

Mycorrhizal response trades off with plant growth rate and increases with plant successional status

LIZ KOZIOL¹ AND JAMES D. BEVER

Department of Biology, Indiana University, Bloomington, Indiana 47405 USA

Abstract. Early-successional plant species invest in rapid growth and reproduction in contrast to slow growing late-successional species. We test the consistency of trade-offs between plant life history and responsiveness on arbuscular mycorrhizal fungi. We selected four very early-, seven early-, 11 middle-, and eight late-successional plant species from six different families and functional groups and grew them with and without a mixed fungal inoculum and compared root architecture, mycorrhizal responsiveness, and plant growth rate. Our results indicate mycorrhizal responsiveness increases with plant successional stage and that this effect explains more variation in mycorrhizal response than is explained by phylogenetic relatedness. The mycorrhizal responsiveness of individual plant species was positively correlated with mycorrhizal root infection and negatively correlated with average plant mass and the number of root tips per unit mass, indicating that both plant growth rate and root architecture trade off with investment in mycorrhizal mutualisms. Because late-successional plants are very responsive to mycorrhizal fungi, our results suggest that fungal community dynamics may be an important driver of plant succession.

Key words: *arbuscular mycorrhizal fungi; growth rate; prairie; root architecture; succession; trade-offs.*

INTRODUCTION

Succession, the predictable serial replacement of species over time, is omnipresent, yet the mechanisms driving species turnover during succession remains a central question in plant ecology. Life history trade-offs play a central role in succession as early successional plants feature adaptations to the rapid colonization of disturbed lands such as fast growth, early maturation, and heavy allocation to reproduction (Grime 1977, Van Kleunen et al. 2010). Later-successional species are often slower growing with lower investment in reproduction and can be more competitive, better defended against antagonists, and invest greater resources in mutualists (Reynolds et al. 2003, Van der Putten 2003, Martin et al. 2010). However, the relative importance and universality of trade-offs between colonization ability and competitive ability, vs. trade-offs between colonization ability and investment in, or defense against, biotic interactions, remains to be investigated. In this paper, we focus on the consistency of trade-offs between plant life history and plant response to, and investment in, a very common belowground mutualism between plants and soil fungi called arbuscular mycorrhizal fungi.

Arbuscular mycorrhizal (AM) fungi are known to improve the growth of some plants through the assimilation and delivery of nutrients from the soil that are difficult for plants to acquire, such as inorganic

phosphorous. AM fungi can also provide nonnutritional benefits to their plant host through alleviation of environmental stressors such as drought (Davies et al. 1993, Koziol et al. 2012) and herbivory (Bennett and Bever 2007). Although AM fungi are commonly present in soils, AM fungi in early-successional environments may be limited due to reduced abundance and infectivity in disturbed soil (Abbott and Robson 1991, Jasper et al. 1991) and restricted propagule dispersal, potentially selecting for plants with lower mycorrhizal responsiveness (Seifert et al. 2009). If early-colonizing plants are poor hosts for AM fungi, their dominance early in succession could be reinforced thereby delaying establishment of mycorrhizally responsive species (Vogelsang and Bever 2009).

While it has long been suggested that early-successional plants may benefit less than late-successional plants from association with mycorrhizal fungi (Janos 1980), evidence for this pattern has been largely anecdotal and individual studies have been conflicting. For example, high mycorrhizal responsiveness has been demonstrated for early-successional woody tropical species (Siqueira et al. 1998, Zangaro et al. 2003), while other studies demonstrate that late-successional, but not early-successional, plants are responsive to fungal inoculation (Middleton and Bever 2012). Meta-analyses of published results reported shifts in mycorrhizal responsiveness associated with plant life-history categories, with non-N-fixing forbs, woody plants, and C₄ grasses responding more positively to mycorrhizal inoculation than plants with N-fixing bacterial symbionts and C₃ grasses (Hoeksema et al. 2010) and

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Corresponding Editor: C. V. Hawkes.

¹ E-mail: ekoziol@indiana.edu

perennials being more responsive than annuals (Reinhart et al. 2012). While perhaps consistent with differences in successional stage, the categories are too crude to permit strong inference on the role of AM fungi in succession. The way in which plants from different successional stages invest in mycorrhizal fungi could trade off with other nutrient gathering strategies of these plants, as successful plants in a disturbed environment may allocate more heavily toward resource acquisition via finely branched roots and reduce responsiveness on mycorrhizal symbionts because more fine roots have been shown have higher nutrient concentrations (Gordon and Jackson 2000). Such a trade-off of mycorrhizal responsiveness and root architecture has been observed across different plant populations (Schultz et al. 2001, Seifert et al. 2009) and across plant species (Hetrick et al. 1991), but the generality of this trade-off has been questioned (Maherali 2014). Further work is required to assess the generality of shifts in mycorrhizal responsiveness and root architecture across plant successional stages and among plant families.

We present a test of potential shifts in mycorrhizal responsiveness, root architecture, and growth rate during plant community succession by comparing shifts in these metrics among a gradient of plant successional stages (see Plate 1). We focus on the tallgrass prairie plant community, which has the advantage that succession is not driven by obvious asymmetries in competition due to plant height, as all plants are adapted to tolerate fire and therefore perennial structures are kept belowground. We evaluate whether early colonizing species are less responsive to mycorrhizal fungi than late-successional plants, as might be expected given that fungi in early-successional environments are often disturbed and less effective.

METHODS

Given that mycorrhizal responsiveness is known to vary across plant phylogeny (Hoeksema et al. 2010, Reinhart et al. 2012), we made efforts to choose both early- and late-successional species from across six plant families (Appendix: Table A1). We selected 30 prairie plant species that included four very early-successional species, seven early-successional species, 11 middle-successional species, and eight late-successional species. Successional stage was assigned using field observations from local naturalists (Schramm 1990, Swink and Wilhelm 1994, Betz et al. 1996; see Appendix: Methods 1 for more information).

Seeds, soil, and AM fungi were obtained from Kankakee Sands Prairie in northern Indiana, USA. We used a mixture of eight species of AM fungi to represent the native diversity. Background soil was a sterilized 1:1:1 mixture of sand, Indiana topsoil, and calcined clay. Five replicates of each plant species were planted into both non-inoculated and AM-fungi-inoculated soil treatments for a total of 320 plants (see Appendix: Methods 2 for more information).

We analyzed the root architecture of each plant by determining the number of root tips per unit mass (see Appendix: Methods 3 for more information). A subsample of roots from each plant was stained with Trypan Blue to confirm AM fungi colonization using the magnified intersections method (McGonigle et al. 1990).

We test for general differences between successional stage by treating plant species as a random effect. We also test for generality of response to mycorrhizal fungi by analyzing absolute biomass differences with inoculation (e.g., Schultz et al. 2001) and response ratios (e.g., Hoeksema et al. 2010). Direct analysis of plant biomass was performed using Proc Mixed in SAS (SAS Institute 2012) with successional stage, plant family, inoculation, and the interactions of successional stage and plant family with inoculation as fixed effects and plant species nested within plant family and successional stage and their interaction with inoculation as random effects. Within this analysis, differences in biomass due to inoculation are tested within the interactions of inoculation with successional stage or plant family and the mixed-model tests for consistent differences across plant species within these categories. We then decomposed successional stage into six a priori orthogonal contrasts corresponding to very early vs. early, middle vs. late, very early and early vs. middle and late (henceforth referred to as early vs. late), and each of the three contrasts by a soil treatment interaction. We remove the effects of initial plant size difference by using initial plant size as covariate analyses of final size. Plant biomass and number of root tips per unit mass were log-transformed and measures of root infection were arcsine-square-root transformed prior to analysis.

Increases in proportion of biomass is analyzed by constructing the mycorrhizal response ratio of the mass of AM inoculated plants relative to the mass of non-inoculated plants (Hoeksema et al. 2010). To generate metrics of mycorrhizal response ratios, we calculated the best linear unbiased predictor (BLUP), the appropriate estimate of means for random effects, for each plant species from the mixed model for the metric of non-transformed plant mass. Construction of the log-transformed mycorrhizal response ratio from the BLUPs, which we henceforth refer to as mycorrhizal responsiveness, allows a second direct test of the relative importance of successional stage and plant family as predictors of mycorrhizal responsiveness using standard general linear models. We also calculated BLUP means for plant mass (averaged across inoculation treatment), the number of root tips per unit mass, and root infection. These data were log-transformed to test correlations with mycorrhizal responsiveness. We corrected the correlations of mycorrhizal responsiveness with average plant mass and root tips per unit mass for nonindependence due to phylogeny using phylogenetic generalized least squares multiple regression using the caper package in R (see Appendix: Methods 4 for more information).

TABLE 1. The general linear model of the log-transformed best linear unbiased predictors (BLUPS) for species average mass, mycorrhizal responsiveness, and the number of root tips per unit mass for plant successional stage, plant family, and the contrast of early-successional vs. late-successional plants.

Predictor	df	Average species mass		Mycorrhizal responsiveness		Root tips per unit mass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Succession	3, 21	11.0	0.0001	9.8	0.0003	3.1	0.04
Plant family	5, 21	3.0	0.04	1.2	0.35	9.0	0.0001
Early vs. late	1, 21	31.9	<0.0001	28.1	<0.0001	4.2	0.05

RESULTS

Plant growth, mycorrhizal responsiveness, and root architecture

Analyses of absolute biomass (see Appendix: Results 1, Table A2, and Fig. A2) gave identical interpretations as analyses of species mean values, including mycorrhizal response ratios, presented here. We found that plant successional stage was a strong predictor of the mycorrhizal responsiveness of plant species (Table 1, $F_{3,21} = 9.8$, $P = 0.0003$), with late-successional species being significantly

more responsive to AM fungi inoculation than early-successional species (Fig. 1a, Table 1, $F_{1,21} = 28.8$, $P < 0.0001$). Plant family (Table 1, $F_{5,21} = 1.2$, $P = 0.4$) was not a significant predictor for mycorrhizal responsiveness. Successional stage (Fig. 1b, Table 1, $F_{1,21} = 11.0$, $P = 0.0001$) was a stronger predictor of average plant biomass than plant family (Table 1, $F_{5,21} = 3.0$, $P = 0.04$), with early-successional species growing twice as quickly as late-successional species (Table 1, $F_{1,21} = 31.9$, $P < 0.0001$). Both plant family (Table 1, $F_{5,21} = 9.0$, $P = 0.0001$) and successional stage (Fig. 1c, Table 1, $F_{3,23} = 3.1$, $P = 0.04$)

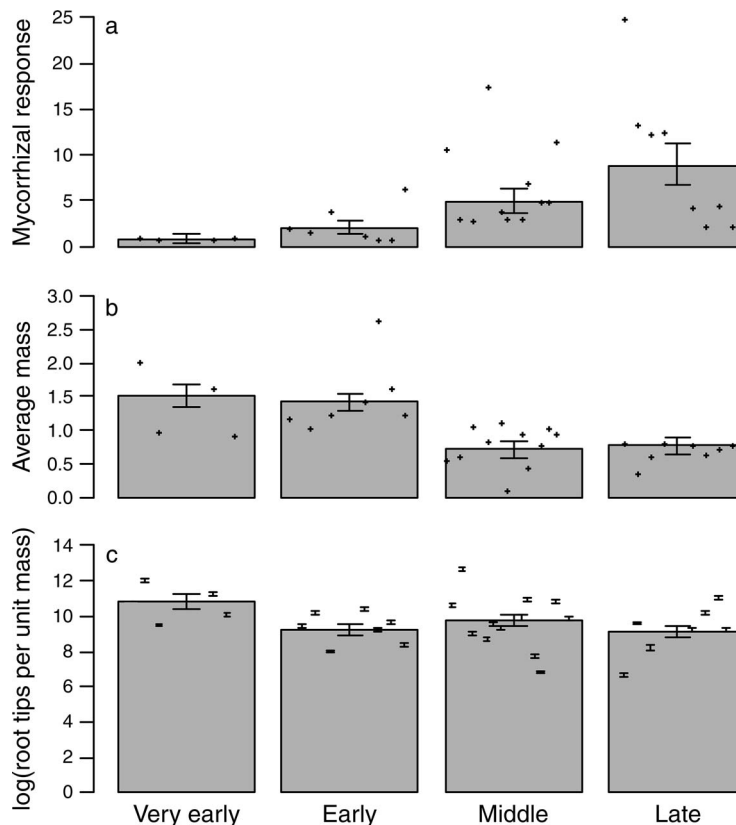


FIG. 1. The effects of successional stage on mycorrhizal responsiveness, average mass, and the number of root tips per unit mass. Bars represent the best linear unbiased predictor (BLUP) species means for (a) mycorrhizal responsiveness, (b) the average plant mass, and (c) the log-transformed number of root tips per unit mass (measured as no./g) for the non-inoculated plants for each successional stage. Large error bars represent variation between plant species in each successional stage, while dots or small error bars represent the mean and variation of individual plant species within a given successional stage. Panels (a) and (b) do not have error bars because the BLUPS are expressed as a ratio and an average, respectively.

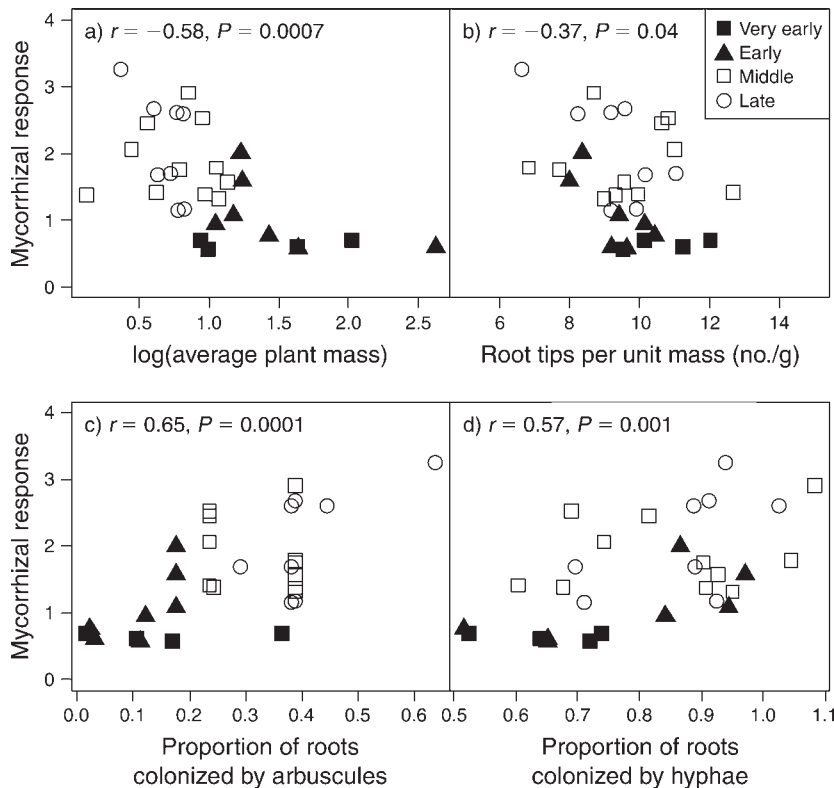


FIG. 2. Correlations of the BLUPs for mycorrhizal responsiveness with (a) the log-transformed average plant mass, (b) the number of root tips per unit mass, (c) the proportion of roots colonized by AM arbuscules, and (d) the proportion of roots colonized by AM hyphae for each species in the very early, early, middle, and late successional stages.

were significant predictors of root architecture, with early-successional species having more root tips per unit mass than late-successional species (Table 1, $F_{1,21}=4.2$, $P=0.05$).

AM fungal colonization

AM fungal infection was negligible in non-inoculated plants and we therefore focus on level of infection in inoculated plants. Early-successional species had significantly fewer arbuscules (Appendix: Fig. A1, Table A3, $F_{1,20}=23.1$, $P=0.001$), the site of nutrient exchange within the plant–fungal mutualism, and significantly less hyphal colonization (Appendix: Fig. A1, Table A3, $F_{1,20}=5.1$, $P=0.04$) than late-successional species. Plant family was a significant but weaker predictor of root infection within the contrast of early vs. late-successional species for both the proportion of roots colonized by both AM hyphae (Appendix: Table A3, $F_{5,20}=5.2$, $P=0.05$) and arbuscules (Appendix: Table A3, $F_{5,20}=2.7$, $P=0.05$). Vesicles were rarely present in the roots and there were no significant patterns in vesicle abundance (Appendix: Table A3).

Correlations and regressions of mycorrhizal responsiveness with biomass and root architecture and infection

The mean root tips per unit mass of non-inoculated and AM inoculated plants were very strongly correlated

(data not shown, $r = 0.96$, $df = 30$, $P < 0.0001$). Mycorrhizal responsiveness of plant species was negatively correlated with average plant mass (Fig. 2a, $r = -0.58$, $df = 30$, $P = 0.0007$) and the number of root tips per unit mass (Fig. 2b, $r = -0.37$, $df = 30$, $P = 0.04$). Phylogenetic multiple regression indicated that average plant size was a very strong predictor of mycorrhizal response independent of shared phylogeny (regression coefficient, $\beta = -2.4 \pm 0.18$ [mean \pm SE], $P < 0.0001$), while the effect of root architecture was weak and not significant (Appendix: Table A4). Mean mycorrhizal responsiveness of plant species was also positively correlated with the mycorrhizal infection of inoculated plants (proportion of arbuscules, Fig. 2c, $r = 0.65$, $df = 30$, $P = 0.0001$; proportion of hyphae, Fig. 2d, $r = 0.57$, $df = 30$, $P = 0.001$).

DISCUSSION

Our results provide the strongest support to date that mycorrhizal responsiveness shifts with the successional status of plant species. In fact, late-successional species grew an average of eight times larger with mycorrhizal inoculation and this declined to a parasitic response with very early-successional plant species. This relationship with successional status was consistent whether we use absolute or relative biomass increase to measure



PLATE 1. (Upper) Late successional remnant prairies can have higher plant diversity, functional diversity, and average coefficient of conservatism than comparable (lower) early successional prairies. Early successional prairies are dominated by plant species that have low responsiveness to arbuscular mycorrhizal fungi, while late successional remnant prairies are dominated by plant species that have high responsiveness to arbuscular mycorrhizal fungi. Photo credits: J. D. Bever.

mycorrhizal response and whether successional status of the plant is measured from field observations on colonization following disturbance (Fig. 1a) or by the average rate of growth within the experiment (Fig. 2a), and it was consistent across 30 plant species. Our result is in contrast to observations of higher mycorrhizal responsiveness in early-successional woody tropical species than late-successional species (Siqueira et al. 1998, Zangaro et al. 2003), but we note that short-term tests of responsiveness in these species can be confounded by their large seed reserves in late-successional plants (R. Herrera, *personal communication*).

Analysis of correlations of plant species means demonstrated that mycorrhizal responsiveness was significantly negatively correlated with average plant biomass and the number of root tips per unit mass. However, when correcting for covariation of average

plant mass, root architecture, and phylogeny, we find that plant growth rate to be a superior predictor, while root architecture is not significant. A negative correlation of root tips per unit mass with mycorrhizal responsiveness suggests that the reduced mycorrhizal responsiveness of early-successional plants may have been facilitated by the increased surface area of finely branched foraging roots (Gordon and Jackson 2000, Seifert et al. 2009). Because fine roots may be more likely to find and assimilate resources, the benefit of mycorrhizal partners could become redundant for these early-successional plants. Our evidence of such a correlation is consistent with observations of genetic correlations of reduced fungal responsiveness with increased root branching in grassland species (Schultz et al. 2001, Seifert et al. 2009). However, phylogenetic correction removes this effect, consistent with a recent meta-

analysis (Maherali 2014), suggesting that the correlation of root architecture and mycorrhizal responsiveness in species means may be due to features of root architecture determined deeper in evolutionary history of plants. Further work is needed to assess the relationship between mycorrhizal responsiveness and root architecture in different plant communities.

We also found a negative correlation between the mycorrhizal response and average plant biomass of the plant species. This correlation provides internal confirmation of our major result as differences in average plant biomass will result from differences in plant growth rate, which is strongly correlated with plant successional status. This correlation likely resulted from correlational selection, as plants that best take advantage of large scale soil disturbance, such as tillage, would have rapid growth rates as well as reduced dependence on mycorrhizal fungi, which may be in low densities or ineffective following disturbance (Jasper et al. 1991). On the other hand, species that are adapted to persist within late-successional environments can rely upon the presence of AM fungi and often allocate to survival rather than rapid growth (Herms and Mattson 1992).

We found successional status to be a more important predictor of plant response to AM fungal inoculation than plant family, suggesting that mycorrhizal responsiveness can evolve quickly to match the plants' current ecological properties. The relatively weak effect of plant phylogeny stands in contrast to previous analyses (Hoeksema et al. 2010, Reinhart et al. 2012). We note that previous studies did not test plant successional stage, nor did they represent early- and late-successional species within each plant family as we have done with this experiment design, so it is possible that strong plant phylogeny effects emerge in these studies as spurious correlations. Additionally, it has been shown that the mycorrhizal responsiveness of intraspecific populations can evolve to match local ecological conditions (Schultz et al. 2001, Seifert et al. 2009, Koziol et al. 2012). Further work is necessary to resolve the relative importance of plant phylogeny and local ecology in determining plant responsiveness on AM fungi.

Implications for succession and restoration

Our results suggest that reduced AM fungal densities following disturbance will favor early-successional plant species because they are less responsive to, and some species even harmed by, AM fungi. AM fungal communities have been shown to increase in richness and biomass with time since disturbance (Bach et al. 2010). Our demonstration that later-successional prairie species are highly mycorrhizally responsive suggests that AM fungal dynamics during succession may promote the growth of late-successional species while providing little benefit to early-successional species. Our results indicate that AM fungal dynamics should be considered as a driver of succession in grasslands along with other factors, such as resistance to drought, fire, and plant

longevity. It should be noted that our AM fungal species were collected from late-successional prairies that contain both early- and late-successional plants.

Generally restoration practices do not include fungal amendments (Schramm 1990, Heneghan et al. 2008, Ohsowski et al. 2012), although there is evidence of its benefits (Scheublin et al. 2004, Middleton and Bever 2012, Veresoglou and Rillig 2014). Our results suggest that the absence of effective AM fungal symbionts following anthropogenic disturbance (Abbott and Robson 1991, Jasper et al. 1991, Bach et al. 2010) may limit the establishment of highly valued late-successional grassland plant species. Inoculation with native AM fungi could improve the success of such restoration efforts by promoting late-successional plant species and future work should address whether fungal amendments advance grassland succession.

A critical issue in predicting plant dynamics during succession is the quality of the early- and late-successional plant species as hosts for AM fungi as this will determine the feedback dynamics (Bever 1999, Umbanhowar and McCann 2005, Bever et al. 2012). Should early-successional species be poorer hosts for AM fungi, as might be supported by our data on density of root infection, then the positive correlation with plant growth promotion would generate a positive feedback in which establishment of late-successional prairie plant species would increase the density of AM fungi, which would then increase the future success of other late-successional plant species. Consistent with this dynamic, late-successional plant species have been found to perform relatively better when inoculated with soil communities isolated near late-successional plants (Kardol et al. 2007, Middleton and Bever 2012). Our results suggest that AM fungi can play an important role in succession, the exact nature of which will require additional work to test the strength and direction of feedbacks during succession of grassland communities.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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