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AMF, phylogeny, and succession: specificity of response to mycorrhizal fungi increases for late-successional plants

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Abstract. Arbuscular mycorrhizal (AM) fungal communities are important to plant community productivity and diversity; however, the importance of AM fungal composition to community dynamics remains largely unknown. Specificity of plant response to different AM fungal species is a prerequisite for AM fungal composition to have an effect on plant community dynamics. We test determinants of specificity of plant response to AM fungi across six early- and six late-successional tallgrass prairie plants by growing them with one of seven different AM fungal species and a non-inoculated control. We found that late-successional species were more responsive, and demonstrated greater specificity, toward individual AM fungal taxa than early-successional species. There was no phylogenetic signal for plant responsiveness or specificity of plant response. Phylogenetic multiple regressions indicated that successional stage, plant growth rate, and overall responsiveness were significant predictors of fungal specificity independent of shared phylogeny. These results suggest that plant response to mycorrhizal fungi is evolutionarily labile and coevolves with plant life history. Our results also suggest that AM fungal community dynamics can be particularly important for the establishment and subsequent dynamics of late-successional plants.

Key words: arbuscular mycorrhizal fungi; coefficient of variation; feedbacks; fungal specificity; mycorrhizal dependency; phylogenetic signal; plant and fungal ecology; plant community dynamics; plant succession.

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Introduction

Belowground symbionts such as arbuscular mycorrhizal (AM) fungi can play an important role in plant community dynamics by improving plant community productivity (van der Heijden et al. 1998, Vogelsang et al. 2006, Bauer et al. 2012). Individual AM fungal isolates have been shown to differ from each other in several dimensions, including their effect on plant host P, N, K, and Na+ uptake (Aggangan et al. 2010), the carbon elicited from a host plant (Bever et al. 2009), and their ability to provide non-nutritional benefits to their host plant through the alleviation of drought stress (Marulanda et al. 2003), providing resistance to herbivores (Bennett and Bever 2007), and pathogen resistance (Sikes et al. 2009). Thus, although AM fungi associate with a wide variety of plants, individual plant species may vary in their responses to different fungal partners (Bever 2002, Klironomos 2003).

Plant response to specific AM fungal taxa can also be linked with ecological processes such as community dynamics and species coexistence. For instance, variation in plant response to specific fungal taxa may drive plant diversity and productivity response to manipulations of AM fungal richness (van der Heijden et al. 1998, Vogelsang et al. 2006, Wagg et al. 2011). Plant composition can also alter AM fungal composition, as plant species can differ in their quality as hosts to different AM fungal species (Bever et al. 1996, Bever 2002, Burrows and Pfleger 2002, Johnson et al. 2004, Antoninka et al. 2011). Taken

together, specificity within the plant and fungal mutualism can lead to feedbacks, the strength and direction of which can alter community dynamics and lead to species coexistence or species turnover and succession (Bever 1999). While there is evidence of changes in AM fungal composition generating positive (Mangan et al. 2010) and negative (Bever 2002, Castelli and Casper 2003) feedbacks, ecologists currently have little basis for predicting which plants might be most sensitive to mycorrhizal feedbacks as well as the impacts of mycorrhizal feedbacks on plant community dynamics.

The relative importance of AM fungal composition in plant community dynamics will depend on patterns of plant response to AM fungal species in that community. Significant variation in plant response to AM fungal species has been demonstrated (Klironomos 2003, Pringle and Bever 2008), and patterns of this specificity would guide assessments of the importance of AM fungal composition. It has been hypothesized that mycorrhizal-responsive plants might be more sensitive to AM fungal composition, but tests of this hypothesis have been inconclusive (van der Heijden et al. 1998, Hart and Klironomos 2003, Reynolds et al. 2003, 2005), possibly because the plant species utilized in these studies had low overall variation in mycorrhizal responsiveness. Phylogeny has been suggested as an important predictor of plant response to mycorrhizal fungi (Reinhart et al. 2012) and other soil organisms (Anacker et al. 2014). However, the phylogenetic patterns of specificity of plant response to different species of AM fungi have not been tested. Moreover, plant successional stage has been found to be a very good predictor of plant response to mycorrhizal fungi and more important than plant phylogeny (Koziol and Bever 2015). Specificity of plant response may also be expected to vary with plant successional stage. However, at present, this possibility is also untested, in spite of the speculation that changes in AM fungal composition can be important to plant succession (Johnson et al. 1991).

Here, we assess the specificity of plant growth response to one of seven different AM fungal taxa across plants of different successional stages in the tallgrass prairie. We use this comparison to test for correlations of specificity of response with average responsiveness, with phylogenetic relatedness, and with plant successional stages. We have previously found that overall mycorrhizal responsiveness increases with plant successional status in this system (Koziol and Bever 2015). Should late-successional plants also be more sensitive to AM fungal composition, then fungal composition could promote or inhibit late-successional plant species, and changes in AM fungal composition could mediate plant species turnover during succession.

Materials and Methods

Experimental design

We chose six early- and six late-successional plant species paired within four plant groups: grasses, legumes, composites, and lilies (Appendix S1: Table S1). Plants were classified as early or late successional based on field observations (Betz 1986, Schramm 1992, Swink and Wilhelm 1994, Betz et al. 1996) as discussed in Koziol and Bever (2015). Seeds were obtained from Spence Nursery (Muncie, Indiana, USA). Seeds were cold-moist-stratified in sterilized sand for one month prior to germination. Seven replicates of two-week-old seedlings of each plant species were planted into non-inoculated soil and soil inoculated individually with one of seven AM fungal species. Soil was collected from the Kankakee Sands Nature Preserve (Morocco, Indiana, USA) and was mixed 1:1 with Indiana river sand. The background soil mix had a pH of 8.2, with 0.1% organic matter, 70 ppm nitrate, 19 ppm P, 33 ppm K, and 102 Mg (Mehlich-3). The background soil mixture was steam-sterilized twice for 4 h with a one-day rest period between sterilization.

Plants were grown in a glasshouse during the summer of 2012 (Bloomington, Indiana, USA). Plant height was taken immediately after starting the experiment, and these initial size measurements were used as covariates in our statistical analyses. After four months, plants were harvested and dry mass were collected for roots and shoots. The growth during these four months is henceforth called the plant growth rate. Mycorrhizal responsiveness was evaluated using average total plant mass for each plant by fungal species combination by determining the weight of inoculated/non-inoculated plants as follows:

$$\text{Mycorrhizal responsiveness (MR)} = \frac{\log(\text{average plant biomass with inoculation})}{\log(\text{average plant biomass without inoculation})}$$

Overall mycorrhizal responsiveness is the averaged mycorrhizal responsiveness across all fungal species.

Fungal material

Arbuscular mycorrhizal fungal spores were isolated from prairies near the Kankakee Sands Nature Preserve. Pure cultures were grown with sorghum grass on mixture of sand and Indiana soil (Vogelsang et al. 2006). The AM fungi included in this experiment were as follows: *Claroideoglomus claroideum, Racocetra fuldiga, Funneliformus mosseae, Cetraspora pellucida, Claroideoglomus lamellosum, Acaulospora spinosa,* and *Entrophospora infrequens.* These cultures have been maintained by the Bever laboratory and have been used in many field and glasshouse experiments (Bauer et al. 2012, Larimer et al. 2013, Koziol and Bever 2015, Middleton et al. 2015). The AM-inoculated pots were filled with 950 cm^3 of sterile soil with 50 cm^3 of single-species fungal inoculum placed at the center pot depth. Non-inoculated pots received 1000 cm^3 of the sterilized soil mixture. During harvesting, a subsample of roots from each plant was washed and stained with Trypan Blue and analyzed to confirm AM fungal colonization (McGonigle et al. 1990). In a similarly inoculated parallel study, a mean infection percentage (MIP) assessment was conducted prior to the experiment to assess mean fungal infection for each of our fungal species (Vogelsang et al. 2006). MIP plants were harvested after four weeks at which time the infection percentage of hyphae and arbuscules was not significantly different among fungal species ($F_6 = 2.6$, $P = 0.08$ and $F_6 = 2.7$, $P = 0.07$), indicating that similar initial infection levels can occur with these fungal species even though arbuscular structures in plants inoculated with the fungal species *E. infrequens* and *F. mosseae* tended to be slightly lower after four weeks than what was found with the other species. We found that the differences in MIP did not predict final proportion of root infected by AM fungal hyphae ($F_{1,5} = 0.1$, $P = 0.8$), infection by arbuscules ($F_{1,5} = 0.007$, $P = 0.9$), or plant response to mycorrhizal fungi ($F_{1,5} = 1.5$, $P = 0.2$).

Statistical analysis

We analyzed plant growth response of total weight, shoot mass, and root mass using a mixed model with plant species within successional stage identified as a random effect to test for general patterns across plant species. We deconstructed plant growth responses into four a priori orthogonal contrasts comparing inoculated vs. non-inoculated, differences among fungi, and these contrasts by successional stage within the model. Specificity of response is tested with fungal treatment by successional stage interaction and the fungal treatment by plant species within successional stage variance component. Contrasts within the fungal inoculation-by-successional stage interaction tested for consistent differences between early- and late-successional plant species in specificity of response to particular AM fungal species.

Variation in levels of specificity of response between successional stages was tested by calculating values of mycorrhizal responsiveness (MR = inoculated plant biomass/non-inoculated plant biomass) from the best linear unbiased predictor means for individual plant and fungal combinations, as in Koziol and Bever (2015). Mycorrhizal responsiveness was log (1 + MR)-transformed prior to testing for differences in (1) average mycorrhizal responsiveness, (2) variation in mycorrhizal response, and (3) the coefficient of variation, hereby abbreviated CoV (variance in mycorrhizal response/average mycorrhizal response), using a general linear model with plant successional stage (early or late) and plant family as predictors. In separate analyses, we tested correlations of mycorrhizal responsiveness and the coefficient of variation in mycorrhizal responsiveness using plant growth rate and successional status as predictors after correcting for phylogeny using phylogenetic generalized least squares multiple regression using the caper package in R (Orme 2013). Our plant phylogeny was constructed using the methods outlined in Koziol and Bever (2015). After searching for ITS1 and ITS2 regions in the GenBank database, a maximum likelihood tree was aligned using MEGA (Tamura et al. 2013) (see Appendix S1: Methods M1 for additional information on phylogenetic analyses). We tested for a phylogenetic autocorrelation signal in our phylogeny for plant successional stage, mycorrhizal responsiveness, variation in mycorrhizal responsiveness, and CoV by calculating

Table 1. Results of a mixed model assessing plant growth where we identified species within successional stage as a random effect to test for general patterns across plant species.

Effect	Num DF	Den DF	Log (total weight)		Log (root weight)		Log (shoot weight)		Log (root:shoot)	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Initial height	1	461	45.1	<0.0001	33.1†	<0.0001	38.6‡	<0.0001	0.2	0.7
Block	6	461	1.5	0.2	1.5†	0.2	1.5‡	0.2	1.2	0.3
Successional stage	1	10	6.5	0.03	3	0.1	12.6	0.005	0.03	0.8
Fungi	7	70	9.7	<0.0001	8.6	<0.0001	7.2	<0.0001	0.7	0.6
AM fungi vs. non-inoculated	1	70	22.2	0.0001	19.5	<0.0001	14.1	0.003	2.1	0.1
Differences among fungal species	6	70	7.6	<0.0001	6.8	<0.0001	6.05	<0.0001	0.5	0.8
Successional stage × fungi	7	70	10.6	<0.0001	10.1	<0.0001	7.5	<0.0001	0.2	1
AM fungi vs. non-inoculated × successional stage	1	70	1.6	0.2	3	0.09	0	1	0.06	0.8
Differences among fungal species × successional stage	6	70	12.1	<0.0001	11.2	<0.0001	8.8	<0.0001	0.2	1

Notes: Plant growth was measured as the log-transformed dry total weight (g), root weight (g), shoot weight (g) or root weight (g)-to-shoot weight (g) ratio. Den DF of 476† and 470‡ for log (root weight) and log (shoot weight), respectively.

Moran's *I* using the picante, adephylo, and phylobase packages in R (Jombart and Dray 2008, Kembel et al. 2010, Hackathon et al. 2016). Tests of phylogenetic autocorrelation signal indicate whether these traits are evolutionarily labile and weakly predicted by phylogeny, as is the case with weak autocorrelation. All other statistical tests were performed using SAS version 9.4 (SAS 2015).

Results

Mycorrhizal responsiveness across succession

Soil treatment was a significant predictor of plant size (Table 1, $F_{7,70} = 9.1$, $P < 0.0001$), with early-successional plants growing 40% smaller with AM inoculation and late-successional plants growing 383% larger with AM inoculation relative to the non-inoculated controls (Fig. 1, Table 1, $F_{7,70} = 10.6$, $P < 0.0001$). Further results on overall plant mycorrhizal responsiveness, variance components, and plant growth across successional stages can be found in Appendix S1: Results S1, and the remainder of these results focus on the specificity of plant response to different AM fungal taxa across succession.

Variation in levels of specificity of growth response across succession

We analyzed both average total variation and the coefficient of variation (CoV) in mycorrhizal responsiveness among the different fungi for each plant species (Appendix S1: Table S2). We found that plant successional stage was a significant predictor of variation in mycorrhizal responsiveness among the different plant species, where late-successional plants averaged more than 10 times the variation in mycorrhizal responsiveness among the different fungal species compared to early-successional plants (Appendix S1: Table S2, $F_{1,11} = 9.3$, $P = 0.02$). The highest average variation in mycorrhizal responsiveness for any early-successional plant was much lower than the lowest average variation in mycorrhizal responsiveness found for any late-successional plant, with 0.03 and 0.06 for *Elymus* and *Schizachyium*, respectively (Appendix S1: Table S2). Successional stage was also the most significant predictor for the coefficient of variation in mycorrhizal responsiveness (Fig. 2a, $F_{1,11} = 7.6$, $P = 0.03$), where late-successional plants had significantly greater average CoV than early-successional plants (0.05). Plant family was not a significant predictor of either average variation or the coefficient of variation in mycorrhizal responsiveness for these plant species (both $F_{3,11} = 1.1$, $P = 0.4$).

Fungal-specific growth responses and root infection across plant successional stage

Early- and late-successional plants consistently differed in their response to inoculation with particular AM fungal species (Fig. 3, Table 1, $F_{6,70} = 7.1$, $P < 0.0001$). Late-successional plants tended to grow largest when inoculated with the fungal species *E. infrequens and C. lamellosum*, while early-successional plants preferred the

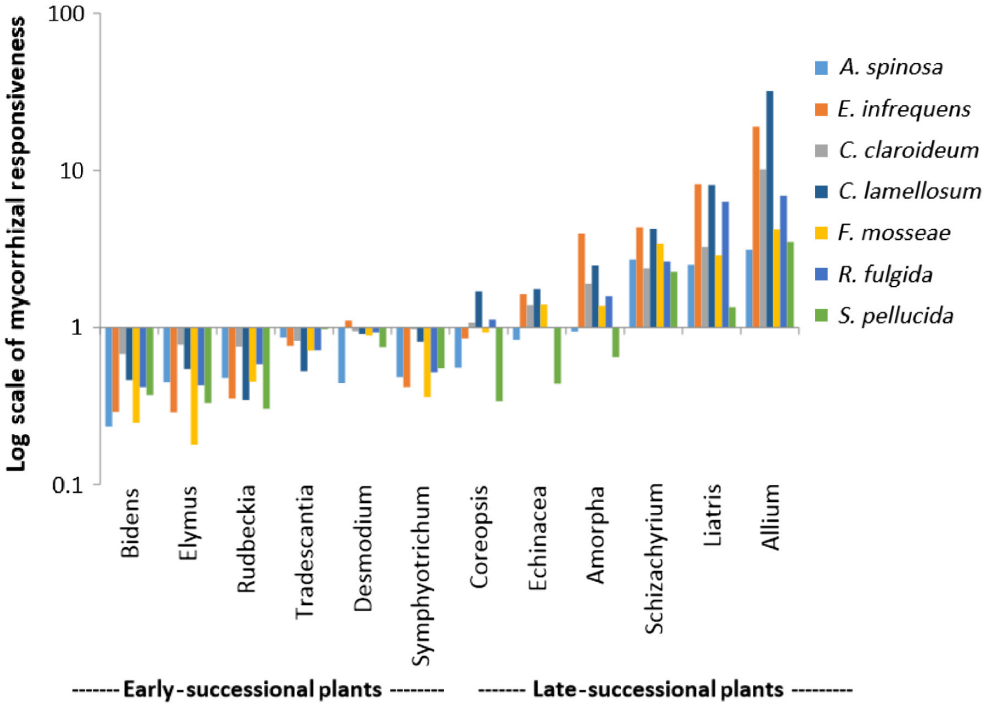

Fig. 1. The log (mycorrhizal responsiveness) for each of the 12 plant species grown with one of seven different fungal species plotted on a log scale. Bars represent the mean mycorrhizal responsiveness that was calculated as the dry weight of inoculated plants/non-inoculated plants. Plants were ordered by overall mycorrhizal responsiveness within each successional stage so that the left six plants are early successional and the right six plants are late successional. Late-successional species had greater overall responsiveness ($F_{7,70} = 10.6$, $P < 0.0001$) and 10 times more variability in responsiveness to individual AM fungi species ($F_{1,11} = 9.3$, $P = 0.02$) than early-successional species.

non-inoculated treatment (Figs. 1, 3). We found that plant successional stage was also a significant predictor of the percentage of roots infected by the different fungal species, where late-successional plants had a higher proportion of roots infected with hyphal (Appendix S1: Fig. S1a, $F_{6,65} = 17.5$, $P < 0.0001$), arbuscular (Appendix S1: Fig. S1b, $F_{7,65} = 5.4$, $P < 0.0001$), and vesicular (Appendix S1: Fig. S1c, $F_{6,65} = 10.2$, $P < 0.0001$) structures when inoculated with some AM fungal species. *Racocetra fulgida* had the highest hyphal colonization, *R. fulgida* and *C. lamellosum* had the greatest arbuscular colonization, and *E. infrequens* and *C. lamellosum* had the greatest vesicular colonization (Appendix S1: Fig. S1).

Plant growth across succession

Plant successional stage was a significant predictor of the average growth rate of plant species (Fig. 3, Table 1, $F_{1,10} = 6.8$, $P = 0.03$). Early-successional plants grew twice as large as late-successional plants (Table 1, $F_{1,10} = 6.8$, $P = 0.03$) in terms of both roots (Table 1, $F_{1,10} = 3$, $P = 0.1$) and shoots (Table 1, $F_{1,10} = 12.6$, $P = 0.005$). Plants from different successional stages did not differ in root-to-shoot ratio (Table 1, $F_{1,10} = 0.02$, $P = 0.8$).

Correlations and phylogenetic regressions of variations in mycorrhizal response

Overall, we found that the coefficient of variation in mycorrhizal responsiveness was strongly correlated with overall mycorrhizal responsiveness (Appendix S1: Table S2; Fig. 2b, $R = 0.63$, df = 10, $P = 0.03$), the total variation in mycorrhizal responsiveness (Appendix S1: Table S2, $R = 0.95$, df = 10, $P < 0.0001$), and average plant growth rate (Appendix S1: Table S2; Fig. 2c, $R = -0.64$, df = 10, $P = 0.02$). Multiple regressions correcting for plant phylogeny indicated that the coefficient of variation was significantly predicted by overall mycorrhizal responsiveness, average plant growth rate,

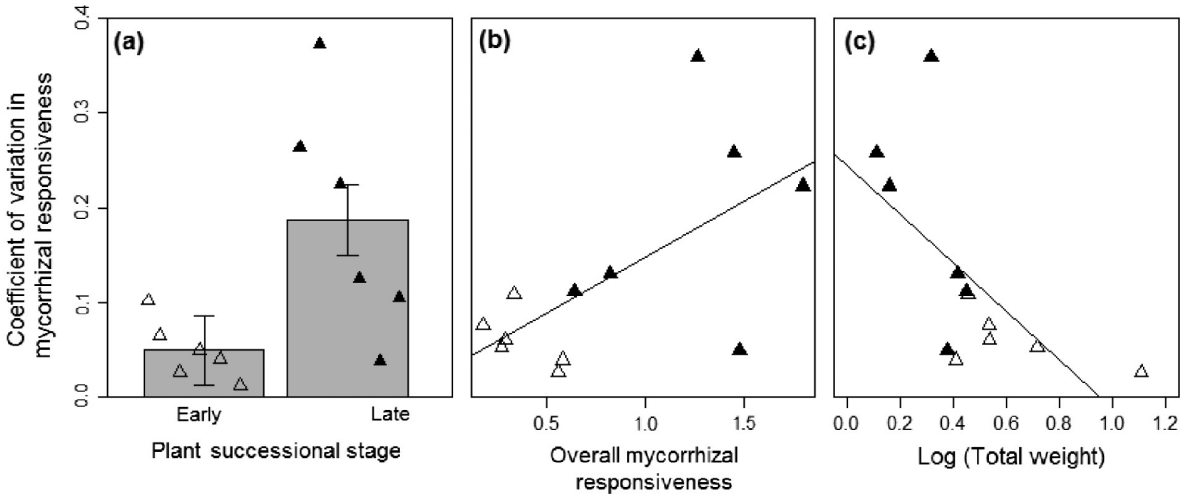

Fig. 2. The coefficient of variation in mycorrhizal responsiveness among fungal species was strongly predicted by plant successional stage (a), overall mycorrhizal responsiveness (average dry weight of inoculated plants/non-inoculated plants across all fungal treatments) (b), and plant growth rate (c). Bars and error bars (a) represent successional stage means and SE, points represent an individual plant species where early-successional species are marked by Δ, late-successional species are indicated by ▲, and lines represent best fit (b and c). We found that the coefficient of variation in mycorrhizal responsiveness was significantly correlated with both overall mycorrhizal responsiveness (b, $R = 0.63$, df = 10, $P = 0.03$) and average plant growth rate (c, $R = -0.64$, df = 10, $P = 0.02$).

and successional stage independent of shared phylogeny (Appendix S1: Table S3; Fig. S2, $\beta = 0.1 \pm 0.04$ [mean/SE], $P = 0.02$, $\beta = -0.3 \pm 0.1$ [mean/SE], $P = 0.02$, $\beta = 0.02 \pm 0.006$ [mean/SE], $P = 0.004$, respectively). We found no phylogenetic signal for successional stage (Appendix S1: Fig S3, Moran's $I = -0.5$, $P = 1.0$), as we controlled for pairs of early- and late-successional plants within a plant family in our species selection. Interestingly, we also found no phylogenetic signal for average overall mycorrhizal responsiveness (Appendix S1: Fig. S3, Moran's $I = -0.4$, $P = 0.9$), variation in mycorrhizal responsiveness among fungal species (Appendix S1: Fig. S3, Moran's $I = -0.3$, $P = 1.0$), the coefficient of variation in mycorrhizal responsiveness (Appendix S1: Fig. S3, Moran's $I = -0.3$, $P = 1.0$), or plant growth rate (Appendix S1: Fig. S3, Moran's $I = -0.4$, $P = 1.0$).

Discussion

Late-successional plants demonstrate greater fungal specificity

The results of this study suggest that mycorrhizal fungal species identity and turnover during succession may play an important role in plant community dynamics, as we found that late-successional prairie plant species have greater variability in response to individual AM fungal species than early-successional plants. The importance of microbial biotic drivers in species turnover during succession remains a poorly understood area in community ecology, with previous work suggesting that microbial pathogens and mutualists could be important to these processes (Kardol et al. 2006, Bauer et al. 2015, Koziol and Bever 2015, Meiners et al. 2015). Previous conjecture on the role of AM fungi in succession has focused on changes in AM fungal density (Janos 1980, Reynolds et al. 2003). We and others have previously found strong evidence that late-successional plant species are highly dependent on AM fungi while early-successional species are not (Middleton and Bever 2012, Koziol and Bever 2015), suggesting that changes in AM fungal density play a key role in shaping plant communities during succession. Previous work has demonstrated that changes in fungal composition occur during field succession (Johnson et al. 1991). Because late-successional plant species are sensitive to fungal species identity, our results suggest that changes in AM fungal composition during

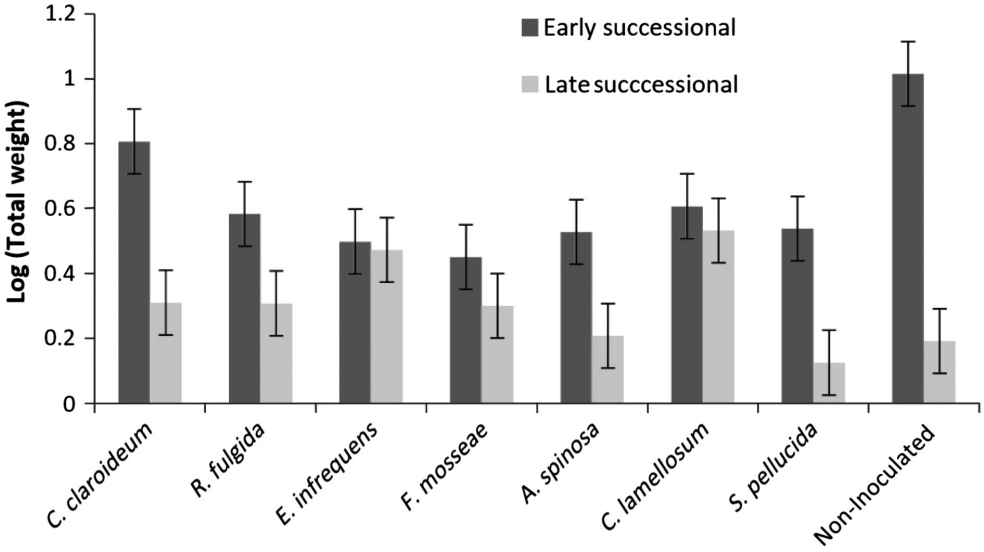

Fig. 3. Bars represent the average log total weight for plants within a successional stage when grown with each different AM fungal species and a non-inoculated control. SE bars represent variation between plant species in each successional stage. The late-successional plants grew significantly more slowly than early-successional plant species ($F_{1,10}$ = 6.5, P = 0.03), especially in the non-inoculated treatments. However, late-successional plants grew an average of 400% larger with fungi, while early-successional plants grew 40% smaller with inoculation relative to the controls, and we found significant differences across successional stages for plant growth differences when inoculated with the different fungal species ($F_{6,70}$ = 12.1, P < 0.0001). Thus, early- and late-successional plants had similar growth rates when inoculated with the AM fungal species *Entrophospora infrequens, Claroideoglomus lamellosum*, and *Funneliformus mosseae*.

succession will matter most for some late-successional prairie plant species. Thus, the presence of specific fungal species could potentially shift plant community composition toward late-successional prairie plants, and future work should test this assumption. Our results were very consistent within successional stages, demonstrating that all late-successional plants exhibited greater variation in plant growth due to fungal specificity than each early-successional plant used in this study. However, whether specific fungal species shift plant community composition toward late-successional plants will depend on whether the observed plants benefit from inoculation with AM fungi under glasshouse conditions are consistent under field conditions under which other AM fungi exist. Previous observations have found that plant response to AM fungi under greenhouse conditions can be consistent in the field (Pringle and Bever 2008).

Our study is the first to test the effects of plant phylogeny and life-history traits on specificity of plant response to mycorrhizal fungi. We found that plant successional stage was the strongest predictor of the coefficient of variation among fungal species when using average plant growth rate, successional stage, and average responsiveness as predictors within phylogenetic multiple regressions as well as in using successional stage and plant family as predictors within an ANOVA. Using Moran's *I*, we found no evidence of a phylogenetic signal for plant growth rate, overall mycorrhizal responsiveness, or specificity in mycorrhizal responsiveness. The lack of phylogenetic signal for plant growth rate is a logical consequence of our purposeful sampling of early- and late-successional species across the phylogeny. It is interesting and novel that we found no phylogenetic signal for average and specificity of plant response to mycorrhizal fungi. Taken together, these results demonstrate that plant response to specific fungi and overall mycorrhizal responsiveness are not constrained by phylogeny; rather, these traits may evolve

rapidly in response to local ecology and coevolve with other aspects of plant life history.

Previous studies that have found a significant pattern of overall mycorrhizal responsiveness across phylogeny (Hoeksema et al. 2010, Reinhart et al. 2012) have not controlled for plant successional stage in their analyses. In one of the few studies that have included both plant successional stage and plant relatedness in assessing patterns in overall mycorrhizal responsiveness, plant successional stage has been found to be a very good predictor of plant response to mycorrhizal fungi and more important than plant phylogeny (Koziol and Bever 2015). Our results suggest that covariation of plant successional stage with phylogeny due to incomplete taxon sampling could generate spurious phylogenetic correlations. However, our work is based on limited taxon sampling. We recommend that future work should include broad sampling across both successional status and phylogeny to resolve their relative importance.

Correlation of average response and specificity of response

Our results are consistent with the predictions of Hart and Klironomos (2003) that overall responsiveness and specificity in responsiveness to mycorrhizal fungi are positively correlated. Using prior knowledge of plant mycorrhizal responsiveness (Koziol and Bever 2015) to inform our experimental design, our study was able to assess the relationship between average mycorrhizal responsiveness and variation in responsiveness among specific fungal taxa across plants exhibiting a wide range of overall mycorrhizal responsiveness. We suggest that the absence or weakly observable pattern of this relationship found in previous studies (van der Heijden et al. 1998, Klironomos 2003, Reynolds et al. 2003, 2005) may be due to overrepresentation of early-successional plant species with low variation in mycorrhizal responsiveness. The strong positive correlation we observed between overall responsiveness to AM fungi and specificity in responsiveness to specific fungal taxa indicates a general pattern where plants that benefit strongly from AM fungi may also be more sensitive to the fungal species in their local environment. As many mid- and late-successional plant species have been shown to have a high overall beneficial response to AM fungi (Wilson and Hartnett 1998, Koziol and Bever 2015), these species are also likely to be more sensitive to the presence of particular beneficial AM fungi species in their environment.

Implications for the restoration of late-successional species

Our results show that late-successional prairie plant species benefit from inoculation with AM fungi and that these plants are more sensitive to specific AM fungal identity than early-successional plants. Consistent with this pattern, a recent grassland restoration found that late-successional prairie species benefited most from locally adapted native AM fungi relative to commercially grown non-native AM fungi (Middleton et al. 2015). Our results suggest that a subset of native AM fungi might be particularly effective at promoting late-successional plant species. Specifically, we found that late-successional plants showed the best growth response when inoculated with the fungal species *E. infrequens* and *C. lamellosum*, while early-successional plants grew best in non-inoculated soil. Reflecting these preferences, early- and late-successional plants had similar growth rates when inoculated with *E. infrequens*, *F. mosseae*, and *C. lamellosum* (Fig. 1), because late-successional plants grew more quickly and early-successional plants grew more slowly with these species relative to other inoculation treatments. Whether specific fungal species could be applied to restorations to improve the growth of late-successional plants will depend on whether AM fungi consistently provide benefits to plants under field conditions where other AM fungi exist, which has been previously observed (Pringle and Bever 2008, Middleton et al. 2015). Taken together, these data can inform grassland restoration practitioners on which particular AM fungi may be most useful to their restoration goals. For instance, if late-successional diversity is the management goal, inoculating plants with consistently beneficial fungal species, such as *E. infrequens* or *C. lamellosum* in this experiment, may best promote the growth of late-successional plants that strongly benefit from some AM fungi. Plant sensitivity to fungal identity has been shown to be important in the restoration of non-prairie plant communities as well. For example, a

recent meta-analysis found that across shrublands, temperate and tropical forests, coastal dunes, savanna, and grasslands, plants are more sensitive to locally sourced fungal inocula relative to commercial fungal inocula (Maltz and Treseder 2015). Thus, fungal specificity appears to play a key role in plant community dynamics across many systems. Future work should more fully assess the role of specific AM fungal species within community dynamics of these sensitive systems and should focus on the usefulness of particular AM fungal symbionts in plant community restoration in addition to assessing the consistency of plant response to particular AM fungi in varied field conditions, such as across restoration sites with more or less disturbed microbial communities including AM fungi.

Future directions

Our results suggest that soil symbionts could drive plant community dynamics through the promotion or inhibition of certain plant species. Because late-successional plant species are more sensitive to AM fungal identity than early-successional species, our results suggest that changes in AM fungal composition may mediate plant species turnover during succession. From a management perspective, inoculation with specific fungal species could potentially shift plant community composition toward late-successional prairie plants. We also found substantial variation in patterns of specificity among late-successional species, suggesting that host-specific changes in AM fungal composition could mediate interactions among late-successional species (Bever 1999). These data contribute to a predictive framework addressing the role of AM fungi in plant community dynamics and suggest that future work should address the importance of (1) changes in AM fungal composition during succession, (2) changes in AM fungal composition with particular hosts, and (3) whether certain fungal species may improve the restoration of sensitive plant communities by improving the establishment of late-successional species.

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