated paradigm for recycled phosphorus fertilizers? Plant Soil 424:367–388. https://doi.org/10.1007/s11104-017-3545-x

Müller A, Ngwene B, Peiter E, George E (2017) Quantity and distribution of arbuscular mycorrhizal fungal storage organs within dead roots. Mycorrhiza 27:201–210. https://doi.org/10.1007/s00572-016-0741-0

Nziguheba G, Zingore S, Kihara J, Merckx R, Njoroge S, Otinga A, Vandamme E, Vanlauwe B (2015) Phosphorus in smallholder farming systems of sub-Saharan Africa: implications for agricultural intensification. Nutr Cycl Agroecosyst 104:1–20. https://doi.org/10.1007/s10705-015-9729-y

Plassard C, Dell B (2010) Phosphorus nutrition of mycorrhizal trees. Tree Physiol 30:1129–1139. https://doi.org/10.1093/treephys/tpq063

Powell C (1979) The effect of mycorrhizal fungi on recovery of phosphate fertilzier from soil by ryegrass plants. New Phytol 83:681–694. https://doi.org/10.1111/j.1469-8137.1979.tb02300.x

Powell CL, Daniel J (1978) Mycorrhizal Fungi stimulate uptake of soluble and insoluble phosphate fertilizer from a phosphate-deficient soil. New Phytol 80:351–358

Qiu S, Lian B (2012) Weathering of phosphorus-bearing mineral powder and calcium phosphate by Aspergillus Niger. Chin J Geochem 31:390–397. https://doi.org/10.1007/s11631-012-0589-8

Ramirez R, Mendoza B, Lizaso JI (2009) Mycorrhiza effect on maize P uptake from phosphate rock and superphosphate. Commun Soil Sci Plant Anal 40:2058–2071. https://doi.org/10.1080/00103620902960583

Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability update on microbial phosphorus. Plant Physiol 156:989–996. https://doi.org/10.1104/pp.111.175448

Rosling A, Lindahl BD, Finlay RD (2004) Carbon allocation to ectomycorrhizal roots and mycelium colonising different mineral substrates. New Phytol 162:795–802. https://doi.org/10.1111/j.1469-8137.2004.01080.x

Roy ED, Richards PD, Martinelli LA, Coletta LD, Lins SRM, Vazquez FF, Willig E, Spera SA, VanWey LK, Porder S (2016) The phosphorus cost of agricultural intensification in the tropics. Nature Plants 2:16043. https://doi.org/10.1038/nplants.2016.43 https://www.nature.com/articles/nplants201643#supplementary-information

Ruzicka DR, Barrios-Masias FH, Hausmann NT, Jackson LE, Schachtman DP (2010) Tomato root transcriptome response to a nitrogen-enriched soil patch. BMC Plant Biology 10(1):1–19

Ruzicka DR, Hausmann NT, Barrios-Masias FH, Jackson LE, Schachtman DP (2012) Transcriptomic and metabolic responses of mycorrhizal roots to nitrogen patches under field conditions. Plant Soil 350:145–162. https://doi.org/10.1007/s11104-011-0890-z

Saia S, Aissa E, Luziatelli F, Ruzzi M, Colla G, Ficca AG, Cardarelli M, Rouphael Y (2020) Growth-promoting bacteria and arbuscular mycorrhizal fungi differentially benefit tomato and corn depending upon the supplied form of phosphorus. Mycorrhiza 30:133–147. https://doi.org/10.1007/s00572-019-00927-w

Satter MA, Hanafi MM, Mahmud TMM, Azizah H (2006) Influence of arbuscular mycorrhiza and phosphate rock on uptake of major nutrients by Acacia mangium seedlings on degraded soil. Biol Fertil Soils 42:345–349. https://doi.org/10.1007/s00374-005-0033-x

Sharif M, Claassen N (2011) Action mechanisms of Arbuscular Mycorrhizal Fungi in phosphorus uptake by Capsicum annuum L. Pedosphere 21:502–511. https://doi.org/10.1016/S1002-0160(11)60152-5

Sharpley A, Daniel TC, Sims JT, Pote DH (1996) Determining environmentally sound soil phosphorus levels. J Soil Water Conserv 51:160–166

Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of Arbuscular Mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in Arbuscular Mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiol 156:1050–1057. https://doi.org/10.1104/pp.111.174581

Smits M, Bonneville S, Haward S, Leake JR (2008) Ectomycorrhizal weathering, a matter of scale? Mineral Mag 72:131–134

Smits MM, Johansson L, Wallander H (2014) Soil fungi appear to have a retarding rather than a stimulating role on soil apatite weathering. Plant Soil 385:217–228. https://doi.org/10.1007/s11104-014-2222-6

Syers J, Johnston A, Curtin D (2008) Efficiency of soil and fertilizer phosphorus use. FAO Fertil Plant Nutr Bull 18

Szilas C, Semoka JMR, Borggaard OK (2007) Establishment of an agronomic database for Minjingu phosphate rock and

examples of its potential use. Nutr Cycl Agroecosyst 78:225–237. https://doi.org/10.1007/s10705-006-9086-y

Talboys PJ, Heppell J, Roose T, Healey JR, Jones DL, Withers PJA (2016) Struvite: a slow-release fertiliser for sustainable phosphorus management? Plant Soil 401:109–123. https://doi.org/10.1007/s11104-015-2747-3

Tarafdar JC, Marschner H (1994) Phosphatase activity in the rhizosphere and hyphosphere of VA mycorrhizal wheat supplied with inorganic and organic phosphorus. Soil Biol Biochem 26:387–395. https://doi.org/10.1016/0038-0717(94)90288-7

Tawaraya K, Naito M, Wagatsuma T (2006) Solubilization of insoluble inorganic phosphate by Hyphal exudates of Arbuscular Mycorrhizal Fungi. J Plant Nutr 29:657–665. https://doi.org/10.1080/01904160600564428

Thirkell TJ, Charters MD, Elliott AJ, Sait SM, Field KJ (2017) Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. J Ecol 105:921–929. https://doi.org/10.1111/1365-2745.12788

Thomson B, Robson A, Abbott L (1992) The effect of long-term applications of phosphorus fertilizer on populations of vesicular-arbuscular mycorrhizal fungi in pastures. Aust J Agric Res 43:1131–1142. https://doi.org/10.1071/AR9921131

Toljander JF, Artursson V, Paul LR, Jansson JK, Finlay RD (2006) Attachment of different soil bacteria to arbuscular mycorrhizal fungal extraradical hyphae is determined by hyphal vitality and fungal species. FEMS Microbiol Lett 254:34–40

Trimmer JT, Guest JS (2018) Recirculation of human-derived nutrients from cities to agriculture across six continents. Nature Sustain 1:427–435. https://doi.org/10.1038/s41893-018-0118-9

Ulrich AE, Frossard E (2014) On the history of a reoccurring concept: phosphorus scarcity. Sci Total Environ 490:694–707. https://doi.org/10.1016/j.scitotenv.2014.04.050

Uroz S, Turpault MP, Delaruelle C, Mareschal L, Pierrat JC, Frey-Klett P (2012) Minerals affect the specific diversity of Forest soil bacterial communities. Geomicrobiol J 29:88–98. https://doi.org/10.1080/01490451.2010.523764

Vaccari DA, Strigul N (2011) Extrapolating phosphorus production to estimate resource reserves. Chemosphere 84:792–797. https://doi.org/10.1016/j.chemosphere.2011.01.052

van der Heijden MG, Boller T, Wiemken A, Sanders IR (1998) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79(6):2082–2091

Van Geel M, De Beenhouwer M, Ceulemans T, Caes K, Ceustermans A, Bylemans D, Gomand A, Lievens B, Honnay O (2016) Application of slow-release phosphorus fertilizers increases arbuscular mycorrhizal fungal diversity in the roots of apple trees. Plant Soil 402:291–301. https://doi.org/10.1007/s11104-015-2777-x

Wang P, Wang T-Y, Wu S-H, Wen M-X, Lu L-M, Ke F-Z, Wu Q-S (2019) Effect of arbuscular mycorrhizal fungi on rhizosphere organic acid content and microbial activity of trifoliate orange under different low P conditions. Arch Agron Soil Sci 65:2029–2042. https://doi.org/10.1080/03650340.2019.1590555

Watson C, Clemens J, Wichern F (2019) Plant availability of magnesium and phosphorus from struvite with concurrent nitrification inhibitor application. Soil Use Manag 35:675–682. https://doi.org/10.1111/sum.12527

Watts-Williams SJ, Cavagnaro TR (2014) Nutrient interactions and arbuscular mycorrhizas: a meta-analysis of a mycorrhiza-defective mutant and wild-type tomato genotype pair. Plant Soil 384:79–92. https://doi.org/10.1007/s11104-014-2140-7

Watts-Williams SJ, Cavagnaro TR (2015) Using mycorrhiza-defective mutant genotypes of non-legume plant species to study the formation and functioning of arbuscular mycorrhiza: a review. Mycorrhiza 25:587–597. https://doi.org/10.1007/s00572-015-0639-2

Wu Q-S, Cao M-Q, Zou Y-N, He X-h (2014) Direct and indirect effects of glomalin, mycorrhizal hyphae and roots on aggregate stability in rhizosphere of trifoliate orange. Sci Rep 4:5823. https://doi.org/10.1038/srep05823

Yao Q, Li X, Feng G, Christie P (2001) Mobilization of sparingly soluble inorganic phosphates by the external mycelium of an abuscular mycorrhizal fungus. Plant Soil 230:279–285. https://doi.org/10.1023/A:1010367501363

Yoneyama K, Yoneyama K, Takeuchi Y, Sekimoto H (2007) Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. Planta 225:1031–1038. https://doi.org/10.1007/s00425-006-0410-1

Zou Y-N, Srivastava AK, Ni Q-D, Wu Q-S (2015) Disruption of mycorrhizal extraradical mycelium and changes in leaf water status and soil aggregate stability in rootbox-grown trifoliate orange. Front Microbiol 6. doi: https://doi.org/10.3389/fmicb.2015.00203