Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits

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INTRODUCTION

Globally, 80% of plant species are estimated to be mycorrhizal, many ecosystems are dominated by mycorrhizal plants (Brundrett 2002; Wang & Qiu 2006), and meters of mycorrhizal hyphae can be in a gram of soil (e.g. Jastrow et al. 1998). This suggests mycorrhizal fungi may represent the most abundant plant mutualist (Trappe 1987; Wang & Qiu 2006). Arbuscular mycorrhizal fungi (AMF) are one of the most common types of mycorrhizal fungi and have the ability to affect plant nutrition (Koide 1991), improve the water status of plants (Augé 2001), reduce plant disease (Newsham et al. 1995), enhance productivity (Hart & Klironomos 2002), and improve measures of soil health (Jastrow et al. 1998; Wilson et al. 2009). Thus, AMF have the potential to affect plant populations, communities, and ecosystems (Van Der Heijden & Sanders 2003; Smith & Read 2008). However, plant responses to mycorrhizae range from negative (i.e. parasitism) to positive (i.e. mutualism) (Johnson et al. 1997; Klironomos 2003). This variability among species complicates efforts to discover and interpret the importance of mycorrhizae to plant populations and communities. Further, understanding the factors that influence the benefit of mycorrhizae on plants has the potential to help guide management decisions and maximize desirable ecosystem functions.

The effect of mycorrhizal fungi on plant performance is often described using metrics referred to as mycorrhizal responsiveness (MR) or mycorrhizal dependency (e.g. Siqueira & Saggín-Júnior 2001). MR describes plant growth in the presence versus absence of mycorrhizae. Mycorrhizal dependency further evaluates the effect of mycorrhizae on plant growth across a range of soil phosphorus levels (e.g. Siqueira & Saggín-Júnior 2001). These approaches often compare several plant species (e.g. Wilson & Hartnett 1998; Siqueira & Saggín-Júnior 2001) or genotypes (e.g. Clement & Habte 1995; Johnson et al. 2010). Thus, these measures provide a direct measure of the interaction strength and direction, which is thought to provide one of the best metrics for interpreting whether mycorrhizae affect plant community structure, diversity, and ecosystem function (Van Der Heijden 2003). Though possibly the most important metric, relatively few studies attempt to quantify MR for an entire plant community (but see Wilson & Hartnett 1998). Furthermore, the experiments necessary to quantify mycorrhizal effects generally manipulate only a small fraction of the abiotic (Johnson 1993; Augé 2001; Siqueira & Saggín-Júnior 2001) and biotic factors (e.g. Clement & Habte 1995; Newsham et al. 1995; Siqueira & Saggín-Júnior 2001; Klironomos 2003; Johnson et al. 2010) known to affect MR. Despite these shortcomings, it is widely believed that mycorrhizae could serve as a management tool to improve plant establishment and growth (e.g. Sieverding 1991). However, their utilization has lagged because evidence justifying their value is lacking for most plant species. Since direct evidence of responses to mycorrhizae exist for only a few species, there is a need for a system to predict which plant species will benefit from mycorrhizae.

Phylogenetic analyzes can help to understand variation in functional attributes among species and even predict the outcome of species interactions (Cavender-Bares et al. 2009). For example, phylogenetic similarity among plant species has been correlated with their similarity in responses to foliar (e.g. Ness et al. 2011) and soil-borne pathogens (e.g. Liu et al. 2012). Here our goal is to rigorously test whether mycorrhizal interactions and associations also vary by plant phylogeny. Previously, Wilson & Hartnett (1998) documented the MR and root colonization (RC) of 95 tallgrass prairie species. We constructed a phylogeny for these 95 species using molecular data. This allowed us to (1) Quantify whether MR and RC vary according to plant phylogeny and exhibit a phylogenetic signal and (2) Test whether adding a phylogenetic predictor (i.e. MR or RC of the most closely related species in the dataset) to a model with predictors for species traits (e.g. annual versus perennial, legume vs. non-legume) improved the ability of the model to predict MR and/or RC.
MATERIALS AND METHODS

Phylogeny construction

We constructed a phylogeny for 95 species of herbaceous angiosperms from molecular data. The phylogeny was estimated using a Bayesian approach. We searched the GenBank database for four gene sequences often used in published angiosperm phylogenies: matK, rbcL, ITS1 and 5.8s (e.g. Cadotte et al. 2009). Multiple gene sequences are necessary to differentiate plant species because some sequences represent conservative coding regions (e.g. rbcL) and others represent more rapidly evolving portions (e.g. matK) (e.g. Cadotte et al. 2009). When a sequence was not available for the exact same species for a marker, we used sequences available for species of the same genus, and when possible of species also native to North America. 93 of the 95 species had at least one gene of these four genes represented for it or a congeneric relative in GenBank. We included one representative from an early diverging angiosperm lineage as an outgroup species, Magnolia grandiflora (L.). Sequences of these 94 species were aligned using MUSCLE version 3.7 (Edgar 2004). We edited the alignment using MEGA version 4. We reformatted the files from FASTA to NEXUS using the program Concatenator version 1. We identified the best-fit maximum likelihood models of nucleotide substitution for each gene using Akaike Information Criterion using MrModeltest version 2.3 (Nylander 2004). We concatenated the aligned sequences for the four gene sequences using Concatenator version 1 (Environmental Biology Centre, University of Lisbon, Lisbon, Portugal).

Using the concatenated sequence alignments, we performed a partitioned Bayesian Inference, estimating the posterior probability distribution of all possible phylogenies using a Markov Chain Monte Carlo algorithm (i.e. Metropolis algorithm) implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2001). Two independent Markov Chains were run, each with 4 heated chains for 10 million generations. The final average standard deviation of split frequencies was 0.008, indicating good convergence of the two independent runs. We sampled runs every 1000 generations and used a burnin of 5000 trees to generate a majority rule consensus tree (i.e. phylogram). Two species [Andropogon bladhii (Retz.), Andropogon virginicus (L.)] which were not included in the consensus tree were added as polytomies with the average branch length of the representative congener (sensu Cadotte et al. 2009). The resulting phylogram was transformed with nonparametric rate smoothing into a chronogram using APE version 2.5 (Mesquite, http://mesquiteproject.org/packages/mesquite.R/MesquiteCallsR/ape/ aAPEIntro/index.html) in R. The chronogram is shown in Fig. 1.

Mycorrhizal dependency and RC among plants

The MR and RC by AMF of 95 tallgrass prairie species were quantified in a greenhouse study (Wilson & Hartnett 1998). Ideally, the MR and RC data would be collected under a range of field conditions; however, to our knowledge attempts to characterize plant-microbial interactions under widely varying conditions have only been done for individual species (e.g. Reinhart et al. 2005) and not large groups of species. While this is a limitation of this and other similar datasets (Tilman & Kareiva 1997), we believe this is the best available dataset for this purpose, particularly because tests to determine the extent that phylogeny explains the ecological similarity of species are thought to require trait data for roughly a minimum of 20 species (e.g. Blomberg et al. 2003).

Briefly, their experiment tested the effect of pasteurized field soil versus pasteurized soil with two AMF species (Glomus spp.) added from Trifolium pratense pot cultures versus unpasteurized field soil containing 10 species of AMF on plant growth (n = 7 per treatment) (Wilson & Hartnett 1998). Plants were grown in a controlled environment and soils were a silty clay loam containing 5–10 mg kg⁻¹ plant-available phosphorus. They justified pooling the data for pasteurized soil with Glomus spp. additions and unpasteurized soil treatments into one treatment [i.e. mycorrhizal treatment vs. pasteurized soil]. This is shown in Fig. 1.

Figure 1 Molecular phylogeny (chronogram) of 95 tallgrass prairie species to the left of mycorrhizal responsiveness (MR) and root colonization (RC) data. RC data are redrawn (Wilson & Hartnett 1998) and MR data were re-calculated using a different equation (see Methods). Bars are shaded to convey positive (gray filled), negative (black filled), or neutral (white filled) effects of arbuscular mycorrhizal fungi according to Wilson & Hartnett (1998). Horizontal dashed lines delinate the family of taxa between dashed lines. Family names are not shown for taxa where only a single representative species per family is in the dataset. Subfamily names are provided for the grass family (Poaceae).
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(n = 14) after determining the effects of Glomus spp. and pasteurization were highly correlated (P = 0.0001; r = 0.894) (Wilson & Hartnett 1998). Further details on the experiment can be found in the original study (Wilson & Hartnett 1998). One important change is that we re-calculated MR using a different equation. The original equation was MR = [(dry mass mycorrhizal plant − dry mass non-mycorrhizal plant)/dry mass mycorrhizal plant] × 100. The new equation is MR = ln (AM/NM), where AM is the mean total dry weight of plants grown with AMF and NM is the mean total dry weight of plants grown without AMF. Positive values indicate enhanced growth when associated with mycorrhizae. The main benefit of this index compared to the original is that simulated data are symmetrically distributed around zero. These data were handled as continuous quantitative trait data for each of the 95 plant species. Dissimilarity metrics were calculated for the phylogenetic data (i.e. phylogenetic distance among pairs of plant species) using Patristic. Then the trait and phylogeny data were integrated to assess if a species’ MR and RC can be accurately predicted from its taxonomic group and/or the MR and RC of the most closely phylogenetically related species in the dataset.

Statistical analyses

Our ultimate goal was to determine whether phylogeny or other factors could be used to predict the MR and RC of plant species. First, we needed to confirm the presence of a phylogenetic signal (i.e. trait conservatism) among plant species for interactions with mycorrhizal fungi and RC. We quantified phylogenetic signal using a generalization of the Abouheif’s test (Pavoine et al. 2008) in adephylo (Jombart et al. 2010) implemented by abouheif.moran using the Abouheif method. This test is designed to detect phylogenetic autocorrelation in quantitative traits (MR, RC) based on a proximity matrix (i.e. phylogenetic distance among species). The significance test compares the autocorrelation of the actual data for a trait to the autocorrelation of simulated data where taxa are randomly assigned to the tips of the phylogeny. The estimates of autocorrelation effectively compare the mean squared differences between two successive observations in a sequence of continuous observations to the sum of all successive squared differences (Pavoine et al. 2008). We used 999 random permutations to obtain P-values. Significance test results using this approach were similar to those using Blomberg’s K statistic (Blomberg et al. 2003) (data not shown).

After checking for potential phylogenetic dependence in the data set, information for five plant traits, based on previous groupings by Wilson & Hartnett (1998), was used in a hierarchical cluster analysis to construct a phenogram. PC-ORD software was used to perform the hierarchical cluster analysis. The resulting phenogram (i.e. dendrogram) depicts the similarity among 95 tallgrass species based on their photosynthetic pathways (e.g. C3 vs. C4), lineages (e.g. monocot vs. dicot), life form (forb vs. grass), life history (annual vs. perennial), and capacity for nitrogen-fixation (legume vs. nonlegume). We used the phenogram like the phylogeny, and performed an Abouheif’s test to determine whether variation in the phenogram explained variation in MR and RC.

To assess the accuracy with which a species’ MR and RC can be predicted from MR and RC of the most phylogenetically related species in the dataset and/or other information, we performed multiple regressions with MR and RC as response variables. The multiple regressions included a maximum of six predictor variables in every possible combination: taxonomic family, functional type (grass, dicot forb, or monocot forb), nitrogen fixation (legume or nonlegume), life history (annual or perennial), photosynthetic pathway (photopath; C3 or C4), and phylogenetic predictor (phylo). A null model was developed that bases predictions on the mean response variable of all other species.

We used a jackknife procedure to determine which model/hypothesis was most consistent with the data (Hjorth 1994). This entailed omitting a species from the dataset, fitting the models, using the fitted models to devise point predictions for the deleted species, and repeating these steps for each species in the dataset. This allowed us to calculate a jackknife coefficient of variation (JCV) for each combination of response variable (MR, RC) and model. All computations were performed in Mathematica version 6.0 (Wolfram Research, Inc. 2007, Campaign, IL, USA).

RESULTS

The measures of MR and RC relative to the phylogeny (i.e. chronogram) of the plant species is shown in Fig. 1. The most obvious phylogenetic pattern across the 95 taxa is for the subfamily Pooidae (family Poaceae). Although this subfamily was colonized by mycorrhizal fungi, levels of colonization appeared lower than in other phylogenetic groups, and the species were predominately neutrally affected by associations with AMF (Fig. 1 and Fig. S1 in the Supporting Information).

Across the entire plant community, the Abouheif’s test confirmed the presence of a phylogenetic signal for MR and RC indicating that related species have more similar interactions with mycorrhizae than expected by chance (P = 0.003). This was true whether using the chronogram (P < 0.001) or phylogram (P ≤ 0.003). Because visual examination of Fig. 1 suggested a phylogenetic signal for taxa of the Poaceae, we then analyzed their MR and RC separately. The Poaceae taxa also exhibited phylogenetic signals for MR and RC when using the chronogram (P < 0.003) and phylogram (P ≤ 0.002) (Fig. S1).

A hierarchical cluster analysis of five plant traits revealed nine distinct clusters of plant species (Fig. 2). Visual examination of the groupings of plant taxa revealed some variation in MR and RC, especially clusters of taxa that were relatively unresponsive to mycorrhizal fungi. Clusters of species that were unresponsive to mycorrhizal fungi included three annual forbs, six C3 perennial grasses, seven C3 annual grasses and eight C4 annual grasses. Other groupings of taxa revealed greater levels of variation among taxa. We used the Abouheif’s test to identify whether the phenogram from the hierarchical cluster analysis of species’ traits explained variation in MR and RC of species. These analyses identified that variation in MR (P < 0.0001) and RC (P = 0.004) is explained by the phenogram.

To assess if a species’ MR and RC can be accurately predicted from the MR and RC of the most phylogenetically related species in the dataset or other criteria, we performed multiple regressions and compared the Jackknife coefficient of variation (JCV) of models used in the multiple regressions to null models. When RC was the response variable, the null model’s JCV was relatively small (Table 1) indicating that all plants had relatively similar RC values. Thus, the top five regression models used to predict RC resulted in only minor improvements to the JCV values (Table 1). When MR was the response variable, the null model had a large JCV...
value indicating MR values varied among plant species. Four of the top five regression models included phylogeny as a predictor. However, the model ranked fifth excluded phylogeny as a predictor and was otherwise identical to the top model. The JCV values for these two models are relatively similar (Table 1). Thus, terms (i.e. functional type, life history, and photosynthetic pathway) other than phylogeny provide much of the explanatory power to predict MR values. A comparison of models with only a single term; however, revealed that phylogeny was the strongest predictor (JCV = 0.88 vs. life history = 0.90, null model = 0.94, photosynthetic pathway = 0.96, nitrogen-fixer = 0.99, functional type = 1.0, and family = 1.0). Though the top ranked models for predicting MR improved JCV values relative to the null model, JCV values remained large indicating that predictions were relatively imprecise.

**DISCUSSION**

We used one of the best available datasets (Wilson & Hartnett 1998) on plant-mycorrhizal interactions to reveal plant phylogenetic signals for both plant MR and RC. Additional, phylogenetic analyses revealed that grass taxa in the subfamily Pooidae typically do not depend on AMF while grass taxa from other subfamilies typically do benefit from AMF. In addition, we determined that phylogeny and other variables can be used to predict the MR and RC of plant species. Plant phylogeny improved predictions of MR but combinations of other variables contributed more to predicting MR. While phylogeny and other factors explained variation in MR, much variation remained unexplained.

Results from our study reveal some phylogenetic patterns in how plants interact with AMF but across the entire dataset phylogenetic similarity was an unreliable predictor of a species’ MR and RC. These findings suggest that interactions with AMF are relatively open to evolutionarily change. These results can be interpreted in the context of the long evolutionary history between plants and mycorrhizae. Geologic evidence suggests that terrestrial plants have a long evolutionary history with mycorrhizal fungi dating back c. 40 MY (Brundrett 2002). This suggests that plants share a common history of associating with mycorrhizae, especially AMF. Other studies, tabulating whether plant species either associate with mycorrhizae or not, report variation among taxa at the level of genus and family (c.g. Harley & Harley 1987). We found that evolutionary history explains some but not all of the variation in MR and RC. The benefit of mycorrhizae did vary among grass subfamilies. Grasses

<table>
<thead>
<tr>
<th>Model</th>
<th>MR (JCV)</th>
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<tr>
<td>Type + life history + photopath + phylo</td>
<td>0.76</td>
</tr>
<tr>
<td>Type + legume + life history + photopath + phylo</td>
<td>0.77</td>
</tr>
<tr>
<td>Family + legume + life history + photopath + phylo</td>
<td>0.77</td>
</tr>
<tr>
<td>Family + life history + photopath + phylo</td>
<td>0.77</td>
</tr>
<tr>
<td>Type + life history + photopath</td>
<td>0.78</td>
</tr>
<tr>
<td>Null model</td>
<td>0.94</td>
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<table>
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<tr>
<th>Model</th>
<th>RC (CV)</th>
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</thead>
<tbody>
<tr>
<td>Family + life history + photopath</td>
<td>0.37</td>
</tr>
<tr>
<td>Type + life history + photopath + phylo</td>
<td>0.37</td>
</tr>
<tr>
<td>Family + life history + photopath + phylo</td>
<td>0.37</td>
</tr>
<tr>
<td>Type + life history + photopath</td>
<td>0.37</td>
</tr>
<tr>
<td>Type + legume + life history + photopath + phylo</td>
<td>0.38</td>
</tr>
<tr>
<td>Null model</td>
<td>0.40</td>
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date back 83–89 MY, and a main evolutionary distinction between the three subfamilies (Fig. 1 and Fig. S1) is that the Pooidae diversified in cooler climates (Gibson 2009) and appear to have less plastic root morphologies in the presence vs. absence of mycorrhizae (Hetrick et al. 1991; Miller et al. 1997). We discovered that a plant’s associations and interactions with AMF cannot be accurately predicted by a close relative’s associations and interactions with AMF. This is partly because several non-grass species have independently evolved to be unresponsive to AMF (i.e. facultative mycorrhizal) (Fig. 1). Therefore, the traits associated with being unresponsive to AMF appear to represent distinct cases of either having arisen from shared descent and being similar to close relatives (e.g. Pooidae) or represent multiple cases of recent convergent evolution.

The most obvious phylogenetic pattern to emerge was among grass subfamilies and their varying responsiveness to mycorrhizae (Fig. 1 and Fig. S1). Distinctions among grass subfamilies are ecologically important because grasslands are dominated by grasses from varying subfamilies both at the level of the communities making up major grassland types and among the major grassland types (Table 2). Distinctions among grasses is important because grasslands are typically dominated by only a few grass species (Sims & Risser 2000), hence grasses comprise the majority of the total biomass and are likely to disproportionately affect ecosystem processes (e.g. Grime 1998). Here we summarize the dominant grass genera and their respective subfamilies for the eight main grassland types in the contiguous U.S. (see Table 2). This helps illustrate that the dominant grasses within each grassland type come from one of these three subfamilies and that the importance of individual subfamilies varies by major grassland type. Because of their abundance, the MR of the dominant grasses of a grassland community may be disproportionately influenced on other plants (e.g. Grime 1998), especially those that depend on mycorrhizal fungi and processes related to mycorrhizae including soil carbon sequestration and soil structure (Jastrow et al. 1998; Wilson et al. 2009). Some of the major grassland types shown in Table 2 are dominated by taxa from either Chloridoideae and Panicoideae (Coastal prairie), or Chloridoideae and Pooidae (Palouse prairie). Other important differences also exist among the individual grassland communities making up these major grassland types. For example, since tallgrass communities are often dominated by a highly mycorrhizal dependent species [Andropogon gerardii (Vitman), subfamily Panicoideae], this is an ecosystem where mycorrhizae can impact plant community composition (Smith et al. 1998; Wilson & Hartnett 1998; Hartnett & Wilson 1999), soil health, and ecosystem function (Jastrow et al. 1998; Wilson et al. 2009). However, tallgrass prairie community composition varies across moisture gradients. Thus, they are often dominated by taxa of Chloridoideae in wet areas, and either Panicoideae or Pooidae subfamilies in dry areas (e.g. Taub 2000). Knowledge that grassland communities are dominated by grass taxa that either depend on mycorrhizae or not is likely essential for interpreting the importance of mycorrhizae to a specific grassland; however, further validation of this is needed.

Wilson & Hartnett (1998) originally reported that plant families and functional guilds separately explain variation in MR and RC. We aggregated several plant guilds to produce a phenogram (Fig. 2) that helped to reveal annuals and C3 grasses are relatively unresponsive to mycorrhizae. Separate analyses revealed that phylogeny and some of these plant characteristics helped enable prediction of plant responses to mycorrhizae. While phylogeny was the best individual predictor, groups of other variables appeared to enable the best predictions of MR (Table 1). Unfortunately, even the best models for predicting MR continued to have relatively large Jackknife coefficients of variation. This indicates their continued inability to accurately predict the MR of plant species. RC values were relatively similar among species suggesting there is limited need to explain their variability (Fig. 1 and Table 1).

Knowledge of which plant species benefit from AMF has the potential to improve management practices for sustainable agriculture, mine reclamation, and restoration. Identifying which plant species will benefit from mycorrhizae is one necessary step for developing effective practices that increase plant establishment and yields by either effectively planting seedlings already colonized by suitable mycorrhizae or adding native mycorrhizal inocula

Table 2 Major grassland types in the contiguous U.S. ranked by their historic prominence prior to changes in land use (listed from major to minor) with prominent genera listed

<table>
<thead>
<tr>
<th>Grassland types*</th>
<th>Pooidae</th>
<th>Chloridoideae</th>
<th>Panicoideae</th>
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<tbody>
<tr>
<td>Palouse prairie</td>
<td>Bromus, Elymus, Festuca, Koeleria, Leymus, Pascopyron, Poa, Pseudoroegneria, Stipa</td>
<td>Boetelona, Buchloe, Hilaria, Muhlenbergia, Sporobolus</td>
<td>Andropogon, Panicum, Schizachyrium, Sorostrum</td>
</tr>
<tr>
<td>Shortgrass prairie</td>
<td>Bromus, Koeleria, Oryzopsis, Pascopyron, Stipa</td>
<td></td>
<td>Andropogon, Schizachyrium</td>
</tr>
<tr>
<td>Tallgrass prairie</td>
<td>Elymus, Koeleria, Pascopyron, Pseudoroegneria, Stipa</td>
<td>Boetelona, Buchloe, Calammezidia, Sporobolus</td>
<td></td>
</tr>
<tr>
<td>Mixed-grass prairie</td>
<td>Koeleria, Pascopyron, Poa, Pseudoroegneria, Stipa</td>
<td>Boetelona, Buchloe, Calammezidia, Sporobolus</td>
<td></td>
</tr>
<tr>
<td>Fescue prairie</td>
<td>Festuca</td>
<td></td>
<td>Andropogon, Schizachyrium</td>
</tr>
<tr>
<td>Desert grassland</td>
<td>Oryzopsis</td>
<td>Boetelona, Hilaria</td>
<td></td>
</tr>
<tr>
<td>California grassland</td>
<td>Deschampsia, Elymus, Festuca, Koeleria, Netella, Poa</td>
<td>Muhlenbergia</td>
<td>Andropogon, Panicum, Psytalum, Schizachyrium, Sorostrum, Tripsacum</td>
</tr>
<tr>
<td>Coastal prairie</td>
<td></td>
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(e.g. pellets, slurries and gels) while seeding (Sieverding 1991). Unfortunately, practitioners have neither the expertise nor the tools to gauge the effects of mycorrhizae on plants. To successfully measure these impacts requires access to scientific experts, summaries of scientific studies on the benefits of mycorrhizae for a species/system of interest, tools that will enable them to make predictions about the benefits of mycorrhizae, or combinations of the three. Coarse phylogenetic patterns have been described previously that tabulated patterns of RC and/or association among plant taxa (Harley & Harley 1987; reviewed in Brundrett 2002; Wang & Qiu 2006). These approaches reveal numerous independent cases of plants not associating with mycorrhizae and indicates that individual species may differ from other species in the same family and even genus (Wang & Qiu 2006). Unfortunately, these tabulations emphasize descriptions of RC which is often unrelated to how plants interact with mycorrhizal fungi (e.g. McGonigle 1988). While other studies on host-specific mycorrhizal fungi, other than AMF, indicate the evolutionary relationships of the mycorrhizae correspond with the phylogenetic structure of their orchid hosts (e.g. Jacquemyn et al. 2011), our focus here is on the importance of phylogenetic relationships in explaining whether or not plant growth increases when associating with AMF.

A future goal should be to develop an information system that can predict the degree plants depend on mycorrhizal fungi. Although evolutionary history may be a useful predictor in some limited cases (e.g. Pooidae), precise predictions of whether or not most plants depend on mycorrhizal interactions or not will require other types of information. Others have found that phylogenetic relationships explain some of the variation in plant-herbivore interactions, but that phenograms which were based on a variety of plant characteristics independent of evolutionary relationships explained greater amounts of variation (e.g. Agrawal & Fishbein 2006). Here we show that grouping plants by other criteria such as life history (annual vs. perennial), functional type (grass vs. monocot forb vs. dicot forb), and photosynthetic pathway can improve predictions of plant responses to mycorrhizae (Table 1). More precise predictions may be achieved by developing phenograms (e.g. Fig. 2) that include additional plant traits related to mycorrhizal interactions independent of evolutionary relationships. Some traits known to explain MR include: difference in phosphorus uptake between mycorrhizal and nonmycorrhizal plants, root to shoot ratios, root architecture and plasticity, and colonization of mycorrhizae based on root length or root mass (Hetrick et al. 1991; Miller et al. 1997; Siqueira & Saggin-Júnior 2001; Brundrett 2002). Other useful predictors may include phosphorus levels and/or ratios of nitrogen to phosphorus in foliar or soil samples (Koerselman & Meuleman 1996; Hoeksema et al. 2010). Some of the variation in MR among grasses correspond to their having optimal root foraging characteristics that are plastic and depend on whether they are colonized by mycorrhizal fungi or not while others have a fixed strategy regardless of their association with mycorrhizae (Hetrick et al. 1991; Miller et al. 1997). Uncovering the plant genes associated with MR, or related root traits, will likely provide additional opportunities for predicting plant responses to mycorrhizae. However, validation of improved predictors will continue to rely on the quantification of MR for additional plant species and even entire communities. Broader utilization of mycorrhizae to solve applied problems is likely to depend on tools to reliably predict which plants will, and will not, benefit from mycorrhizal fungii.

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AUTHORSHIP

GWTW provided the primary data set on mycorrhizal responsiveness and root colonization; KOR constructed the phylogeny; KOR and MJR analyzed the data; and all authors contributed in writing, discussions, or comments.

REFERENCES


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