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MARSCHNER REVIEW

The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content

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Abstract
Aims The most common metric of arbuscular mycorrhizal fungal (AMF) abundance is percent root length colonized (PRLC) by mycorrhizal structures. Frequently, plants with greater PRLC are assumed to receive more nutrients (such as phosphorus, P) from their mycorrhizal symbionts, leading to greater plant growth. Nevertheless, the functional significance of this metric remains controversial. In this review, I discuss whether manipulations of PRLC generally led to changes in plant biomass and P content, and whether AMF taxa and plant functional groups influence these relationships.
Methods I conducted a meta-analysis of laboratory- and field-based trials in which mycorrhizal colonization was directly altered compared to unmanipulated controls. For each trial, I calculated (1) the difference in PRLC (ΔPRLC) between the treatments, and (2) the response ratio of plant biomass. In a subset of these studies, the response ratio of P content of host plants could also be calculated.
Results The response ratio of plant biomass and P content rose significantly and exponentially as ΔPRLC increased. Nevertheless, ΔPRLC explained only a fraction of the variation in response ratios in each case. Moreover, AMF taxa varied in their effects on biomass per unit ΔPRLC. In addition, plant functional groups differed in effects on plant P content per unit ΔPRLC, with C4 grasses responding most strongly.
Conclusions It appears that as the extent to which plant roots are colonized by AMF increases, plant growth and P content often increase, although substantial variability exists among trials. As others have found, a likely mechanism for this relationship is increased transfer of P (and perhaps other nutrients) through the more-prevalent mycorrhizal structures.

Keywords Arbuscular mycorrhizal fungi · Meta-analysis · Percent root length colonized · Phosphorus · Plant biomass · Taxonomy

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Introduction

Arbuscular mycorrhizal fungi facilitate the growth of many plants by improving nutrient acquisition from soil (Smith and Read 2008; Smith and Smith 2011b). This generally mutualistic relationship has been well-established via hundreds of studies for more than 50 years (Mosse 1957; Hoeksema et al. 2010 and references therein). Essentially, these studies have compared plant growth or nutrient status between plants growing

with and without AMF inocula. On average, plants that are colonized by AMF grow 3.1 times larger than do uncolonized control plants (Hoeksema et al. 2010). Arbuscular mycorrhizal fungi are thought to be more efficient at scavenging for soil nutrients, owing to their larger surface-to-volume ratios (Sanders and Tinker 1973). This ability is particularly important for acquisition of P, which is relatively immobile in soil (Nye and Tinker 1977). In this review, I will first describe how researchers apply and interpret one metric of AMF dynamics: percent root length colonized (PRLC) by AMF. Although PRLC is often used to infer benefits of AMF on plant growth and P content, a number of factors could modify these relationships. These include AMF taxa, plant functional groups, and environmental conditions. Therefore, I next discuss the state of knowledge regarding relationships between PRLC and benefits to host plants, which factors directly influence PRLC, and how AMF characteristics and plant functional groups can modify the effect of PRLC on plants. Finally, I conduct a meta-analysis of studies that have directly manipulated PRLC and measured effects on plant biomass and plant P content.

How are arbuscular mycorrhizal fungi assessed?

One common interpretation is that greater density of AMF in plant roots leads to greater benefits for the host plant. The standard metric for AMF abundance is PRLC (reviewed in Vierheilig et al. 2005). This technique involves clearing and staining fine roots for AMF hyphae, vesicles, and arbuscules, and using a line intercept method to determine the proportion of root length colonized by these structures (Koske and Gemma 1989; McGonigle et al. 1990). The measurement of PRLC is relatively inexpensive and technically undemanding (albeit time-intensive). For these reasons, this technique is attractive and accessible to a wide variety of researchers.

Consequently, the measurement of PRLC by AMF is frequently reported in the literature, and is often placed in the context of benefits to plants by the AMF fungus. In this case, "benefit" refers to improved growth or P content of AMF-colonized plants compared to uncolonized plants. For instance, 60 original research articles were published by *Mycorrhiza* in 2010 and 2011 that examined AMF. Of these, 40 reported PRLC by AMF. The authors of 23 of the 40 studies interpreted PRLC in relation to some aspect of plant benefit, most commonly plant growth or biomass (12 studies), plant P uptake (10 studies), and/or other nutrients (2 studies). Often, the authors used patterns of PRLC to interpret those of plant growth or P uptake, by suggesting that higher values of PRLC led to greater plant benefits.

Percent root length colonized by AMF structures is not the only measure of AMF abundance (Vierheilig et al. 2005). Some investigators report percent root length colonized by arbuscules, specifically, since arbuscules are often the primary site of nutrient and C exchange between the fungus and plant (Smith and Gianinazzi-Pearson 1990; Ezawa et al. 2002; Smith and Read 2008). Nevertheless, arbuscules are more ephemeral than other intraradical AMF structures, and they can be difficult to observe, so this metric is rarely reported (Allen 1983; Brundrett 2009). In addition, the role of arbuscules have not been fully confirmed, and other exchange sites—including coiling AMF—are possible (Brundrett 2004; Brundrett 2009). Total root length colonized by AMF, either on a per-plant or per-ground area basis, has also been used (e.g., Nadian et al. 1997; Allen 2001). This index may be a closer estimate of AMF abundance within a plant or ecosystem, respectively. Nevertheless, investigators must measure root length to calculate this variable, so it is more time-demanding—and sometimes less feasible—than measuring PRLC alone. Arbuscular mycorrhizal fungi also produce extraradical hyphae that extend into the surrounding soil much further than do root hairs (Rhodes and Gerdemann 1975; Read 1984; Friese and Allen 1991). These hyphae are responsible for nutrient uptake by AMF from soil, so standing hyphal length in soils is another frequently-used index of AMF biomass (e.g., Bardgett 1991; Sylvia 1992; Schweiger and Jakobsen 2000; Hart and Reader 2002a). Quantitative PCR of AMF-specific DNA from roots or soil is another option (Filion et al. 2003; Alkan et al. 2004; Isayenkov et al. 2004; Alkan et al. 2006; Gamper et al. 2008), although this technique is relatively technically demanding and expensive. Finally, phospholipid or neutral lipid fatty acids can indicate biomass of AMF (Olsson et al. 1995; Allison and Miller 2005), although this technique is used less frequently than is PRLC. Each of these assays provides an index of the standing biomass (or gene copy number) of AMF. Thus, they are not necessarily a measure of the activity or function of the symbiosis, especially since nutrient uptake and C use can vary among and within AMF tissues (reviewed in Smith and Read 2008).

Does higher PRLC yield greater plant benefits?

To date, few syntheses have directly tested the robustness of PRLC of AMF as an indicator of plant benefits. In a recent meta-analysis of agricultural systems, Lekberg and Koide (2005) observed that increases in PRLC were associated with stronger effects on biomass of crop plants. Feldmann et al. (2009) examined effects of corn-derived AMF inocula on growth of seven host plants. They concluded that PRLC influenced plant growth in a non-linear fashion, with a threshold at 20–30 % PRLC. Below this threshold, plant benefits of AMF colonization were not evident; above this threshold, plant benefits existed but did not co-vary with PRLC. Sanders et al. (1977) reported that in three of four isolates of AMF, the flux of P into onion roots increased linearly with PRLC. Fitter and Merryweather (1992) did not find striking evidence for relationships between PRLC and plant P uptake in observational studies in which PRLC was not directly manipulated. In a meta-analysis focusing on ectomycorrhizal fungi, Karst et al. (2008) found no significant relationship between plant biomass response and PRLC or percentage root tips colonized by ectomycorrhizal fungi. Altogether, the suitability of PRLC as an index of AMF effectiveness is a matter of debate (Smith and Read 2008), and it has not yet been quantitatively tested across a broad range of studies that include natural as well as agricultural systems.

What influences PRLC?

Percent root length colonized is essentially the product of two variables: standing root length and AMF abundance. Thus, changes in PRLC could result from changes in standing root length, and may not necessarily be related to AMF abundance. Since standing root length (as m root $plant^{-1}$ or m root m^{-2} ground area) varies among plant species (Einsmann et al. 1999; Kembel and Cahill 2005) and developmental stages (Troughton 1956; Bartelink 1998), as well as environmental characteristics such as ecosystem type (Schenk and Jackson 2002a), season (Hendrick and Pregitzer 1996), soil moisture (Schenk and Jackson 2002b), nutrient availability (Chapin 1980; Reynolds and Dantonio 1996; Ostertag 2001), and atmospheric CO_2 (Stulen and Denhertog 1993; Pritchard et al. 2008), any shifts in PRLC may occur due to changes in colonized root length, standing root length, or both.

What might influence the effect of PRLC on plants?

Arbuscular mycorrhizal fungal taxa, morphology, and activity

Arbuscular mycorrhizal fungal taxa vary in their contribution to nutrient uptake by plants (Munkvold et al. 2004; Smith and Smith 2011b). Some genera, such as *Scutellospora* and *Gigaspora*, construct more extensive extraradical hyphae per unit PRLC, which could result in better nutrient acquisition (Hart and Reader 2002a, b; Treseder 2005; Maherali and Klironomos 2007; Powell et al. 2009). Other genera such as *Acaulospora*, *Glomus*, *Funneliformis* (i.e., the *Glomus mosseae* clade), and *Rhizophagus* produce less extraradical hyphal biomass, and may serve as poorer mutualists (Hart and Reader 2002b; Maherali and Klironomos 2007; Powell et al. 2009). Nevertheless, greater production of extraradical hyphae does not always lead to stronger plant benefits (Graham and Abbott 2000; Klironomos 2003). Since ratios between PRLC and extraradical hyphal biomass vary among AMF taxa, it is not clear how well PRLC predicts host plant benefit across diverse AMF taxa (Abbott and Robson 1985; Hart and Reader 2002a). In addition, AMF can in some cases negatively affect plant growth (Smith and Smith 2011a; Smith and Smith 2011b, 2012). High PRLC could cause decreased benefits or negative effects on plants in this instance.

The presence of AMF structures in a root does not necessarily indicate that those structures are translocating C and P (Fitter 1991). Indeed, AMF structures appear to grow most rapidly, and transfer C and P most actively, when they are located near a growing root tip (Buwalda et al. 1982; Walker and Smith 1984). As the AMF structures age and become more distant from the root tip, activities decline (Tisserant et al. 1993; Tisserant et al. 1996). Thus, some fraction of intraradical AMF structures may not be actively contributing to plant P uptake, especially where older roots are present (Allen 2001).

Plant functional groups

Plant functional groups can influence relationships between PRLC and benefits to host plants through a number of mechanisms. Plant functional groups are groups of species that are similar in their role in community or ecosystem dynamics, and classifications include C3 and

C4 grasses, woody plants, forbs, and N-fixers (e.g., Kattge et al. 2011). These functional groups vary in standing root length (Jackson et al. 1997; Einsmann et al. 1999; Kembel and Cahill 2005), which partly determines PRLC (see "What influences PRLC?", above). A number of investigators have suggested that fast- versus slow-growing plants (or roots) should differ in their responses to AMF colonization, with arguments for and against fast-growers being more dependent on AMF (Brundrett 1991; Koide 1991; Allsopp and Stock 1993; Smith and Smith 1996). In addition, plant functional groups may select for AMF taxa that elicit particular C costs or P benefits. As a result, effect sizes for plant biomass or P content could differ per unit PRLC. Indeed, plant and AMF taxa appear to interact in terms of their effects on plant biomass and P content (e.g., McGee 1990; Siqueira et al. 1998; van der Heijden et al. 1998; Helgason et al. 2002; Smith et al. 2004; Bunn et al. 2009; Lendenmann et al. 2011). Hoeksema et al. (2010) performed a meta-analysis of plant responses to the presence versus absence of AMF, and they found that plant functional group explained the greatest amount of variation among studies. Specifically, they reported that C4 grasses and non-N-fixing plants tended to be more responsive to AMF colonization than were C3 grasses and N-fixing plants (Hoeksema et al. 2010). Since these functional groups are relatively sensitive to the presence versus absence of AMF, then they may likewise be more responsive to changes in PRLC.

Meta-analysis

I examined these issues by conducting a meta-analysis of published trials in which PRLC by AMF was directly manipulated, and then responses in plant biomass or plant P content were assessed. In many cases, the taxonomic identity of AMF was provided, so I could also test for phylogenetic effects on relationships between PRLC and host plant benefit. I tested three hypotheses: (1) overall, more extensive colonization of plant roots by AMF leads to greater plant benefits, in terms of increases in biomass and P content; (2) AMF taxa vary in their degree of host plant benefit per unit PRLC; and (3) plant functional groups differ in the benefit they receive from AMF per unit PRLC. In examining the second hypothesis, I capitalized on recent advances in the taxonomy of AMF (Redecker 2002; Da Silva et al. 2006; Redecker and Raab 2006; Krüger et al. 2012; Stuermer 2012; Young 2012). Most of the genera used here as AMF inocula have been sequenced in the 28S rDNA region (Da Silva et al. 2006; Redecker and Raab 2006), which allowed me to estimate phylogenetic relationships. In addition, many taxa previously identified as *Glomus* species have been reassigned to new genera, which allowed higher-resolution assessments of taxon effects.

Methods

Sources of data

Meta-analyses were performed on previously-published data that met specific criteria (Online Resource 1). I selected laboratory and field trials in which AMF colonization was directly manipulated, usually via a combination of soil sterilization, addition of AMF inocula, serial dilution of soils or inocula, or fungicide applications. Most laboratory trials used sterilized soils; control treatments harbored low or no PRLC, while enriched treatments received AMF inocula. Other laboratory trials used whole soil to represent a baseline PRLC level, in comparison with a reduced-PRLC treatment obtained via dilution with sterile soil, fumigation, or treatment with fungicides. Field trials included those with transplanted, AMF-colonized versus uncolonized seedlings; plots augmented with AMF inocula; and plots treated with fumigants or fungicide. Because the baseline nutrient status of host plants can strongly influence responses to AMF (Hoeksema et al. 2010), I included only trials in which no type of fertilizer was applied. This constraint eliminated many trials of AMF benefits on host plants. I also did not include trials that used non-soil based growth media; or soils contaminated with heavy metals, augmented with organic contaminants or additives, or artificially acidified. If a particular publication reported results from more than one study system that could reasonably be considered independent (e.g. geographical location, ecosystem, dominant vegetation type, or AMF inoculum), each system was designated as a different trial.

Of all trials that met these criteria, 195 reported plant biomass for each treatment; 118 reported plant P content (i.e., total P contained within the whole plant or the shoot). Many of the trials with inocula from the order *Glomerales* or inocula with multiple species were also included in the meta-analysis by Hoeksema et al. (2010).

Data assimilation

For each trial, I recorded the mean PRLC of the "lower PRLC" and "higher PRLC" treatments, and calculated the difference between the two as ΔPRLC. The unit is percentage point, which is the arithmetic difference between two percentages. In addition, I recorded the corresponding plant biomass or plant P content for each treatment. Effect sizes were calculated as response ratios (unitless):

$$Biomass\ Effect\ Size = \left(\frac{Biomass_{higher\ PRLC}}{Biomass_{lower\ PRLC}}\right)$$

$$Phosphorus\ Effect\ Size = \left(\frac{P_{higher\ PRLC}}{P_{lower\ PRLC}}\right)$$

where "Biomass" was the total plant biomass (if available). If total plant biomass was not provided, then I recorded aboveground plant biomass instead. In the majority of trials, investigators measured biomass by harvesting standing plant tissue and then determining dry mass, although a few assessed plant height (Online Resource 1). Likewise, "P" was recorded for the whole plant (where available), and for shoots (i.e., all aboveground biomass) otherwise. Phosphorus was provided as units total P per plant (or shoot), and it was primarily determined via colorimetry/spectrophotometry (Online Resource 1).

Estimate of AMF phylogeny

I searched GenBank for representative, high-quality 28S sequences of each AMF genus represented in the selected studies (www.ncbi.nlm.nih.gov/genbank/, accessed May 20, 2012). The taxonomy of Schüßler and Walker (2010) was used to define AMF genera. High-quality 28S sequences were available for each genus except *Sclerocystis*. I downloaded representative sequences for all available genera (Online Resource 2), and trimmed them where necessary to remove extraneous regions. I then constructed an alignment and estimated a phylogeny using SATé under the default Saté-II-fast setting (Liu et al. 2009; Liu et al. 2012). MAFFT 6.717 was used as the aligner (Katoh et al. 2009), and a maximum likelihood tree was created with FastTree 2.1.4 under the GTR CAT model (Price et al. 2010).

Statistics

In every case, tests were performed on ranked data owing to non-normal distributions. Except where noted, Systat version 10.2 software was used. To test Hypothesis 1, general linear models were applied with ΔPRLC as the independent variable and biomass effect size or P effect size as the dependent variable in each case. In addition, I checked for potential influences of inoculum complexity (single taxa versus multiple taxa), study setting (laboratory versus field), and lower PRLC value by conducting sequential general linear models with ΔPRLC as one independent variable plus either inoculum complexity, study setting, or lower PRLC as an additional independent variable. I included lower PRLC value in the analysis to test whether the absolute value of PRLC—in addition to the change in PRLC—influenced plant responses.

To test Hypothesis 2, I focused on trials with single-taxa inocula only. In addition, some *Glomus* species had not received a formal taxonomic designation (i.e., *Glomus* sensu *lato*), so they were omitted from tests of Hypothesis 2. First, I applied general linear models with ΔPRLC and genus of AMF inoculum as independent variables, and biomass effect size or P effect size as the dependent variables. A significant genus effect would support the hypothesis that AMF taxa vary in their effect on plant biomass or P concentration. Second, I calculated the effect size per unit ΔPRLC for each study. Where indicated, Tukey post hoc tests were used to check for pairwise comparisons among AMF genera. Third, a Mantel test with 1000 random iterations was used to check for phylogenetic signals in biomass effect size per unit ΔPRLC (Liedoff 1999). Specifically, sequence identity and the absolute difference between effect size per unit ΔPRLC were calculated for each pairwise comparison among genera. A significant phylogenetic signal (i.e., negative correlation between variables) would indicate that more closely-related taxa elicit similar plant benefits. (Trials with *Sclerocystis* species were not included in tests for phylogenetic signal, since this genus was not represented in the maximum likelihood tree).

For Hypothesis 3, general linear models were applied with ΔPRLC and plant functional group as independent variables, and biomass effect size or P effect size as the dependent variable. Tukey pairwise tests among plant functional groups were conducted where indicated.

Results

Plant biomass

The response ratio of plant biomass increased significantly with ΔPRLC across all trials, within trials with

multiple taxa, and within trials with *Funneliformis* species as single inoculants (Fig. 1, Online Resource 3, $P<0.001$ in each case). However, ΔPRLC explained only a fraction of the variation in the response ratio ($r^2=0.118–0.363$). For trials with single inocula, the genus of the AMF fungus significantly influenced the degree to which plant biomass responded to ΔPRLC (Fig. 2, Online Resource 3). Specifically, *Funneliformis* (i.e., the *Glomus mosseae* clade) had a significantly larger effect on plant biomass per unit ΔPRLC than did *Racocetra*. Nevertheless, there was no significant phylogenetic conservation of plant benefit when all phylogenetic scales were considered ($g=0.132$, $P=0.483$). In other words, more closely-related taxa did not generally produce similar effects on plant biomass per unit ΔPRLC. Inocula with multiple AMF taxa did not significantly differ from inocula with single taxa in terms of their effects on plant biomass (Online Resource 3, $P=0.514$), and neither did laboratory- versus field-based trials (Online Resource 3, $P=0.360$). The lower value of PRLC within each trial was not significantly related to plant biomass effects ($P=0.654$). Plant functional groups differed from one another in biomass effect, but only marginally significantly (Fig. 3, Online Resource 3, $P=0.068$).

Plant P content

Increases in plant P contents were greater when ΔPRLC was more pronounced, and this relationship was significant across all trials (Fig. 4, Online Resource 3, $P<0.001$), in trials with multiple AMF taxa ($P=0.009$), and in trials with single AMF taxa as inocula ($P<0.001$), albeit with high variability in each case ($r^2=0.223–0.274$). Plant P effects did not differ significantly among AMF genera (Online Resource 3). In addition, the lower PRLC value in each trial did not significantly influence P effects ($P=0.468$). Moreover, single-taxa inocula did not differ significantly from multiple-taxa inocula in their effects on plant P concentration (Online Resource 3, $P=0.191$), and neither did laboratory- versus field-based trials (Online Resource 3, $P=0.213$). Plant functional groups were associated with significantly different plant P effects ($P<0.001$); C4 grasses displayed the highest plant P effect per unit ΔPRLC, and N-fixing woody plants the lowest (Fig. 3, Online Resource 3).

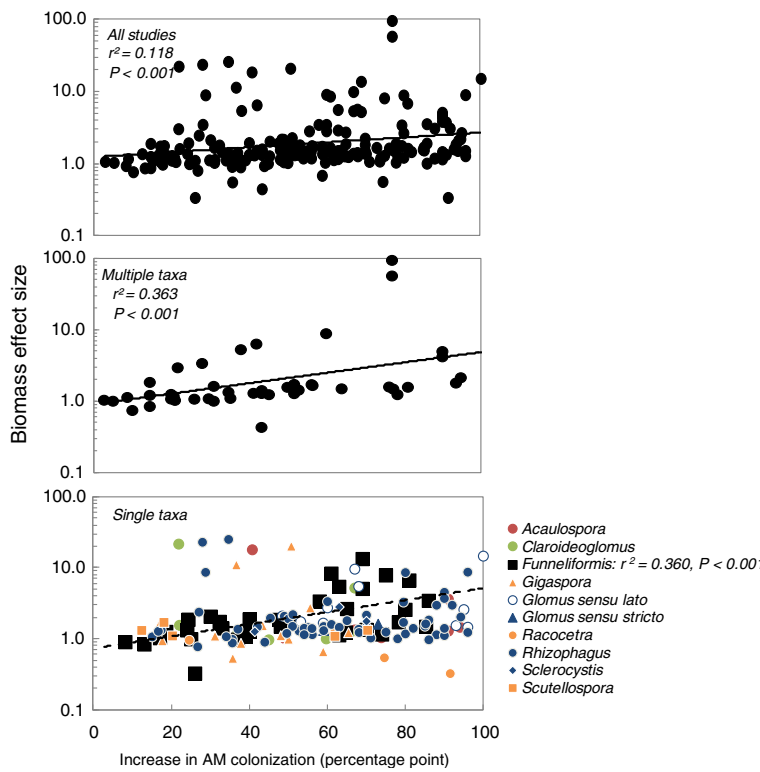

Fig. 1 Relationships between changes in percent root length colonized (higher PRLC – lower PRLC) and effect size of plant biomass ($biomass_{higher}/biomass_{lower}$). Relationships are presented for all studies combined, for studies with multiple AMF taxa in the inoculum, and for studies with single AMF taxa. Each symbol represents one study. *Lines* are best fit regressions for significant relationships only. Statistics were conducted on ranked data. *Dashed black line = Funneliformis*. Note log scale of vertical axis. Effect size is unitless

Discussion

Generally, greater PRLC by AMF was associated with better plant growth (Fig. 1). This relationship was significant when all trials that met the selection criteria were included in the analyses, although PRLC explained only 11.8 % of the variability in biomass effect size. In addition, effects on plant P content were positively related to ΔPRLC (Fig. 4). This potential mechanism is consistent with the characterization of the generally mutualistic relationship between plants and AMF (Mosse 1957, 1973; Smith and Read 2008; Smith and Smith 2011b, 2012). Indeed, a fair amount of evidence has accumulated indicating that AMF are balanced mutualisms that function by a form of regulated exchange, so that plants should support high levels of PRLC only if the AMF provide benefits (reviewed in Brundrett 2004). Nevertheless, Smith and Smith (2012) reported physiological evidence for large differences in P transfer by different AM fungi that would be expected to influence the size (and possible direction) of AM-mediated growth responses and total P uptake. This area requires more research, given that AM roots contain multiple AM fungal taxa. On average, natural ecosystems harbor 15 to 30 AMF species (Kivlin et al. 2011). Thus, trials with multiple AMF taxa in their inocula may be particularly relevant for natural settings. In these studies, PRLC explained

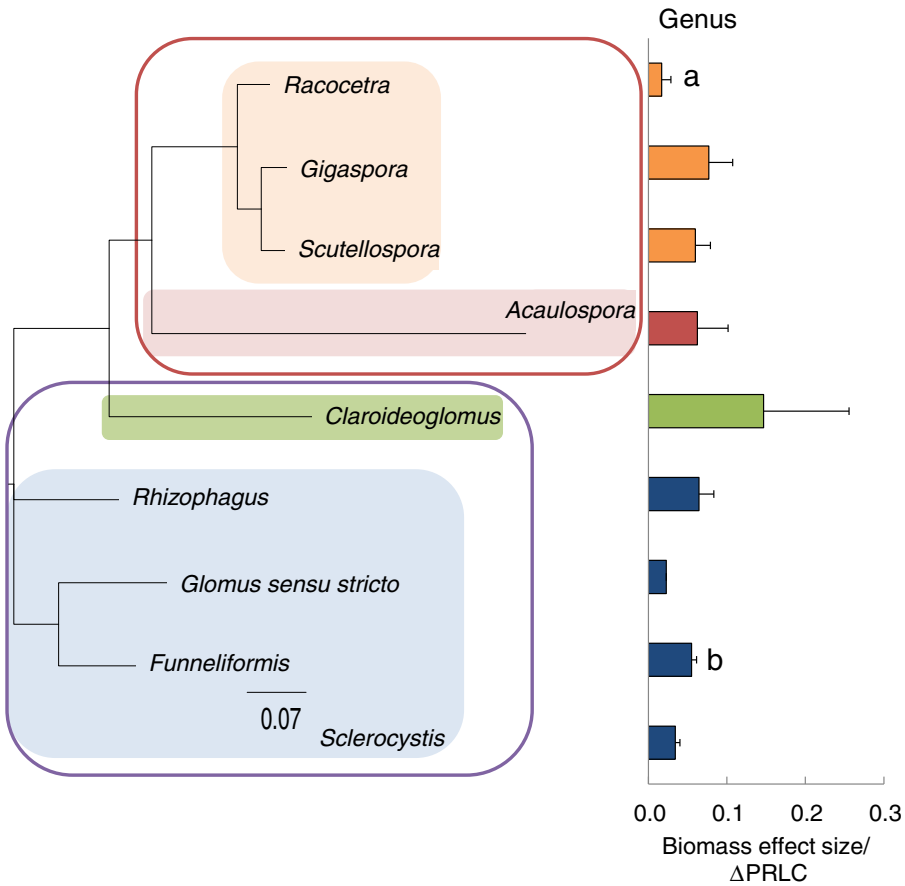

Fig. 2 Maximum likelihood tree of AMF taxa included in meta-analysis, coupled with the relative influence of AMF taxa on effect size of plant biomass per unit ΔPRLC (percentage point^{-1}). Tree was estimated for representative 28S rDNA sequences (Online Resource 2). *Sclerocystis* is a member of the *Glomeraceae*, but it was not included in the tree owing to lack of a high-quality sequence in this region. Colors of shaded boxes represent family (*orange* = *Gigasporaceae*, *red* = *Acaulosporaceae*, *green* = *Claroideoglomeraceae, blue* = *Glomeraceae*). Colors of open boxes represent order (*red* = *Diversisporales, purple* = *Glomerales*). *Bars* are means+SE for each genus. Genera with different letters were significantly different from one another. *Claroideoglomus*, *Funneliformis,* and *Rhizophagus* species were formerly classified as *Glomus*. *Racocetra* species were formerly classified as *Scutellospora* or *Gigaspora*

36 % of the variation in plant biomass effect and 27 % in plant P content. Altogether, the results of this study support Hypothesis 1, and suggest that PRLC indicates (albeit very imprecisely) AMF benefits to host plants.

The relationships between ΔPRLC and plant biomass and P effects were significant despite potential complicating factors that have been previously raised by researchers. First, PRLC is influenced by standing fine root length as well as AMF abundance. If so, variation in standing fine root length could alter PRLC even if AMF abundance (and, presumably, benefits to host plants) remains constant. Instead, it is possible that standing root length increased concurrently with AMF abundance, which could occur if plants grew more fine roots upon colonization by AMF. Second, although AMF can negatively affect the growth of host plants under certain conditions (Bever 1994; Bever et al. 1997; Johnson et al. 1997; Klironomos 2002; Castelli and Casper 2003; Hart et al. 2003; Klironomos 2003; Jones and Smith 2004; Smith and Smith 2011b, 2012), these situations were rare within this meta-analysis. In fact, a reduction in plant growth in response to increases in PRLC (i.e., a response ratio <1.0) was recorded in only 18 of the 195 trials surveyed here (Online Resource 1). Third, even though PRLC does not quantify extraradical biomass of AMF, as cited by Hart and Reader (2002a), there appears to be no substantial trade-off between construction of intraradical and extraradical structures by AMF (Powell et al. 2009). Indeed, Powell et al. (2009) reported that after accounting for shared evolutionary histories, PRLC and extraradical biomass are positively correlated among AMF taxa. Although each of these potentially confounding mechanisms could have obscurred relationships between PRLC and plant biomass and P effects, they do not appear strong enough to negate it.

In support of Hypothesis 2, AMF taxa varied in their influence on plant biomass (Fig. 2). Differences among AMF taxa in effects on plant biomass have been documented in numerous studies (e.g., Abbott and Robson 1985; Guissou et al. 1998; Vosátka and Dodd 1998; Clark et al. 1999; Ozgonen and Erkilic 2007; Sensoy et al. 2007; Powell et al. 2009; Watanarojanaporn et al. 2011). The results of the

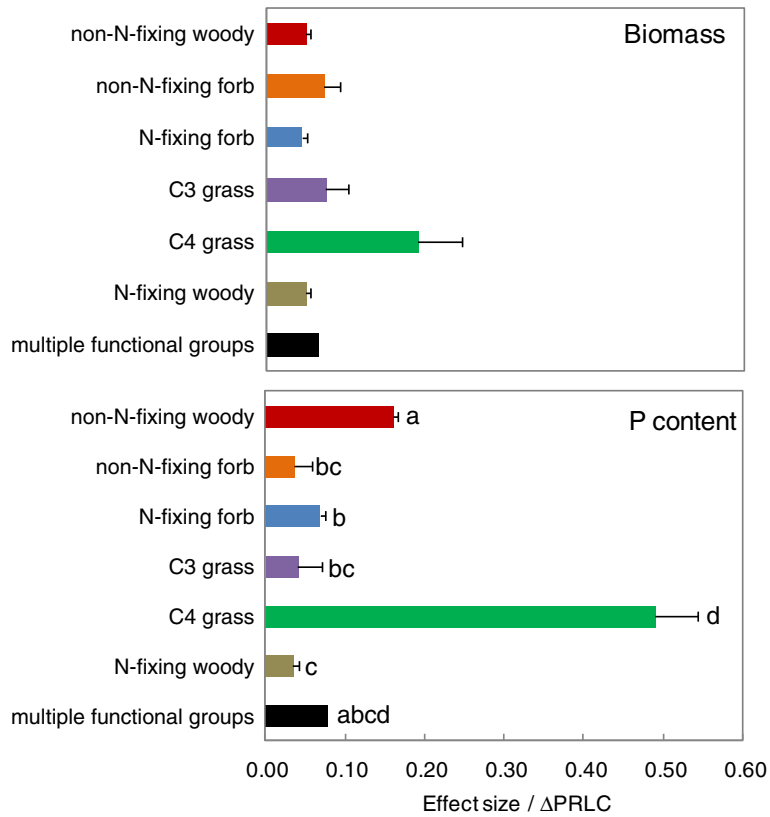

Fig. 3 Effect size of plant biomass and P content per unit ΔPRLC (percentage point^{-1}) for each plant functional group. Plant functional groups differed marginally significantly for biomass (P=0.068), and significantly for P content (P<0.001). Bars are means+SE for each plant functional group. Standard error is not presented for the "multiple functional groups" category, as it contained only one study. Plant functional groups with *different letters* were significantly different from one another

current study are not generally consistent with expectations based on investment in extraradical hyphae, arbuscules, or vesicles by AMF genera (e.g., Hart and Reader 2002a, b; Treseder 2005). *Funneliformis* produced the greatest effect on host plant growth, even though it does not develop extensive extraradical hyphal networks that would facilitate nutrient uptake. It is possible that shorter hyphae require less C to construct, and thus represent a smaller cost to the host plant. Alternately, the differences among AMF taxa could be influenced by variation in propagation biology (e.g., Abbott and Robson 1991; Friese and Allen 1991). Taxa of AMF can also vary in their ability to grow in pot cultures in general, or in specific conditions imposed by greenhouse trials, such as soil pH or P availability (Brundett et al. 1996).

The current study is broadly consistent with the meta-analysis of Hoeksema et al. (2010), who synthesized responses in plant biomass to the presence versus absence (but not PRLC) of mycorrhizal fungi. For instance, they found that plants colonized by AMF grew much larger, on average, and that P-limitation of plant growth influenced the degree of response. Nevertheless, they found that differences in effects among mycorrhizal genera were relatively unimportant, even when ectomycorrhizal and AMF genera were compared. The two studies may be inconsistent in this regard for two reasons. First, different sets of trials were used (albeit with some overlap). In the current study, certain species of *Glomerales* and *Diversisporales* differed from one another in their effects on plant biomass per unit ΔPRLC (Fig. 2). On the other hand, Hoeksema et al. (2010) focused on AMF taxa belonging to the *Glomerales*, so differences between AMF taxa may have been less evident. Second, I essentially tested taxa for differences in the *efficiency* with which they benefitted host plants, on a per-unit basis (i.e., effect size per unit ΔPRLC). This value need not necessarily coincide with total effects on plant growth by the sum of AMF structures colonizing the root system, which is

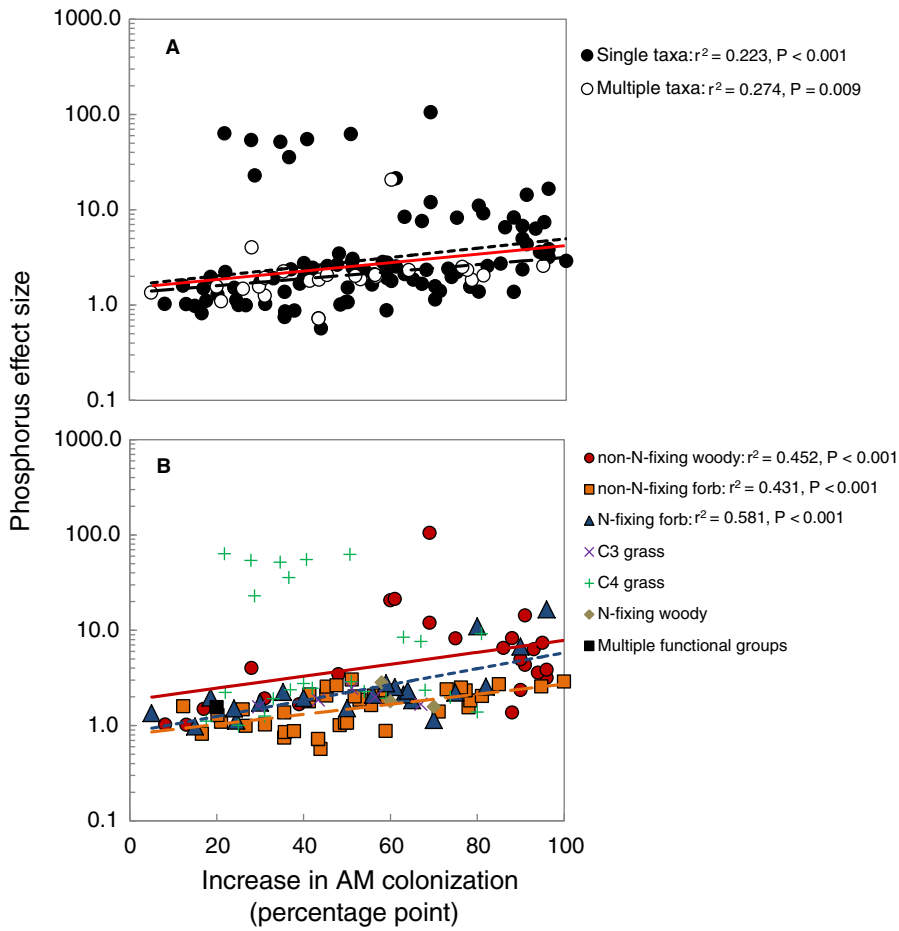

Fig. 4 Relationships between changes in percent root length colonized (higher PRLC – lower PRLC) and effect size of plant P content (P_{higher}/P_{lower}). **a** Relationships for all studies combined (r^2=0.235, P<0.001, red solid line), across all studies with single AMF taxa (*dashed line*), and for studies with multiple AMF taxa in the inoculum (*dotted line*). **b** Relationships for each plant functional group (*red solid line*=non-N-fixing woody, *orange dashed line* = non-N-fixing forb, *blue dotted line* = N-fixing forb). Each symbol represents one study. *Lines* are best fit regressions for significant relationships only. Statistics were conducted on ranked data. Note log scale of vertical axis. Effect size is unitless

the more common assessment (and the one used by Hoeksema and colleagues).

Hoeksema et al. (2010) reported that plant functional groups differed in their responses to the presence versus absence of mycorrhizal fungi, with non-N-fixing forbs and woody plants and C4 grasses displaying the greatest biomass effect. Plant functional groups were similarly influential in the current study. Here, non-N-fixing woody plants and C4 grasses displayed greater sensitivity of plant P content to ΔPRLC (Figs. 3 and 4). For instance, in the C4 grass *Panicum virgatum*, a relatively minor ΔPRLC of 20–30 percentage points resulted in a 20- to 60-fold increase in plant P content (Clark et al. 1999). This pattern could have resulted from better nutrient use efficiency of these plant functional groups compared to the others. Non-N-fixing woody plants and C4 plants can display fairly efficient retention of P within tissues (Chapin 1980; Ehleringer and Monson 1993; Aerts 1996), which could elicit higher total P content within the plant. Thus, small increases in nutrient uptake via AMF could translate to relatively large increases in P content. Soil P supply may also have interacted with plant functional group in influencing P effects in specific studies.

Even though relationships between ΔPRLC and plant biomass and P effects were highly significant, ΔPRLC did not explain the majority of variation in either effect. In analyses that included all studies, ΔPRLC explained only 11.8 % of the variation in plant biomass effect (Fig. 1), and 23.5 % in plant P effect (Fig. 4). These relatively low r^2 values are not uncommon in meta-analyses, which compile data from studies that typically differ in multiple factors. For example, methods of measuring PRLC can vary in terms of type of stain, number of intersects, and identification of AMF (versus non-AMF) structures (Vierheilig et al. 2005). Moreover, the choice of host plants, study settings, AMF taxa, and differences in assessments of plant biomass and plant P content could each have interacted with responses to ΔPRLC. For instance, most studies were conducted in laboratory settings (Online Resource 1), which requires relatively small-statured plants. Furthermore, laboratory studies often harbor artificial conditions such as low initial AMF abundance, lack of established AMF hyphal networks, or atypical P availability. Another issue to consider is that completely effective controls are rare in AMF experiments (reviewed in Brundrett 1991), so PRLC levels are not fully independent of other factors in trials. In addition, two AMF orders were not included: *Paraglomerales* and *Archaeosporales*. Thus, generalizations to natural ecosystems, particularly those with mature forest trees, or those containing the unrepresented AMF taxa, may be problematic.

In conclusion, PRLC significantly influenced AMF effects on plant biomass and P concentrations across a broad selection of field- and laboratory-based based trials with a variety of AMF taxa and plant functional groups. These findings suggest that PRLC can serve as a rough metric of AMF benefits to host plants. Moreover, AMF taxa varied in the efficiency with which they augmented plant biomass, with *Funneliformis* as particularly beneficial to plant biomass. These relationships may allow researchers to interpret changes in PRLC in the context of general effects on plant growth and P status. For example, restoration or agricultural practices that yield an increase in PRLC may likewise augment AMF benefits to host plants, especially where *Funneliformis* is common.

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