Crop growth is increased by arbuscular mycorrhizae for both phosphate rock and soluble phosphorus fertilizers, but fertilizer solubility primarily determines crop growth

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Abstract

Arbuscular mycorrhizae (AM) are thought to improve crop growth by enhancing phosphorus (P) uptake via scavenging and enhancing dissolution. However, AM-mediated crop growth responses to P forms of varying solubility are often crop-species and soil-context dependent. The relative importance of AM associations and P source solubility on crop growth is not conclusively understood, and requires controlled factorial experiments to test their relative and interactive effects. We conducted a meta-analysis to evaluate how AM impact crop growth responses to rock phosphate relative to soluble phosphates across diverse crop species and soil characteristics. A total of 83 observations utilizing a 2×2 factorial design of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates were identified. We found that AM similarly improved crop growth with rock phosphate and soluble phosphates. A distinguishable crop growth benefit from AM coupled with rock phosphate was observed for soils with a low degree of weathering, at soil pH < 6.5 and > 7.5, and when soils were heat-sterilized prior to inoculation with AM. Shoot biomass of legumes was uniquely greater than non-legumes with rock phosphates and AM as compared to soluble phosphates and AM. However, crop growth under rock phosphate fertilization relative to soluble phosphates was still lower irrespective of AM. This meta-analysis reveals that crop growth is more dependent on P fertilizer solubility than AM. Moreover, AM do not appear to close the solubility gap of rock phosphate vs. soluble phosphate fertilizers to support similar crop growth under rock phosphate relative to soluble phosphates. Studies assessing crop growth responses to AM-crop associations effect on contrasting solubility P fertilizers should expand to the field, and greenhouse experiments should be conducted under realistic field growing conditions, such as agronomically appropriate P application rates.

Highlights
- AM-driven crop shoot biomass increased similarly under RP and SP.
- Crop biomass was lower under RP relative to SP fertilization irrespective of AM-enrichment.
- In soil pH < 6.5 and > 7.5, shoot biomass increased with RP but not SP under AM.
- Legume shoot biomass increased two-fold more than all crops for RP with AM.
- Root colonization when fertilized with SP was not lower than RP.

Abbreviations

AM	Arbuscular mycorrhiza
RP	Rock phosphate
SP	Soluble phosphate
PSM	Phosphorus solubilizing microbes
CCE	Calcium carbonate equivalent
SOM	Soil organic matter
SOC	Soil organic carbon
STP	Soil test phosphorus
PCR	Polymerase chain reaction
TSP	Triple superphosphate
TCP	Tricalcium phosphate
MCP	Monocalcium phosphate
USDA-NRCS	United States Department of Agriculture-Natural Resources Conservation Service
RR	Response ratio

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CI   Confidence interval
CV   Coefficient of variation

Introduction

Arbuscular mycorrhizae (AM) are known to improve phosphorus (P) uptake by host crop species in agroecosystems (Ferrol et al. 2019; Jansa et al. 2011). At least four major mechanisms have been hypothesized: (i) physical exploration of soil through fungal hyphae, which serve as root extensions to access distal P and increase the surface area of P uptake, (ii) P exchange among plants through common mycorrhizal networks, (iii) solubilization of insoluble inorganic P forms, and (iv) secretion of extracellular phosphatases to mineralize organic P (Bücking et al. 2016; Fellbaum et al. 2014; Jansa et al. 2011). Of these, solubilization is often assumed to be the chief means through which AM or the AM-hyphosphere-associated microbiome (Faghihinia et al. 2022; Zhang et al. 2022) aids in crop utilization of insoluble or low solubility P forms such as rock phosphates (RP), presumably through AM-mediated secretion of organic acids (e.g., maleic, citric, acetic acid) (Andrino et al. 2021; Tawaraya et al. 2006; Zhang et al. 2022). However, reports of P solubilization from insoluble inorganic P forms have been largely limited to ectomycorrhiza and ericoid mycorrhiza species (Blum et al. 2002; Landeweert et al. 2001; Smits et al. 2012; Van Schöll et al. 2006), rather than for AM that are more common mutualists with crop species (Plassard and Dell 2010). In some cases, crop utilization of RP is not improved by AM as compared to soluble phosphates (SP) such as superphosphate (e.g., Dann et al. 1996). Despite this, many studies continue to propose or assume, but do not test, the hypothesized benefit of AM-acquisition of P from low solubility sources such as RP over SP (Bolan et al. 1987; Klugh-Stewart and Cumming 2009; Parfitt 1979; Yao et al. 2001).

In cases where AM may improve crop P uptake from low solubility forms such as RP, the greater dissolution rate and thus crop availability of SP may outweigh the enhanced dissolution of low solubility P forms, leading to greater net crop P availability (Barrow et al. 1977; Pairunan et al. 1980; Thirkell et al. 2017). In P-deficient soils, crop yields under RP fertilization are generally lower compared to SP (Malhi et al. 2014; Mnkeni et al. 1991; Wahid et al. 2016). AM-driven dissolution of P from RP could close the gap of crop growth under RP fertilization compared to SP, conceptualized as the "solubility gap". For example, in acidic soils, crop yields under RP can be comparable to those with SP due to abiotic dissolution of P from RP acting as an additive benefit to AM-driven dissolution (Chien and Menon 1995; Ellis et al. 1955; Mutuo et al. 1999). Nevertheless, AM could improve crop growth even under SP fertilization. For example, more than 50% of P uptake in wheat (*Triticum aestivum*) can be via AM hyphae, even with SP fertilizers such as ammonium polyphosphate and sodium phosphate (Li et al. 2006). Even if AM-driven chemical dissolution of inorganic P from SP is negligible, AM access to distal P up to several centimeters beyond the root (Jansa et al. 2003) can increase crop P uptake, especially in the early stages of plant growth when nascent root systems access a limited portion of bulk soil P (Barber 1995; Grant et al. 2001) and in fields with broadcast application of P fertilizers (Bolan et al. 1987; Shen et al. 2012).

Reported benefits of AM for crop growth have been critiqued for overemphasizing AM effects in pot-scale greenhouse studies (Ryan and Graham 2018; Thirkell et al. 2017). There is a general lack of field scale evaluations that assess the impact of AM-crop associations on crop growth and yield with varying P solubility sources in biotically and abiotically complex agroecosystems (Lekberg and Helgason 2018; Thirkell et al. 2017), despite historically recognized needs for field scale evaluation of AM function in crop P acquisition (Johnson et al. 1997; Read 1991). Field studies provide evaluation of the impact of AM associations on crop growth across management practices such as tillage and a range of complex biotic and abiotic interactions not replicable at the greenhouse scale (Thirkell et al. 2017). On the other hand, the effect of AM on crop growth may be confounded in a field experiment with multiple biotic interactions and spatiotemporally variable abiotic conditions compared to a controlled greenhouse experiment. High root densities in pots could negate physical P acquisition benefits of AM, though P dissolution from RP would likely be greater at high plant root densities. Additionally, the method of inducing AM colonization differences such as soil sterilization by heat or fumigants could adversely affect the complex soil biological community, overemphasizing AM effects (Forero et al. 2019; Heinze et al. 2016; Schittko et al. 2016).

Apart from experimental methods, crop species and soil conditions can account for conflicting reports of how AM impact crop growth under contrasting P fertilizer solubilities. Differences in root densities and rhizosphere acidification of legumes vs. non-legumes could potentially impact AM-driven crop growth response with different solubility P fertilizers (Bekele et al. 1983; Truog 1916). Legumes generally have greater rhizosphere acidification than non-legumes by greater exudation of organic acids and phosphatases (Shen et al. 2012) that could enhance dissolution of RP. Relative effects of AM on RP versus SP are likely to be influenced by pH and soil P fixation (Blal et al. 1990; Powell and Daniel 1978), which in part reflects the degree of soil weathering, as pH influences fertilizer dissolution and P fixation can mitigate greater availability of SP-derived P. In highly weathered soils (e.g., Oxisols) and many Andisols

that are highly P-fixing, greater rate of orthophosphate release from SP will entail a higher rate of P-fixation, hence reduced labile P pools relative to gradual AM-driven RP dissolution. Another soil property that potentially influences RP dissolution is soil organic matter (SOM) content, with higher organic matter content driving RP dissolution by serving as a sink (via complexation) of Ca^{+2} (Chien and Menon 1995). Thus, accounting for crop species and soil properties can help disentangle agroecosystem-specific effects of AM on crop response to RP vs. SP.

To reconcile conflicting arguments about the relative importance of P source solubility and AM associations for crop growth, controlled factorial experiments that test relative and interactive effects of P solubility and AM associations are needed. Given agroecosystem-specific manifestation of AM-driven crop growth responses, meta-analysis affords quantitative assessment of P solubility and AM associations across agroecosystem contexts hypothesized to influence the relative importance of these two factors. We conducted a systematic literature review and meta-analysis to assess AM impact on host crop biomass and root colonization from RP and SP. Specific objectives were to assess AM-crop symbiosis impact on crop growth response when fertilized with (i) RP or (ii) SP, and to evaluate the effect of RP relative to SP on crop growth (iii) with or (iv) without relative presence of AM (expressed as AM-enrichment vs. AM non-enrichment). We hypothesized that AM-enrichment would increase crop biomass (total, shoot, root) and root colonization for both RP and SP relative to AM non-enrichment. Additionally, we expected crop biomass and root colonization would be improved with RP fertilization relative to SP only with AM-enrichment. For each of the response variables, we tested the effect of methodological and contextual variables that could influence interactions of AM and P solubility on crop growth. We hypothesized an increase in crop growth with RP relative to SP with AM-enrichment with a (i) greater degree of soil weathering, (ii) higher soil pH, (iii) low soil P availability as assessed by soil test P values, and (iv) in non-legumes vs. leguminous crops. We anticipated these responses to vary by study scale, crop type, and method of soil sterilization. We also analyzed methodological parameters and contextual variables to identify gaps in study design for evaluating AM benefits hypothesized for host crops for P sources of varying solubility.

Methods

Literature search and review

A comprehensive literature search was conducted on Web of Science on September 24, 2020, using the keywords: *mycorrhiza/mycorrhizae* AND *phosphate rock* within "topic" in "all databases" for the years 1864–2020. This resulted in 739 search results. The full text of initial results was surveyed to select peer-review publications evaluating AM by removing ecto- and ericoid/orchidaceous mycorrhiza studies. A subsequent search with the keywords *mycorrhiza/mycorrhizae*, *arbuscular* AND *phosphate rock* within the original search constraints was also performed to identify potential additional publications, none of which were found. The resulting 229 studies were then screened for robustness of experimental design. To test the effect of relative presence or absence of AM on crop growth responses when fertilized with RP or SP, only studies reporting a full 2×2 factorial of relative presence or absence of AM and fertilization with RP vs. SP were retained. Importantly, studies were selected only if a non-AM control for both RP and SP was included. The non-AM control is referred to as AM non-enrichment describing relative absence of AM. We use this notation because AM uninoculated or even genotypically non-AM plants have reduced AM presence, as opposed to no AM colonization (Bodenhausen et al. 2021; Nair and Bhargava 2012; Shi et al. 2013). Many agronomic evaluations of AM and RP vs. SP had a $2 (\pm AM) \times 1$ (RP) factorial design, which are unable to test AM-enrichment vs. non-enrichment for SP. Such observations were excluded from the meta-analysis because these observations do not permit a comprehensive comparison of AM effects for both RP and SP. Publications were rejected for inclusion in the meta-analysis dataset based on confounded P rates and/or sources, use of non-soil growth media (e.g., tin tailings), and incomplete methods, analysis, or missing experimental design details. This resulted in a final set of 19 peer-reviewed studies yielding $n = 83$ observations. Two studies by Lin and Fox (1987; 1992) were counted as one source, since they report data separately from the same experimental evaluation.

Data extraction

Reference descriptors, descriptive variables, and response variables were extracted from tables or from figures using DataThief software (Tummers 2006). Descriptive variables comprised of study scale (field vs. greenhouse), method of inducing AM colonization (sterilization only, inoculation only, sterilization + inoculation, genotype), geographical region (UN region classification), crop species, crop class (legume vs. non-legume), tillage (conventional tillage vs. no-tillage) and irrigation (irrigated vs. non-irrigated), soil order (USDA Soil Taxonomy), degree of soil weathering (low, intermediate, high), soil particle size fractions (sand, silt, clay; %), soil textural class, soil organic matter (%), soil pH, and available or extractable soil P concentration (mg kg^{-1} soil), measurement method (Mehlich III, Bray I, Bray II, Olsen, Resin) and method of quantification (colorimetric vs. ICP).

Phosphate rock characterization variables extracted were ore source, fineness, calcium carbonate equivalent (CCE), total P (%), and soluble P (%). Soluble phosphate characterization variables extracted were fertilizer type (e.g., ammonium phosphate, superphosphate, potassium dihydrogen phosphate), total P (%), and soluble P (%). Fertilizer P application rates were extracted as mg kg^{-1} for greenhouse studies and kg ha^{-1} for field studies. Extracted mycorrhizal descriptors were type of inoculum (external inoculum vs. native), species composition of inoculum (single vs. mixed species), AM species, confirmation of colonization by the study (yes vs. no), and method to determine colonization (root staining, root staining and spore count, root staining and PCR).

Extracted response variables were AM root colonization counts (%), shoot (aboveground), root (belowground), and total biomass (g plant^{-1} for greenhouse study and t ha^{-1} for field study), P concentration in aboveground, belowground, and total biomass fractions (%) and P uptake in the three biomass fractions (t ha^{-1} for field studies and mg plant^{-1} for greenhouse studies).

Data consolidation

Extracted data were consolidated to be in common units. For unreported data which could not be assigned a value even after assumptions and conversions, NA (not available) was assigned. Crops were classified as legume or non-legume. Percent sand as a soil particle size fraction was calculated from coarse sand and fine sand fractions (%) if only these sub-fractions were reported. Soil textural class was assigned according to USDA classification, and if unreported, was calculated based on particle size fraction (%). Reported SOM values were converted to %, and soil organic carbon (%) was converted to SOM (%) assuming that SOM is 58.1% organic carbon by mass (Van Bemmelen 1890; Wolff 1864). Degree of soil weathering was classified as

low, intermediate, and high according to Brady and Weil (2016); Margalef et al. (2017); and Nakayama et al. (2021). Soil pH was classified as acidic, circumneutral, and alkaline (< 6.5, $6.5–7.5$, and > 7.5) based on USDA NRCS guidelines (Burt 2014; Staff 2014). Available soil P was based on extractable or "soil test" P (STP) on an Olsen basis, though it was originally developed to predict crop yield response and was classified based on agronomic recommendations (Hertzberger et al. 2020; Mallarino and Atia 2005; Mallarino et al. 2013). There were no or low observations for total soil P ($n=0$ studies), soil organic P ($n=0$ studies) or available soil inorganic N ($n=4$ studies).

Phosphate rock and SP fertilizer characteristics were extracted to interpret the effect sizes of P source solubility and AM associations on crop growth. Phosphate rock solubility was assessed by 2% citric acid or formic acid soluble P and consolidated as solubility (% of total P). Phosphate rock fineness and CCE (%) were removed due to large variability in method of reporting and absence of data, respectively. Unreported total P content (%) for SP was assumed based on commercial fertilizer grades and converted from P_2O_5 to P, as follows: diammonium phosphate (DAP) — 20.1% P; triple superphosphate (TSP) — 19.2% P; KH_2PO_4 — 22.8% P; tricalcium phosphate (TCP) — 20.0% P; monocalcium phosphate (MCP) — 24.6% P; calcium-superphosphate (same as single superphosphate) — 7.9% P; superphosphate — 7.9% P. For P application rates (mg kg^{-1} soil and kg ha^{-1}), conversions from reported data were performed assuming 15 cm soil depth and 1.3 g cm^{-3} bulk density.

Response variables were used to gauge plant responses to P source solubility × AM presence. Aboveground biomass was the most abundant response and was used as a direct measure of plant response to treatments. Biomass values reported as kg fed^{-1} were converted to t ha^{-1} using 1 fed = 0.42 ha (Mahmoud et al. 2013). Biomass fraction P uptake was calculated as follows:

Equation 1.

$$\text{P uptake } \left(\text{t ha}^{-1} \text{or mg plant}^{-1}\right) = \frac{\left[\text{Biomass fraction } \left(\text{t ha}^{-1} \text{or mg plant}^{-1}\right) * \text{Biomass fraction P concentration}(\%)\right]}{100}$$

To facilitate testing effect sizes as response ratios, the final dataset was organized into factorial sets each comprised of the 2×2 factorial of relative presence or absence of AM and P source solubility. This allows testing crop response to RP relative to SP in the relative presence or absence of AM, which we refer to as AM-enrichment vs. AM non-enrichment. At the end of data consolidation, only factorial sets were retained which were field and greenhouse studies with at least above ground biomass as a response, for a final dataset of $n=83$ factorial sets from 19 studies.

Calculation of response ratios (RRs) and statistical analysis

The response ratio (RR), referring to effect sizes, is the ratio of mean outcome in the treatment group to that in the control group (Hedges et al. 1999). It indicates treatment response relative to the control. In this case, RR refers to the ratio of mean crop response with RP vs. SP under AM-enrichment or not. Response ratios were calculated as:

Table 1 Distribution of soil order and degree of weathering in a metadataset, comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

Degree of weathering	Observations (n)	Observations (%)	Soil order (USDA)	Observations (n)	Observations (%)
High	6	10.2	Spodosols	2	3.4
			Oxisols	3	5.1
			Ultisols	1	1.7
Intermediate	50	84.7	Andisols	40	67.8
			Vertisols	6	10.2
			Mollisols	4	6.8
Low	3	5.1	Inceptisols	3	5.1
Total reported	59 (71.1%)			59 (71.1%)	

$$\text{Response ratio} = \frac{\text{Treatment response}}{\text{Control response}} \qquad (1)$$

The four RRs in this evaluation were (i) AM effect on RP, (ii) AM effect on SP, (iii) RP vs. SP (+ AM), and (iv) RP vs. SP (− AM). 95% confidence intervals (CIs) were used to determine significance and directionality of treatment effects. A positive treatment effect was inferred if RR was greater than 1 and CI did not overlap with the 1:1 line on the x-axis. A negative treatment effect was inferred if RR was less than 1. An absence of treatment effect was inferred if CI overlapped with the 1:1 line on the x-axis (Akobeng 2005; Egger et al. 1997). RRs with overlapping 95% CIs were considered statistically similar (Zlowodzki et al. 2007). Summary statistics, analyses, and data visualization were conducted in Microsoft Excel, SigmaPlot, and RStudio (Team 2015) using *psych* (Revelle 2020), *FSA* (Ogle et al. 2023), *ggplot2* (Wickham 2016), and *ggpubr* (Kassambara 2020) packages using *summary*, *summarize*, *ggscatter*, and *ggplot functions*.

Results

Approaches to assessing arbuscular mycorrhizal × P source solubility

Most observations of AM and P source solubility effects on plant growth response were inoculation-based greenhouse studies for non-legume species in acidic, P-responsive soils, but with very high field-equivalent P application rates. Geographical distribution of the observations was not uniform across regions, with more than half of the observations from Oceania ($n = 42$, 50.6%). Africa ($n = 11$, 13.3%), Latin America and the Caribbean ($n = 10$, 12.0%), Asia ($n = 8$, 9.6%), Europe ($n = 6$, 7.2%), and North America ($n = 6$, 7.2%) each contributed less than 15% of total observations. Greenhouse studies were more common ($n = 78$, 94%) than field studies ($n = 5$, 6%), the majority of which were tilled ($n = 4$, 80%) and irrigated ($n = 5$, 100%). The predominance of greenhouse studies in the metadataset, which is comprised of experiments that use a full 2×2 factorial design to test AM-enrichment or non-enrichment and fertilization with RP

Table 2 Properties of soils in a metadataset, comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

Sand (%)		Silt (%)		Clay (%)		SOM (%)		pH	
Min	18.2	Min	4.7	Min	4.8	Min	0.07	Min	4.1
1st quartile	26.0	1st quartile	15.2	1st quartile	5.8	1st quartile	0.7	1st quartile	5.4
Median	33.8	Median	30.0	Median	42.0	Median	1.3	Median	5.7
Mean	41.7	Mean	26.5	Mean	32.8	Mean	4.2	Mean	6.1
3rd quartile	58.8	3rd quartile	36.5	3rd quartile	44.0	3rd quartile	6.3	3rd quartile	7.0
Max	90.5	Max	39.8	Max	52.8	Max	18.0	Max	8.2
Not reported	(n=74; 89.2%)	Not reported	(n=74; 89.2%)	Not reported	(n=74; 89.2%)	Not reported	(n=60; 72.3%)	Not reported	(n=4; 4.8%)

vs. SP, represents a critical literature gap of a lack of full factorial field scale evaluations needed to test the AM effect on P sources of varying solubility.

Soils with an intermediate degree of weathering constituted the majority (85%) of observations, with 10% and 5% of observations derived using soils with high and low degrees of weathering (Table 1). Approximately two-thirds of intermediately weathered soils (68%) were from a single soil type (Andisol) from one study in New Zealand. The majority of the studies did not report soil particle size fractions (89%) nor SOM content (72%). Soil particle size fractions varied widely, with a mean of approximately 41% sand, 26% silt, and 33% clay, and textural class of clay loam (Table 2). The sand, silt, and clay content (%) varied by a factor of $\approx$ 5, 8.5, and 11, respectively. Soil organic matter varied by 257-fold from 0.07 to 18%, with a mean of 4.2%. Soil pH, reported for 95% of observations, varied from acidic (4.1) to alkaline pH (8.2) with a mean of 6.1 (Table 2). The majority (75%) of the observations from studies reporting initial soil pH values were from acidic soils ($n = 59$), and circumneutral ($n = 12$) and alkaline soils ($n = 8$) accounted for approximately 15% and 10% of observations, respectively. Available soil P (Olsen) varied by 20-fold from 0.9 to 18.2 mg kg^{-1} (mean 8.1 mg kg^{-1}), and three-fourths of observations were from soils below the threshold of 10–13 mg kg^{-1} considered to merit P fertilization for most crops (Mallarino and Atia 2005; Mallarino et al. 2013) (Table 3). Of the available soil P values reported (87% of observations), most indicated low (40%) or very low (approximately 35%) STP soils that would be expected to have a crop response to P fertilization. Soil pH and STP were positively related ($R = 0.31$; $p = 1.2e-07$), and low and very low STP soils largely (83%) occurred in acidic soils (pH < 6.5). High STP soils ($n = 13$) were associated with low (pH < 6.5) to circumneutral pH (6.5–7.5) soils. Optimal STP soils were found in low pH (< 6.5) ($n = 4$) and circumneutral (pH 6.5–7.5) ($n = 1$) soils. Acidic soils occurred for all STP classifications (low to high), but alkaline soils (pH > 7.5) only had very low STP soils.

Table 4 Classification of rate of applied phosphorus (P) (mg P kg^{-1}) in soils of a metadataset, comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

P application rate (mg/kg soil)	Observations (n)	Observations (%)
0–30	24	28.9
30–120	6	7.2
120–150	40	48.2
150–480	13	15.7
Total reported	83 (100%)	

Soil P application rates varied by a factor of 1170-fold from 0.4 to 480 mg kg^{-1} soil. Only 29% of the observations used P applications at a field-equivalent realistic rate of 0–30 mg kg^{-1} (Table 4). In most soils (71%), P was applied at a rate exceeding harvest removal and thus recommended P application rates for grain crops such as maize (*Zea mays*), soybean (*Glycine max*), and wheat in low STP soils (Fernández and Hoeft 2009; Kaiser et al. 2011; Mallarino and Atia 2005). Soil P application rate was unrelated to STP of the soil used for the study ($R = -0.13$, $p = 0.025$) (Fig. S1). In already high STP soils, P was applied at rates exceeding 120 mg P kg^{-1} (Table 5). In contrast, P was applied at less than 30 mg P kg^{-1} in most soils with optimal STP (80%). Distribution of soil P application rates was more varied in low and very low STP soils, but in at least half of the very low (60%) and low (70%) soils, P rate was still greater than 120 mg kg^{-1}. Field-equivalent realistic P rates were only observed in 21% of low and 32% of very low STP soils.

Approximately one-fifth of crop species were legumes, comprised of lentil (*Lens culinaris*), fava bean (*Vicia faba*), soybean, alfalfa (*Medicago sativa*), and subterranean clover (*Trifolium subterraneum*) (Table 6). The 82% of observations that were non-legumes were largely grasses (66%) such as wheat, tall fescue (*Festuca arundinacea*), maize,

Table 3 Soil test phosphorus (STP) and STP classification of soils in a metadataset comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

STP (mg/kg)		Quantification method	Obs[a] (n)	Obs[a] (%)	STP classification	Obs[a] (n)	Obs[a] (%)
Min	0.9	Colorimetric	71	98.6	High	13	18.1
1st quartile	4.0	ICP	1	1.4	Optimal	5	6.9
Median	6.9	Total reported	72 (86.7%)		Low	29	40.3
Mean	8.1				Very low	25	34.7
3rd quartile	9.2				Total reported	72 (86.7%)	
Max	18.2						
Not reported	11 (13.3%)	Not reported	($n = 11$; 13.3%)		Not reported	($n = 11$; 13.3%)	

[a]Obs (n) refers to the number of observations and Obs (%) refers to the percent of observations

Table 5 Distribution of soil test phosphorus (STP) and rate of P applied (from $n=72$ observations (87% of total) which contained values for both STP and soil P application rates) in a metadataset comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

P application rate classification (mg kg^{-1} soil)	Very low STP (n, %)	Low STP	Optimal STP	High STP
0–30	8 (11.1%)	6 (8.3%)	4 (5.6%)	
30–120	2 (2.7%)	3 (4.2%)		
120–150	10 (13.9%)	20 (2.8%)	1 (1.4%)	10 (13.8)
150–480	5 (6.9%)	-	-	3 (4.2%)
Total reported = 72				

Table 6 Distribution of crop class and species classification in a metadataset comprising of a 2×2 factorial of relative presence or absence of arbuscular mycorrhizae (AM) and fertilization with rock phosphate vs. soluble phosphates, used to evaluate AM effect on crop growth

Crop	Obs (n)	Obs (%)	Crop species	Latin name	Obs (n)	Obs (%)	Obs (%)
Legume	15	18.1	Lentil	*Lens culinaris*	3	17.6	3.5
			Faba bean	*Vicia faba*	4	23.5	4.7
			Soybean	*Glycine max*	2	11.8	2.4
			Alfalfa	*Medicago sativa*	4	23.5	4.7
			Subterranean clover	*Trifolium subterraneum*	2	13.3	2.4
Non-legume	68	81.9	Wheat	*Triticum aestivum*	7	10.3	8.3
			Tall fescue	*Festuca arundinacea*	2	2.9	2.4
			Banana	*Musa spp.*	3	4.4	3.5
			Maize	*Zea mays*	5	7.4	5.9
			Tabasco pepper	*Capsicum frutescens*	6	8.8	7.1
			Tomato	*Solanum lycopersicum*	1	1.5	1.2
			Sugarcane	*Saccharum officinarum*	2	2.9	2.4
			Perennial ryegrass	*Lolium perenne*	40	58.8	47.1
			Sweet fennel	*Foeniculum vulgare*	2	2.9	2.4

sugarcane (*Saccharum officinarum*), and perennial ryegrass (*Lolium perenne*); vegetable crops (7%) such as Tabasco peppers (*Capsicum frutescens*); fruits ($\approx$ 5%) such as tomato (*Solanum lycopersicum*); and herbs (2%) such as fennel (*Foeniculum vulgare*). Nearly half of the total observations (47%) were from perennial ryegrass.

All studies used AM inoculum to induce AM but approximately one-fourth of observations first sterilized soils before inoculation (Table S1). Use of external inoculum was more common (75%) than relying on soil native AM species. No study used sterilization alone or genotypic models to induce AM. Most (87%) inoculations were performed with a single AM species (Table S2), most commonly *Gigaspora margarita* (24%), *Funneliformis mosseae* (17%), and *Planticonsortium tenue* (22%). The majority of studies and thus observations (95%) confirmed colonization, largely by root staining. Less than 10% observations were from studies that confirmed colonization by either spore count ($n=5$, 6.0%) or PCR ($n=2$, 2.4%) in addition to root staining.

Overall effects of AM-crop symbiosis and P solubility sources on crop biomass

Shoot biomass increased with AM-enrichment and when fertilized with either RP or SP but did not increase with RP relative to SP irrespective of AM colonization (Fig. 1a). The increase in shoot biomass response was similar by P source (AM effect on RP and SP).

Greenhouse studies (94% of observations) reflected the trends in overall shoot biomass responses (Fig. 1b). No differences in shoot biomass by P solubility (AM effect on RP and SP) or AM (RP vs. SP [$\pm$ AM]) were observed for field studies (6% of observations). Biomass responses for $n=11$ observations that measured total biomass as shoot (aboveground) and root (belowground) fractions showed distinct responses to AM and P solubility compared to shoot-only biomass observations ($n=83$) (Fig. 2a–c). Total, shoot, and root biomass increased with RP but not SP fertilization under AM-enrichment. However, shoot biomass but not root biomass, as a proportion of total biomass, did

Fig. 1 (**a**) Effect of arbuscular mycorrhizae (AM)-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset ($n=83$) comprising of a 2×2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates. (**b**) Impact of study scale on AM-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset ($n_{field}=5$; $n_{GH}=78$) comprising of a 2×2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates
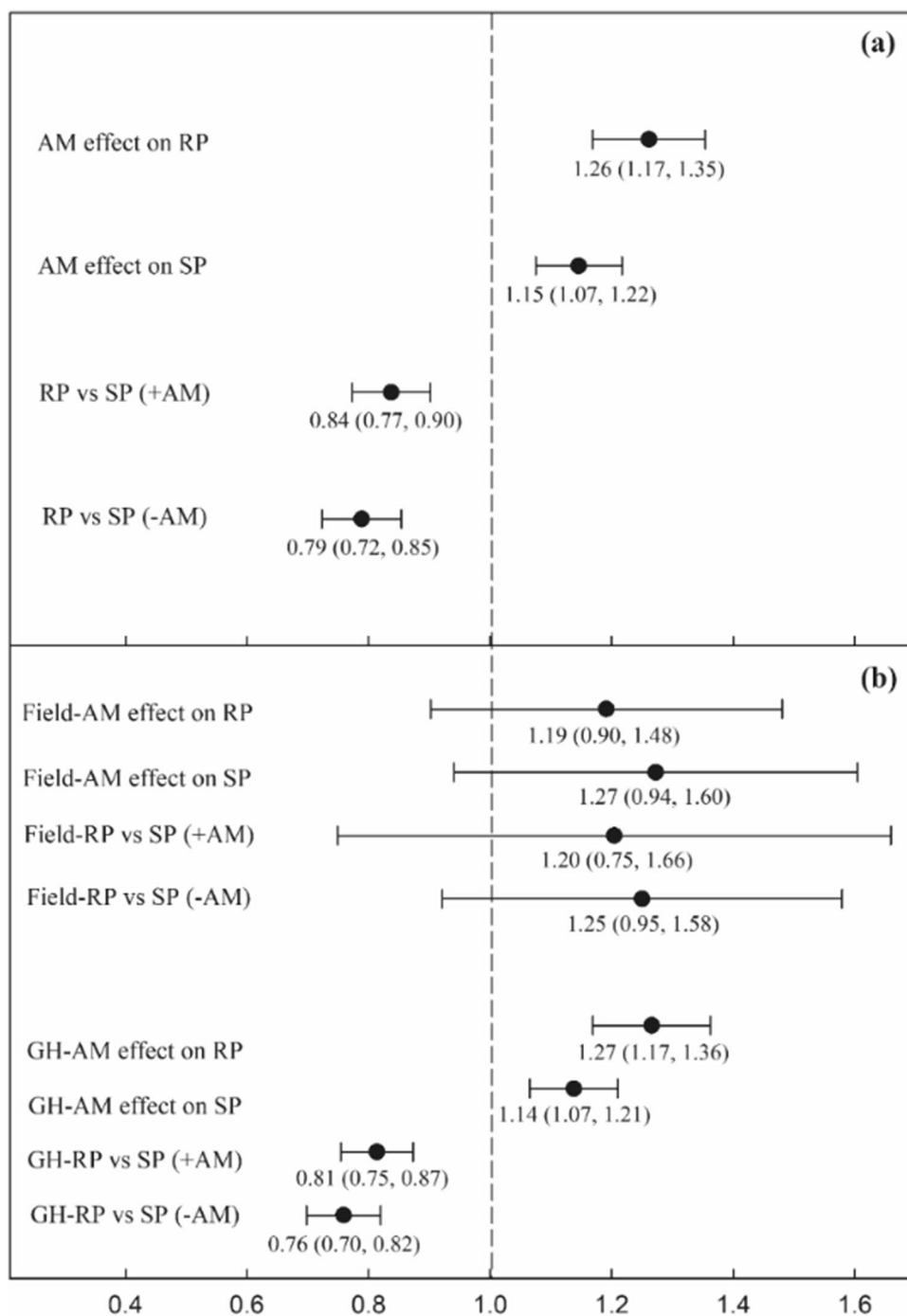
not follow the same trend as the absolute biomass values (Fig. 3a, b). No differences in shoot biomass as a proportion of total biomass by P solubility or AM were observed. Root biomass increased most (54%) under AM-enrichment and RP fertilization, followed by total (30%), and shoot (27%) biomass. Root but not shoot or total biomass increased with RP fertilization relative to SP fertilization under AM-enrichment (45%).

Influence of soil properties and P application rates

The overall crop shoot biomass responses varied by soil classification and properties of degree of weathering, pH, and STP (Fig. 4a–c) and by P application rates (Fig. 4d). Only in low weathered soils did AM-enrichment entail 32% greater shoot biomass for RP relative to SP (Fig. 4a). In highly weathered soils, shoot biomass decreased compared
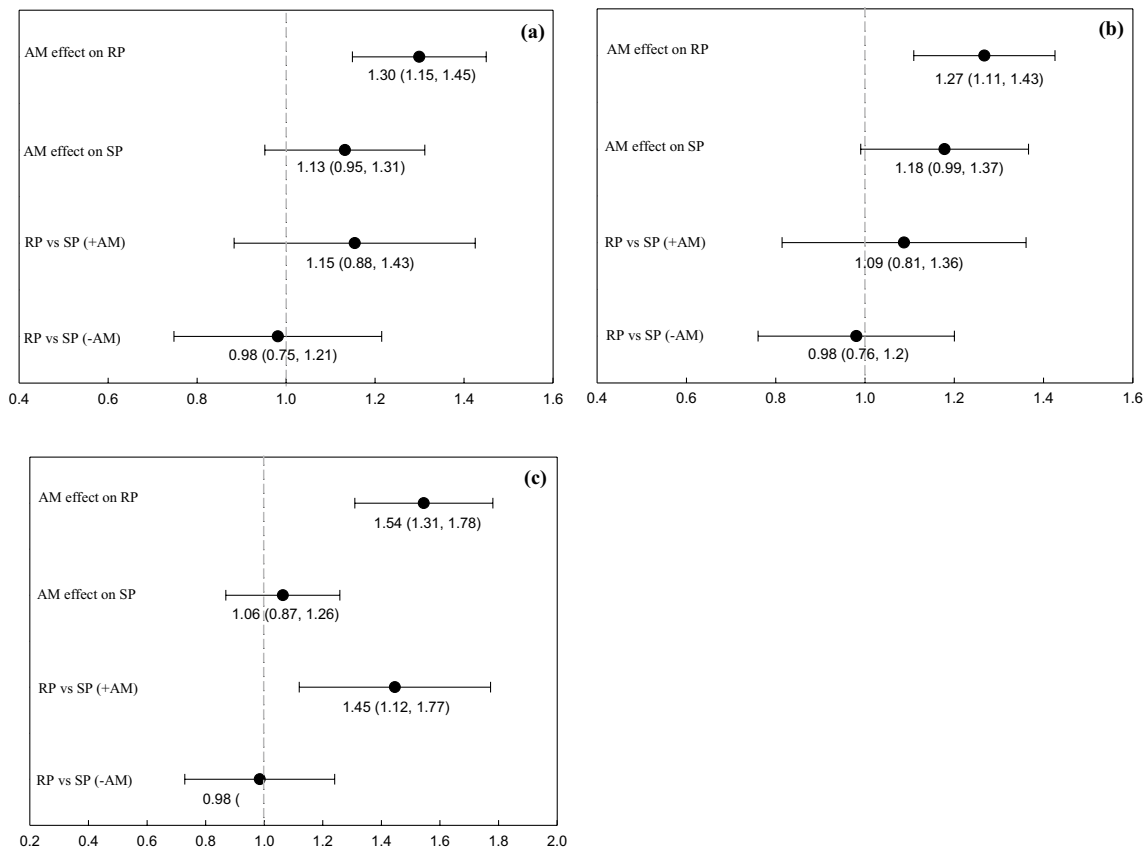
Fig. 2 Effect of arbuscular mycorrhizae (AM)-crop symbiosis and P solubility sources on (a) total (aboveground and belowground) shoot biomass response, (b) shoot (aboveground) biomass response, and (c) root (belowground) biomass response in a subset of ($n=11$) containing observations for total, shoot, and root biomass response

to low and intermediately weathered soils, regardless of P source solubility or AM-enrichment, and decreases in shoot biomass with RP relative to SP (45%) were nearly double in magnitude compared to shoot biomass responses across soils (≈20%). In intermediately weathered soils, which accounted for over 80% of observations, shoot biomass was lower with RP than SP irrespective of AM-enrichment but the decrease was similar to the mean response across soils. However, in contrast to highly weathered soils, shoot biomass increased with AM-enrichment regardless of P source solubility. In low weathered soils, shoot biomass increased under AM-enrichment with RP but not with SP, and the increase was 33% in contrast to a 14% increase in intermediately weathered soils.

Related to but separate from degree of weathering, soil pH also modulated shoot biomass response to P source solubility and AM (Fig. 4b). Shoot biomass increased under AM-enrichment and RP fertilization in tandem with soil pH, albeit inconsistently. Shoot biomass increase was ≈ 1.8- or 1.5-fold higher for RP or SP in circumneutral soils as compared to mean responses across soils (1.3- and 1.1-fold increase). In acidic and alkaline soils, shoot biomass

increased with RP but not with SP under AM-enrichment. In contrast, shoot biomass increased regardless of P source solubility under AM-enrichment in circumneutral soils by + 77%, which was greater than acidic soils (+ 15%) and similar to alkaline soils (+ 29%). Similar to mean responses across soils, shoot biomass did not increase with RP relative to SP irrespective of AM-enrichment. In contrast to highly variable shoot biomass responses with soil pH, shoot biomass increases under AM-enrichment was similar across STP classes, but only for RP (Fig. 4c). Shoot biomass responses with SP fluctuated across STP classes with an increased shoot biomass only observed in low STP soils. Similar to mean responses across soils, across STP classes, shoot biomass did not increase with RP relative to SP irrespective of AM-enrichment.

At P application rates that are agronomically typical (<30 mg kg^{-1} or <60 kg ha^{-1}), shoot biomass responses were similar between P solubility sources under AM-enrichment (Fig. 4d). At P application rates greater than 30 mg kg^{-1}, shoot biomass varied inconsistently by P source solubility and was not necessarily proportionate to the application rate. At 30–120 mg kg^{-1} P application rate,

Fig. 3 Effect of arbuscular mycorrhizae (AM)-crop symbiosis and P solubility sources on (**a**) shoot biomass as a proportion of total biomass and (**b**) root biomass as a proportion of total biomass in a subset of ($n = 11$) containing observations for total, shoot, and root biomass responses
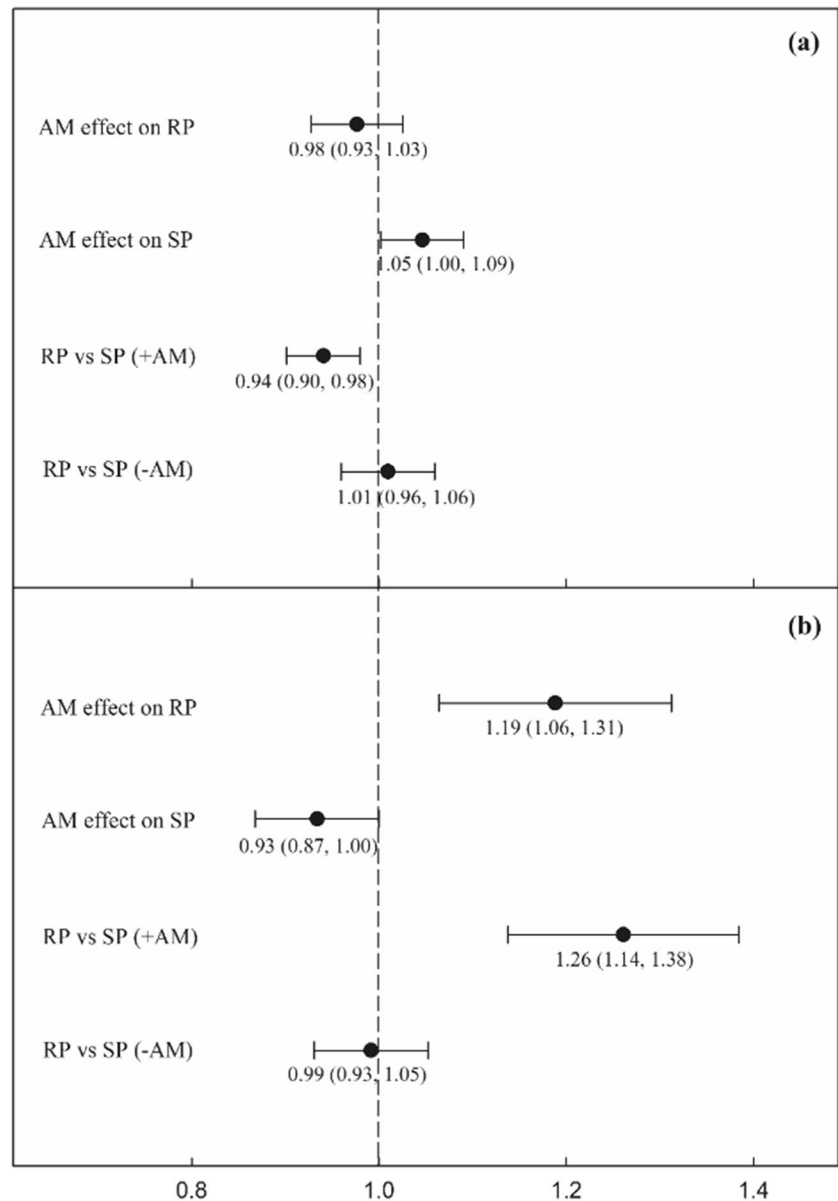
shoot biomass increased with RP but not SP fertilization under AM-enrichment. In contrast, at 120–150 mg kg^{-1} application rate, shoot biomass did not increase with either P solubility source regardless of AM-enrichment. At P application rates exceeding 150 mg kg^{-1}, shoot biomass increased with both RP and SP only under AM-enrichment. Across P application rates, shoot biomass was similar regardless of P source solubility and AM-enrichment. However, at the highest P application rates (> 150 mg P kg^{-1}), shoot biomass was lower with RP relative to SP under AM-enrichment compared to the lowest application rates (< 30 mg P kg^{-1}). Even without AM-enrichment, shoot biomass with RP relative to SP fertilization was greater at the lowest P application rate (< 30 mg kg^{-1})

than at the highest P rates (> 150 mg kg^{-1}), but an increase with RP compared to SP was not observed.

Influence of crops and method of AM-enrichment

Crop shoot biomass responses varied across P solubility sources depending on the crop species and how AM-enrichment was induced (Figs. 5 and 6). Legume shoot biomass increased under AM-enrichment for RP but not SP (Fig. 5). Legume shoot biomass increased by approximately 50% for RP under AM-enrichment compared to approximately 25% across all crop classes. In contrast, non-legume shoot biomass increased under AM-enrichment regardless of P solubility sources, and the increase was similar to the mean response across crops.
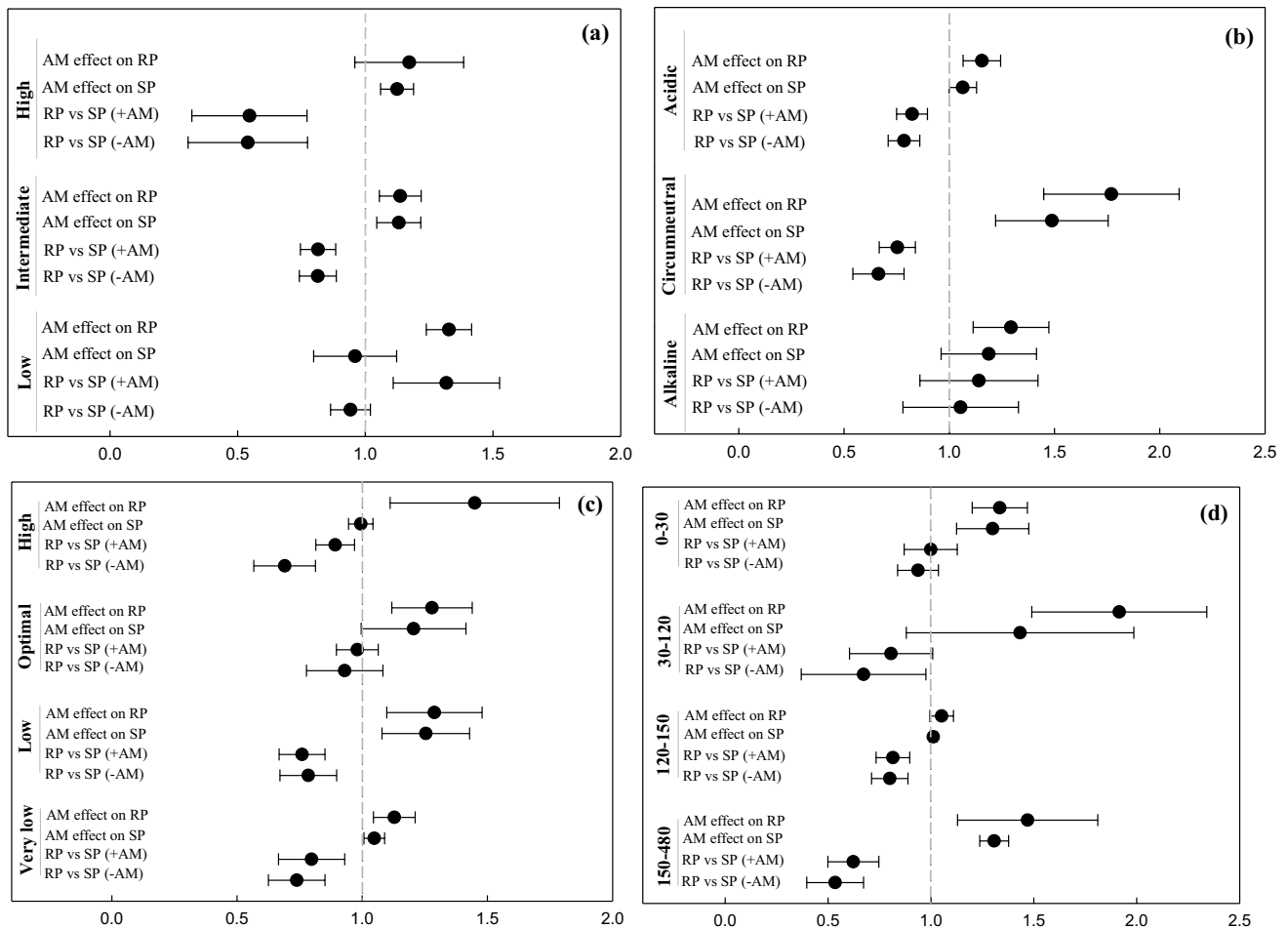
Fig. 4 Impact of soil properties and P application rates on arbuscular mycorrhizae (AM)-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset comprising of a 2×2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates. (**a**) Impact of degree of soil weathering which were high ($n=6$), intermediate ($n=50$), and low ($n=3$); (**b**) Impact of soil pH (acidic ($n=59$), circumneutral ($n=12$), and alkaline ($n=8$)); (**c**) Impact of soil test phosphorus (STP) (high ($n=13$), optimal ($n=5$), low ($n=29$), and very low ($n=25$); (**d**) Impact of P application rate, expressed as mg P kg.$^{\pm 1}$ ($n_{[0–30]}=24$; $n_{(30–120)}=6$; $n_{(120–150)}=40$; $n_{(150–480)}=13$)

Shoot biomass of legumes and non-legumes did not increase with RP relative to SP, irrespective of AM-enrichment.

Though all soils generated AM contrasts though AM inoculation, soils that were first sterilized had a mean $+54\%$ greater shoot biomass with RP than the mean response (26%) across soils, and $+76\%$ if heat sterilized or $+19\%$ if chemically sterilized (Fig. 6a). In contrast, inoculating without sterilization led to largely similar shoot biomass with AM-enrichment for both RP and SP. In chemically sterilized soils, shoot biomass responses under AM-enrichment across P solubility sources were similar to the mean responses in inoculated soils as well as across soils (Fig. 6b). However, in heat-sterilized soils, shoot biomass increased under AM-enrichment only for RP but not SP. Regardless of how AM-enrichment differences were induced, shoot biomass was consistently lower with RP relative to SP. When reported, root colonization rates were elevated by approximately

3-fold for RP and SP fertilization under AM-enrichment (Fig. 7). Under AM-enrichment, root colonization rates for plants fertilized with RP varied from 16% lower to 69% higher than those fertilized with SP. Without AM enrichment, root colonization rates varied from 49% lower to 3-fold higher for RP relative to SP.

Discussion

AM improve crop growth with both RP and SP, but not for RP relative to SP

Similar increases in shoot biomass with AM regardless of P solubility indicate enhanced crop P acquisition from RP and SP, though potentially by different mechanisms. Whereas AM can increase crop P acquisition from RP by P
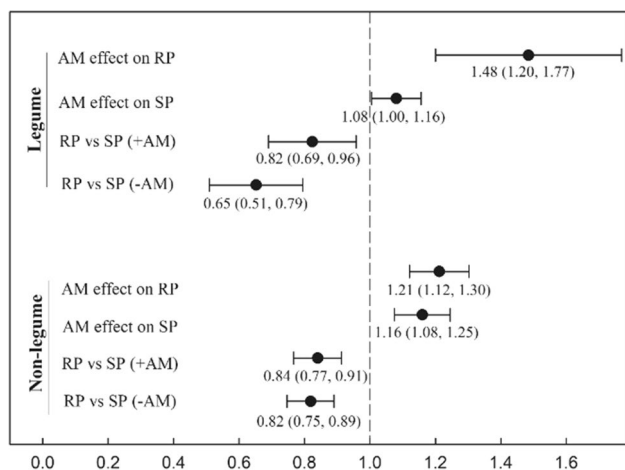
Fig. 5 Impact of crop class on arbuscular mycorrhizae (AM)-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset ($n_{legume} = 15$; $n_{non-legume} = 68$) comprising of a 2×2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates

dissolution and/or P scavenging, the high water solubility of SP means that AM could improve crop growth with SP fertilizers primarily via scavenging. However, lower shoot biomass with RP relative to SP irrespective of AM-enrichment was opposite to our hypothesis. These results demonstrate that AM-enrichment impacts on P availability — proxied by crop growth in these largely P-limited soils — when fertilized with RP are secondary in importance to inherent differences in fertilizer solubility. More broadly, this suggests that AM alone cannot fully close the gap in P availability between RP and conventional soluble fertilizers as has been often proposed (e.g., Covacevich et al. 2006; Murdoch et al. 1967). Though AM-enrichment may increase P availability from low solubility P sources such as RP, the often-asserted AM dissolution mechanism of P access from RP may not operate at sufficient magnitude to compensate for lower solubility, which is 5.6×10^5 to 1.4×10^9 fold lower than superphosphates (66% of observations) (Wei et al. 2013). The absence of studies reporting RP fineness, which affects RP dissolution rates, is a critical research gap in evaluating AM impact on RP dissolution.

For limited studies that reported belowground biomass, we identified differential responses to AM than aboveground biomass that are consistent with previous evaluations of impacts of this mutualism on biomass allocation of the host plant. The distinct increase in absolute biomass of roots but not shoots with RP relative to SP as well as the root biomass as a proportion of total biomass suggests greater root growth to increase P acquisition with AM associations. An increase in plant root biomass with RP fertilization in conjunction with AM species such as *Rhizophagus fasciculatus* and *Rhizophagus irregularis* and P solubilizing microorganisms

such as *Bacillus cereus*, *Bacillus subtilis*, and *Pseudomonas striata* has been observed in sesame (*Sesamum indicum* L.), mung bean (*Vigna radiata*), and maize (Duponnois et al. 2005; Gaind and Gaur 1991; Sabannavar and Lakshman 2009; Singh and Reddy 2011; Yasmeen et al. 2022). We can hypothesize that under potential P starvation induced by RP fertilization, an increase in plant root: shoot ratio could have led to an increase in the root biomass (Hetrick 1991; Powell 1974). However, the limited number (12%) of total observations reporting available soil P at the end of the experiment (12%) and the very few studies reporting root biomass (13%) prevents evaluation of this potential mechanism that could mediate in part effect of AM on crop growth.

That P source did not affect root colonization ensured that comparisons of AM effects on crop growth and P uptake between RP and SP were not confounded. The lack of root colonization suppression by SP compared to RP also indicates that AM colonization of plant roots is unaffected by the relatively solubility and consequent P availability of P sources. Though reduction in AM root colonization with increasing KH_2PO_4 application has been reported (Thomson et al. 1986; 1991), this occurred at very high application rates (up to 280 mg P kg^{-1}). Moreover, plant P status (Menge et al. 1978; Sanders 1975) and specifically the root P concentration in the colonized root tissues (Lu et al. 1994) regulate AM colonization, rather than soil P availability and thus application rate or P fertilizer solubility necessarily (Lu et al. 1994; Sobat and Whalen 2022). Thus, differing solubilities of SP and RP would not affect AM root colonization rates if P concentration in colonized root tissues was similar. Though the absence of reported data on root colonization and colonized root tissue P concentration differences between P sources precludes testing this mechanism, Lin and Fox (1992) found a 43% increase in root P concentration in AM vs. non-AM roots in unfertilized soil, but similar root P % between RP and TSP. Greater variability in root colonization rates with and without AM enrichment than by P source could suggest that P source solubility does not affect AM root colonization.

Influence of experimental scale

Crop shoot biomass response to AM and P source varied by whether experiments were conduct at the greenhouse or field scale. The minority of field studies (6% of total observations) — a key limitation of current evaluations — means that crop responses largely reflected greenhouse studies. Shoot biomass was unresponsive to RP or SP under AM-enrichment in the field scale evaluations, but this could be partly attributable to the limited number of field scale observations with subsequent high variability (CV of shoot biomass in field scale observations = 33%). Higher crop biomass response to AM in

Fig. 6 (**a**) Impact of method of arbuscular mycorrhizae (AM) colonization induction on AM-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset ($n_{sterilization+inoculation}$ = 18; $n_{inoculation\ only}$ = 65) comprising of a 2 × 2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates; (**b**) Impact of method of AM colonization induction on AM-crop symbiosis and P solubility sources on shoot biomass response in the complete metadataset ($n_{heat\ sterilization}$ = 11; $n_{chemical\ sterilization}$ = 7; $n_{inoculation\ only}$ = 65) comprising of a 2 × 2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates
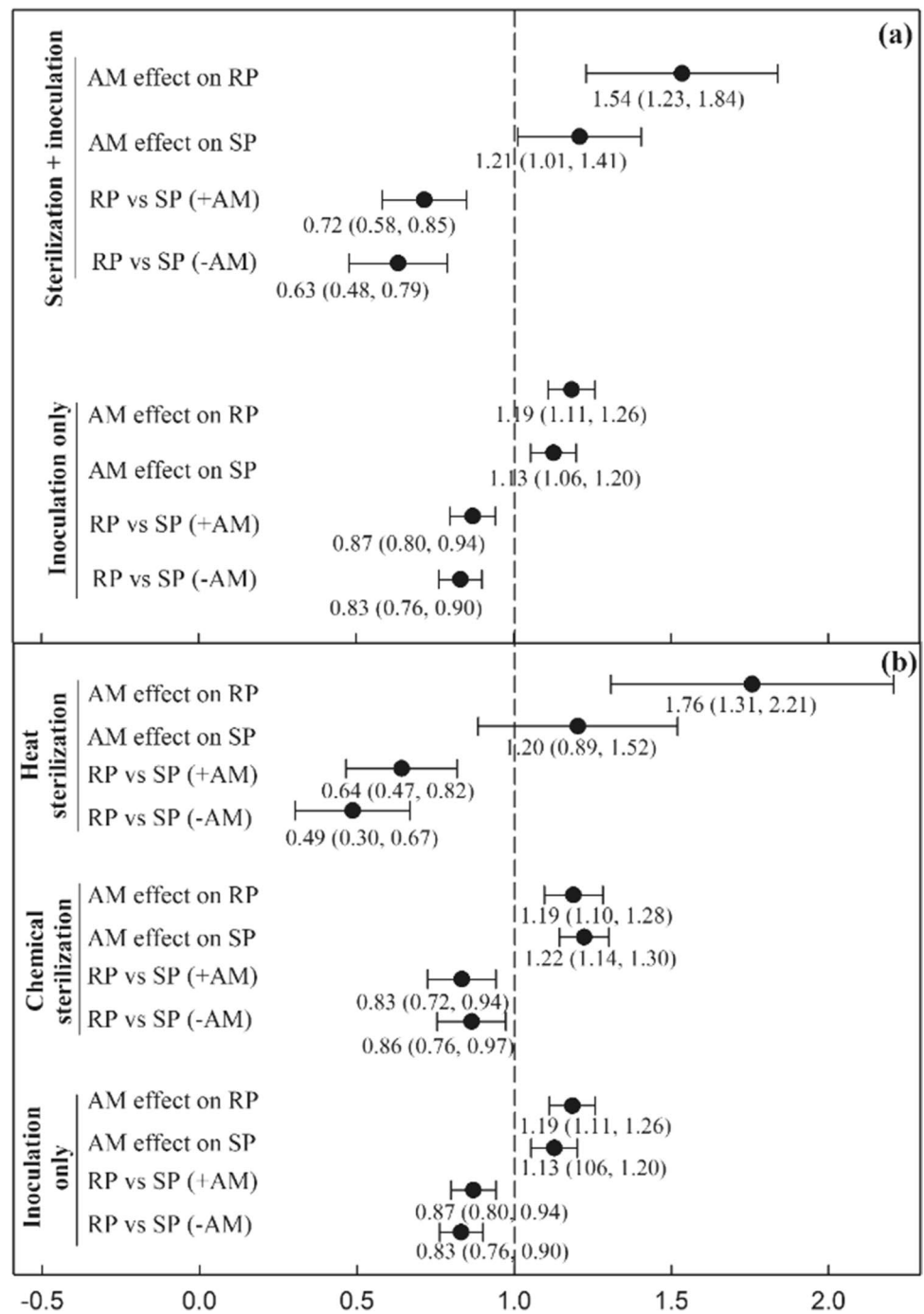
greenhouse studies could be due to reduced biotic and abiotic interactions expected at the field-scale, such as native AM species and variable weather (Ryan and Graham 2018). A possible reason for limited number of field studies comparing AM effects on crops growth could be the difficulty in furnishing AM treatment differences by sterilization. However, the results of this meta-analysis indicate that inoculation alone appears to be sufficient to generate AM treatment differences for crop shoot biomass response to P solubility sources — based on

largely greenhouse studies. Soil sterilization can eliminate non-AM microbiota and have considerable microbial necromass for heterotrophic survival (Kästner et al. 2021), which can confound observed plant responses. Moreover, sterilizing soil is not necessary for generating AM presence or absence contrasts in field studies if these can be achieved by genotypic models (Ruzicka et al. 2012). For example, plant genotypic models such as the mycorrhiza-defective tomato mutant (*rmc*) and its mycorrhizal wild-type progenitor (76R MYC +) (Barker
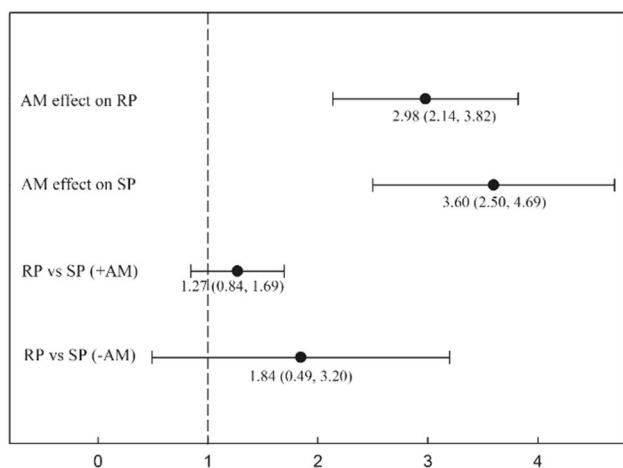
Fig. 7 Effect of arbuscular mycorrhizae (AM) enrichment and P solubility sources on crop root colonization rate response (from $n = 18$ observations that reported root colonization %) from a metadataset comprising of a 2×2 factorial of relative presence or absence of AM and fertilization with rock phosphate vs. soluble phosphates

et al. 1998) avoid the confounding factors due to soil sterilization. The tomato AM genotypes have similar growth under various environmental conditions including non-AM conditions (Cavagnaro et al. 2008) and have been used both in field and greenhouse studies to study AM effect on plant P uptake and growth (e.g., Di Tomassi et al. 2021; Poulsen et al. 2005).

Influence of soil properties

Soil pH and P availability as determined by soil tests largely impacted AM-driven crop response under different solubility P fertilizers. Lower shoot biomass with a greater degree of soil weathering regardless of AM-enrichment under RP fertilization is inconsistent with P limitation effects in highly weathered soils. Though highly weathered and acidic soils (median soil pH = 6.3) in our metadataset were severely P limited with Olsen P equivalent ≤ 2.5 mg kg^{-1} (median 1 mg kg^{-1}) well below critical values of 12–15 mg kg^{-1} (Mallarino et al. 2013), shoot biomass was not responsive to RP under AM. The absence of an AM effect for RP in these highly weathered and P-deficient soils could be due to the high P application rates (all > 30 mg kg^{-1} and ~80% > 150 mg kg^{-1}) leading to high soil P availability. Even under AM non-enrichment, crop shoot biomasses were statistically similar to AM-driven biomass response under RP, suggesting that the crop response was determined by fertilizer P addition and not AM in these highly P limited soils. In long-term experiments in severely P limited (1.2 mg kg^{-1} Bray P equivalent) Oxisols in Western Kenya, application of P as either Minjingu RP or TSP at 50 kg P ha^{-1} similarly

increased maize and soybean yield and biomass, which were both significantly higher compared to the P-unfertilized control (Savini et al. 2016).

In the acidic soils that dominated this metadataset, higher shoot biomass for RP but not SP under AM-enrichment signifies abiotic dissolution via soil acidity, which could occur independently of hyphal-driven dissolution. Bolan and Hedley (1990) observed an increase in North Carolina RP dissolution from 30 to 83% and Nauru RP dissolution from 12 to 60% as soil pH decreased from 6.5 to 3.9. However, it is not possible to assess the magnitude of AM and abiotic dissolution mechanism without quantifying dissolution or derivation of P from P sources. This would require mass-based dissolution data (e.g., Di Tomassi et al. 2021) or direct dissolution measured by radiolabeling (e.g., Cruz-Paredes and Gavito 2020). The distinct shoot biomass increase with RP but not with SP also in alkaline soils supports hypothesized AM-driven RP dissolution. Since abiotic dissolution of RP is low to negligible in alkaline soils, our finding that AM support relatively higher crop biomass with RP in alkaline soils points to a soil-specific benefit of AM for low solubility P forms. Finally, we note that this metadataset had a geographical skewness towards observations from Oceania, which were primarily Andisols, and a comparatively lower representation of observations from primary global consumers of P and RP (i.e., North America, Asia). This reflects the reality of where research on comparing AM effects on RP and SP are being performed, presenting a gap in full factorial evaluation of AM effect on P solubility in regions of major consumption of P and RP.

Influence of P application rate

That the large proportion of soils in our meta-dataset were fertilized at agronomically unrealistic P rates challenges evaluation of crop growth response to AM and P source solubility. As argued by Thirkell et al. (2017), under high nutrient availability due to high rates of chemical fertilizer addition in intensive agriculture systems, AM may act as neutral mutualists or even parasites. AM benefits to crop P uptake tend to be reduced under high soil P availability because host plants tend to reduce carbon allocation to roots and AM (Johnson 2010; Johnson et al. 2003). However, within this metadataset, soil P application rate was not correlated ($r = -0.1$) with AM colonization of crop roots, contradicting the hypothesized reduction in host carbon allocation to AM under high P application rate. Several studies in the metadataset published before 1990 (e.g., Badr El-Din and Moawad 1988) used the root slide technique (Phillips and Hayman 1970) to estimate colonization counts, and more recent studies in the 2000s (e.g., Rubio et al. 2003; Zarei et al. 2006) used the gridline intersect method (Giovannetti and Mosse 1980). The absolute colonization counts from

both these methods are not comparable given the potential overestimation or underestimation of AM colonization by the root slide technique (McGonigle et al. 1990). However, the observations used in the correlation that report the use of specific methods are limited: $n = 8$ observations report root slide technique and $n = 16$ observations report gridline intersect method, with $n = 48$ observations that do not report the method of colonization count estimation. Additionally, due to the weak correlation ($r = -0.1$) between P application rate and AM root colonization, the differences in absolute colonization counts of the two methods are expected to not have impacted the correlation. At high P application rates, the same proportion but a greater net amount of RP would dissolve to generate a crop growth response similar to SP. However, shoot biomass was lower with RP relative to SP irrespective of AM enrichment. Contrary to the plant biomass responses with AM and P source solubility across P rates, the reduced plant biomasses with both RP and SP at the 120–150 mg P kg^{-1} rate is unexpected, and not fully explained.

The absence of studies reporting RP CCE, which can be of significant magnitude (59–63%) (Sikora 2002), underscores liming effects of RP, particularly at high P application rates as observed for many studies. The absence of CCE data being reported is critical since the appreciable CCE of RP makes it a liming source along with a P fertilizer, potentially confounding comparisons between RP and SP. For example, a P application rate of 150 mg P kg^{-1} is equivalent to adding $\sim$750 mg RP [Ca$_3$(PO$_4$)$_2$] kg^{-1} soil, which assuming a conservative CCE of 50% entails the addition of 375 mg CaCO$_3$ kg^{-1} soil or approximately 0.75 Mg CaCO$_3$ ha^{-1} soil assuming incorporation into the 0–15 cm depth. The liming effect of addition of high quantities of RP will increase soil pH and potentially influence the AM effect on RP. Hence, any direct comparisons of RP and SP as P fertilizers would require a reporting of CCE values of the corresponding RP.

Influence of crop species

The distinct increase in legume shoot biomass with RP but not SP under AM-enrichment could reflect generally greater rhizosphere acidification due to proton release during nitrogen fixation of legumes (Hinsinger et al. 2003). However, if RP dissolution limited P availability and thus legume shoot biomass, legume rhizosphere acidification would mute the beneficial effect of AM for legumes fertilized with RP – yet, the opposite was observed. Legumes generally have higher root acid phosphomonoesterase activity relative to non-legumes (Lambers et al. 1998; Richardson 2001) particularly under conditions of low P availability (Olde Venterink 2011). Such low soil P availability conditions could occur under fertilization with low solubility fertilizers such

as RP, which could favor production of extracellular phosphomonoesterases by legume roots to acquire P from organic matter via mineralization. In the case of potential P limitation with RP fertilization, legume root phosphatases would be expected to mineralize more organic P than without P limitation, as with SP fertilization. Increased P availability from organic P mineralization may have resulted in greater shoot biomass under RP fertilization compared to SP. However, shoot biomass with RP relative to SP under AM nonenrichment was not greater in legumes compared to nonlegumes. This suggests that increased legume shoot biomass with RP but not SP under AM was not due to increased organic P mineralization caused by root phosphatases production under P limitation.

A possible confounding effect on crop response to P source solubility and AM could be soil P availability. Since majority of the non-legumes (78%, Fig. S2) as well as legumes (63%, Fig. S2) in the metadataset were grown in P-limited soils, non-legumes benefitted from AM for both RP and SP. Legume shoot biomass did not increase with SP due to possibly a competition effect for photosynthate between rhizobia and AM (Kiers and Denison 2008). Competition for photosynthate between rhizobia and AM in legumes could explain the legume-specific reduction in biomass with SP. With SP fertilization, a flush of readily available orthophosphates is available soon after application, potentially negating the AM dependance for P dissolution, unlike RP. Since colonization was similar between legumes and non-legumes and across P sources, the photosynthate sink to AM in legumes could have led to reduced shoot biomass compared to non-legumes. Finally, while other possible comparisons of AM effect across crop classifications such as annuals vs. perennials, monocots vs. dicots could be performed, we focused on the legume vs. non-legume comparison because of known rhizobia-AM interactions and their effects on crop growth.

How AM contrasts are established influence crop response to P source

Increased shoot biomass with RP alone when soils were heat sterilized before inoculation could reflect increases in soil N and P availability due to pyromineralization of organic N and P (Giardina et al. 2000; Nye and Greenland 1961; Raison 1979). Higher relative plant response to AM inoculation in sterilized soils has been observed under low P or P-deficient soils than when soil P is high or under high P application rates (Ortas 2003). For example, Ortas (2003) observed AM dependency values up to 81% with *Funneliformis mosseae* and *Claroideoglomus etunicatum* with zero P addition to sterile soil and 38% and 21% with 125 mg P kg^{-1} soil application. Arbuscular mycorrhizal dependence is defined as a plant's dependency on AM to generate its maximum yield or growth at a given soil fertility level (Gerdemann 1975)

and more recently has been modified as inoculation effectiveness, the ratio of yield (or another plant growth metric) differences between inoculated and non-inoculated plants to the yield of inoculated plants (Ortas 2012). Plant P limitation under RP fertilization, especially in early crop growth stages and in P limited soils, would be expected to induce a higher mycorrhizal colonization in response to RP. Since available soil P pools were not reported, we were unable to test how P solubility and AM enrichment may have affected soil P availability.

Reduced shoot biomass in soils fertilized with SP that were heat sterilized compared to chemically sterilized or non-sterilized is unexpected but could be due to increased soil P availability. Extreme sterilization treatments like autoclaving may release large amount of P that mask benefits of AM (Jakobsen and Andersen 1982), though often studies are incubated for a sufficient period of time for re-fixation or immobilization of nutrients before use. Since the majority studies in this metadataset (65%) were steam sterilized, at a temperature of at least 100 °C (40%), with most studies not reporting if the heat-sterilized soils were incubated before use, AM benefits may have been muted in the heat-sterilized soils. In non-sterilized soils, inoculated AM could be acting synergistically with native AM and other microorganisms (Requena et al. 1997). However, both AM inoculation and sterilization produced similar AM root colonization differences between the AM-enrichment and non-enrichment in the metadataset. Nonetheless, similar crop responses to AM treatments after chemical sterilization and non-sterilization suggest that the reduced shoot biomass with SP in heat-sterilized soils is not due a biotic effect of soil sterilization. None of the studies in the metadataset, including the studies employing mixed AM inoculum, confirmed which species of AM colonized plant roots despite AM species being functionally diverse. Additionally, due to limited number of observations using mixed inoculum ($n = 4$), the comparison of crop growth responses to single vs. mixed AM inoculum was not possible. Thus, future evaluations of AM impacts on P acquisition by host crop species should consider resolving colonizing AM species, particularly with multi species inoculum.

Conclusion

This meta-analysis assessed the relative importance of P source solubility and AM associations for crop growth and the agroecosystem context dependency of this relationship under factorial experiments that tested both relative and interactive effects of P solubility and AM-crop associations. In the largely P-limited soils in the metadataset,

AM-driven crop shoot biomass increased similarly under RP and SP, but crop biomass was lower under RP relative to SP fertilization irrespective of AM-enrichment. Thus, though AM-enrichment appears to increase P availability from low solubility P sources such as RP, this appears insufficient in magnitude to compensate for lower solubility relative to SP. In the largely acidic soils that dominated this metadataset, shoot biomass increased for RP but not SP under AM-enrichment suggestive of a strong effect of abiotic dissolution via soil acidity that reduces AM benefits for RP in acidic soils. The distinct shoot biomass increase with RP but not with SP in alkaline soils could point to AM-driven RP dissolution, but studies are needed to quantify dissolution. Crop biomass did not increase for RP relative to SP in highly weathered soils, rejecting the hypothesized benefit of RP over rapidly solubilizing P fertilizers in strongly P-fixing soils. Moreover, that SP did not suppress root colonization compared to RP indicates that AM colonization of plant roots is unaffected by the relative solubility and subsequent P availability of the RP and soluble P fertilizers evaluated for the largely P-deficient, slightly acidic soils used in extracted studies. Arbuscular mycorrhizae therefore appear to improve crop growth response to RP and SP alike under these edaphic conditions. To elucidate the realistic potential of AM-crop associations to improve crop P use efficiency, future evaluations should be conducted under field or greenhouse conditions that reflect realistic field-growing conditions and agronomically sound P application rates.

Declarations

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