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RESEARCH ARTICLE

The Influence of Beneficial Fungi on Plant–Enemy Interactions and Plant Community Structure

Context dependence of grassland plant response to arbuscular mycorrhizal fungi: The influence of plant successional status and soil resources

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Abstract

1. Many of the disturbance-sensitive, late successional plant species in grasslands respond to arbuscular mycorrhizal (AM) fungi more positively via growth and establishment than plants that readily establish in disturbed areas (i.e. early successional species). Inoculation with AM fungi can therefore aid the establishment of late successional species in disturbed areas. If the differential benefit of AM fungi to late versus early successional plants is context-dependent, however, this advantage could be diminished in high phosphorus (P) post-agricultural soils or in future climates with altered precipitation.
2. In this greenhouse experiment, we tested if late successional plant species are less plastic in their reliance on AM fungi than early successional plants by growing 17 plant species of different successional status (9 early and 8 late successional) in full factorial combinations of inoculated or uninoculated with AM fungi, with ambient or high P levels, and with low or high levels of water.
3. AM fungi positively affected the biomass of the 17 grassland plant species, but across all environments, late successional plant species generally responded more positively to AM fungi than early successional plants species.
4. AM fungal growth promotion and change in below-ground biomass allocation was generally diminished with P fertilizer across all plant species, and while there was significant variation among plant species in the sensitivity of AM fungal responsiveness to P fertilization, this differential sensitivity was not predicted by plant successional status.
5. The role of AM fungi in plant growth promotion was not generally altered by variation in watering, however late successional plant species allocated a greater proportion of their biomass below-ground in response to AM fungi in low versus high water conditions.
6. *Synthesis*. Overall greater responsiveness to arbuscular mycorrhizal (AM) fungi by late successional species is consistent with an important role of AM fungi in plant succession, even while AM fungi are less impactful overall in high P soils.

However, the increase in responsiveness of below-ground allocation of late successional species to AM fungi in low water conditions suggests that successional dynamics may be more dependent on AM fungi in future climates that feature greater propensity for drought.

KEYWORDS
arbuscular mycorrhizal fungi, context-dependence, determinants of plant community diversity and structure, drought, fertilization, plant development and life-history traits, plant–soil (below-ground) interactions, succession, symbiosis

1 | INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are obligate plant root endosymbionts that associate with over 80% of terrestrial plant species (Smith & Read, 2008). Through their association with plant roots, AM fungi primarily forage for soil resources like phosphorus (P) and water in the soil via their hyphal network in exchange for photosynthates from their host plants. Via these mechanisms, AM fungi can have large influence on the fitness of individual plants (Hoeksema et al., 2018), and the strength and direction of this influence can depend upon the environmental context (Hoeksema et al., 2010). Plant growth response to AM fungi, called mycorrhizal response (MR), often varies by species and therefore can alter plant–plant interactions and potentially structure plant communities (Bever, 1999; van der Heijden et al., 1998; Vogelsang et al., 2006). Higher MR has been associated with late successional species in grasslands (Bauer et al., 2015; Cheeke et al., 2019) and a plethora of associated life history traits like slower growth rates (Koziol & Bever, 2015) as well as higher root:shoot ratios, longer-living leaves and lower reproductive effort (Bauer et al., 2018), suggesting that AM fungi can play a major role in succession (Bever, 1999; Janos, 1980; Koziol & Bever, 2019). Whether the role of AM fungi in plant community interactions and succession will be modified with anthropogenic disturbances such as eutrophication (i.e. nutrient enrichment) and climate change, will hinge upon the environmental dependence of variation in MR across species and successional status.

A critical role of AM fungi in succession was originally proposed for tropical forests (Allen et al., 2003; Janos, 1980), in which early successional plant species are not dependent on AM fungi and therefore can establish in soils with degraded AM fungal communities, and once beneficial AM fungi establish they facilitate the establishment of late successional plant species which are highly dependent on, and responsive to, AM fungi. In this study and others, a particularly strong case can be made for the importance of AM fungi in grassland succession, built around tests of their importance for restoration of native grassland diversity (Koziol et al., 2018). Native grasslands like tallgrass prairies in the Great Plains region of what is known today as North America are home to diverse, perennial-dominated plant communities. Much of this land has been tilled and used for row-crop agriculture in the past few centuries with settler colonial expansion, and efforts to restore these grasslands are often stymied in early successional stages dominated by a small subset of native ruderals and non-native plant species. Work in this latter ecosystem has shown that late successional plant species often respond more positively to AM fungi via biomass (i.e. have a higher MR) than early successional species that readily establish in disturbed areas (Bauer et al., 2015, 2018; Cheeke et al., 2019; Koziol & Bever, 2015). In these studies, MR often also correlated with other life history traits. Additionally, these late successional plant species are more sensitive in terms of MR to AM fungal identity (Cheeke et al., 2019; Koziol & Bever, 2016). Surveys demonstrate that the AM fungal community composition of late successional 'old growth' grasslands are consistently degraded by agricultural disturbance (House & Bever, 2018), and a growing number of experiments have shown that reintroduction of AM fungi from 'old growth' grasslands consistently improves the establishment and growth of late successional plant species relative to that of early successional species (Koziol and Bever, 2017; Koziol et al., 2020, 2022, 2023; Middleton et al., 2015; Middleton & Bever, 2012). Finally, mesocosm and field dynamics are consistent with positive mycorrhizal feedback between early and late successional species as expected from known patterns of responsiveness; in other words, plant communities grown with beneficial AM fungi (alone or in a mixture of other AM fungal species) established late successional plants at higher rates (Koziol & Bever, 2019). This latter finding is consistent with observations of preferential allocation of plant resources to more beneficial symbionts (Bever et al., 2009).

Despite this evidence of a basic role of AM fungi in succession, the outcomes of plant-AM fungi partnerships can depend on context. Many studies have predicted or empirically shown that environmental conditions with plentiful soil resources, particularly soil P and nitrogen (N), can lead to AM fungi becoming parasitic symbionts and negative plant MR (Johnson, 2010). This contrasts with a recent meta-analysis by Hoeksema et al. (2018) that finds overwhelmingly that recent evolutionary history and plant species identity predict MR rather than the environmental context in which the symbiosis is established. In fact, Wang et al. (2022) found MR, which is correlated with successional status, as the primary predictor of plant community composition change under P and N fertilization after 15 years. Because most tallgrass prairies have been tilled and converted to agriculture, resulting in elevated soil P relative to the native soil (Baer et al., 2012; Bennett et al., 2001), the possibility that high P soils may alter the role of AM fungi in prairie successional dynamics is very relevant to broadscale efforts towards grassland restoration. With respect to water, plants often benefit more from AM fungi under drought conditions via increased biomass through a variety of mechanisms including increasing access to water (Augé, 2001; Kakouridis et al., 2022; Ruiz-Lozano, 2003), but fewer studies have focused on MR under different watering conditions. Plants inoculated with AM fungi also experience physiological benefits (Augé, 2001), and these positive effects have been shown to be lessened in high water conditions (Augé et al., 2015). With global eutrophication of soils and alteration of precipitation patterns with global climate change including in the Great Plains (Dai, 2013), it is becoming increasingly important to understand how environmental conditions like P and water availability will alter community dynamics like succession in the context of plant-AM fungal partnerships.

In this experiment, we tested the consistency and interdependence of the impacts of plant successional status (i.e. early or late successional status), soil P levels and soil water levels on the response of 17 plant species to inoculation with AM fungi. We looked at responses both in terms of total biomass and proportion of total biomass below-ground. Under conventional hypotheses: plants will be equally plastic in their MR under different soil contexts (Figure 1a). We hypothesized alternatively that late successional plants may benefit from AM fungi similarly under low and high soil resource conditions in contrast to early successional plants. In other words, late successional plants would have a less plastic response to AM fungi (Figure 1b). Finally, it is possible that late successional plant species, being more responsive to AM fungi overall, are more sensitive to higher resource levels. In this case, late successional species would have a more plastic response to AM fungi (Figure 1c). It is also possible that variation in prairie plant species' response to AM fungi, soil P fertilization and watering conditions is not well represented by plant successional status. In this case, other categorical predictors (e.g. certain functional trait(s)) may predict the plasticity of MR in plant species. We include species-specific analyses in order to point out this variation among species responses to AM fungi that can be better understood with future categorization and study.

2 | MATERIALS AND METHODS

2.1 | Study system

In this study, we hypothesized that successional status could provide the context needed to predict how tallgrass prairie plants will respond to AM fungi under different soil conditions. We selected the 17 plant species for this experiment as described in Table 1 to reflect a broad variety of families in both early and late successional categories. We considered early successional plants those species with coefficients of conservatism (CC) of 0–4, and late successional plant species with CC of 6–10 as determined by Wilhelm and Rericha (2017); we differentiated *Sorghastrum nutans* and *Schizachyrium scoparium* (both CC of 5) based on personal experience in the field of *S. nutans* as more ruderal. CC's were developed to help measure the 'floristic integrity' of a plant community (Taft et al., 1997), and they can be used for estimates of succession (i.e. the prevalence of disturbance-sensitive plants) within the same ecosystem type (Taft et al., 2006). While CC are generally reliable for distinguishing plant sensitivity to disturbance, occasionally high CC's are assigned to species simply because they are near the edge of their range. By grouping 17 plant species by their successional status in a conservative statistical model, we generalized

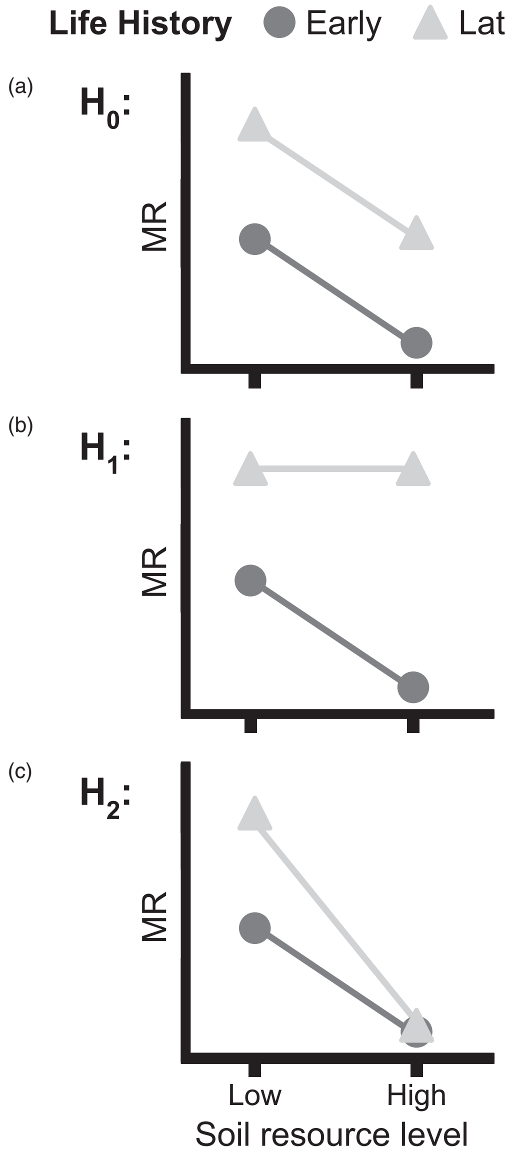

FIGURE 1 Graphical hypotheses of early and late successional plant species' change in mycorrhizal responsiveness (MR) with an increase in soil resources. The three graphs all assume that late successional species generally have a higher MR as in previous studies. The null hypothesis (H_0) is that both early and late successional species will be equally plastic in their MR. Alternatively, (H_1) we hypothesize that late successional plant species will be less plastic than early successional species. A second alternative hypothesis (H_2) is that late successional species will be more plastic in their MR.

TABLE 1 Plant species included in this experiment. Coefficients of conservatism are based on values determined by Wilhelm and Rericha (2017) for the Chicago region.

Family	Species	Coefficient of conservatism	Successional status
Asclepiadaceae	*Asclepias syriaca*	0	Early
	Asclepias tuberosa	8	Late
Asteraceae	*Coreopsis tinctoria*	0	Early
	Helianthus annuus	0	Early
	Echinacea pallida	10	Late
	Liatris pycnostachya	8	Late
	Parthenium integrifolium	8	Late
Commelinaceae	*Tradescantia ohiensis*	3	Early
Fabaceae	*Chamaecrista fasciculata*	4	Early
	Desmanthus illinoensis	3	Early
	Amorpha canescens	10	Late
	Baptisia alba	8	Late
Lamiaceae	*Monarda fistulosa*	4	Early
Poaceae	*Elymus canadensis*	4	Early
	Sorghastrum nutans	5	Early
	Bouteloua curtipendula	8	Late
	Schizachyrium scoparium	5	Late

Note: Based on these scores, we have separated these plants into early or late successional status, which has been shown to generally describe important life history trade-offs.

across many different growth forms and plant families. We have precedence for this generalization as late successional plant species appear to have life history trade-offs that differentiate them from early successional plant species (Bauer et al., 2018; Koziol & Bever, 2015). These features like slower growth, less investment in reproductive structures and longer-lived standing biomass also appear to correspond to a greater response to AM fungi. In fact, Koziol and Bever (2015) found that successional status was a better indicator of MR than phylogenetic relatedness.

2.2 | Experimental set-up

After germination in species-specific trays of sterilized BM7 bark mix (Berger, Saint-Modeste, Quebec, Canada), we planted individuals in 1 L pots filled with a steam-sterilized 1:1 soil-sand mixture using soil from the University of Kansas Field Station and sand from Pine's Garden and Market (Lawrence, KS, USA). This mixture had a pH of 6.8, and it contained 0.82% total organic carbon, 41.7 ppm NO_3-N and 12.6 ppm NH_4-N. Plants in the inoculated treatment received 50 mL of AM fungi inoculum. This inoculum consisted of homogenized cultures of four different species of AM fungi: *Acaulospora spinosa*, *Cetraspora pellucida*, *Claroideoglomus lamellosum* and *Entrophospora infrequens*. These species have been shown to promote the growth of late successional plants (Cheeke et al., 2019; Koziol & Bever, 2015, 2016; Vogelsang et al., 2006). The fungi were derived from cultured remnant prairie soil from Indiana and Illinois and were originally harvested in 2017. Infection with AM fungi was observed in the rehydrated roots of all plants in the AM fungi treatment that had enough biomass to provide at least ten ~1 cm fine root fragments using Trypan Blue and scoring percent root colonization according to the protocol outlined in McGonigle et al. (1990). Most *Tradescantia ohiensis* roots disintegrated during the staining process, and grass species (Poaceae) were de-stained too long for analysis; therefore, data on root colonization for these species is not included in the analysis. No AM fungal infection was observed in a random subsample of plants in the sterile treatment.

To test MR across different soil resource contexts, we manipulated both water and P levels in this experiment. There were two levels of the water treatment: high and low. The 'high' water treatment received twice as much water as the 'low' treatment, though soil moisture was not measured to assess for drought conditions. The treatment was achieved by using two irrigation stakes in pots in the 'high' water treatment compared to one in 'low' water pots. Plants were watered via drip irrigation for 30 s twice daily. There were also two levels of the P treatment: high and low. The 'low' treatment remained at the ambient P levels found in the sterile soil-sand mixture (about 5.4 ppm Mehlich-3 P). For the 'high' treatment, we added dissolved triple super phosphate to increase the concentration of P by 31 ppm (for a total average of 36.4 ppm).

Each treatment combination was replicated five times, and replicates were grown in spatially separated blocks in a greenhouse. We measured the initial height of each plant at the beginning of the experiment. We grew each plant species for 7–12 weeks in an attempt to harvest them before biomass began being allocated to sexual reproduction, an approach to measure plant growth response to AM fungi that is informed by years of working with this system (see Bauer et al., 2015; Cheeke et al., 2019; Koziol & Bever, 2015, 2016, 2019; Vogelsang et al., 2006). At this point, plants were measured for height, harvested, oven-dried and weighed. We recorded the dry mass of both above- and below-ground biomass.

2.3 | Statistical analysis

We analysed total biomass and proportion of total biomass below-ground as response variables in two types of models. In the first model type, the successional status-based model, we tested the hypothesis that a priori grouping of species into successional status categories (i.e. 'early' or 'late-successional') would consistently describe plant responses to AM fungi, soil P, watering, or their interactions. We tested this using successional status, AM fungi, soil P level and water level, as well as all interactions as fixed effects. We then included plant species nested within successional status categories, as well as all interactions with other fixed effects as random effects. Including species identity nested within successional status as a random effect tests for consistency of differences due to successional status, as well as effects of experimental treatments and their interactions, across all species. Therefore, this is a conservative test of successional status effects, as well as the AM fungi, P and water treatments. A parallel model identifying CC as a factor (rather than successional status categories) revealed similar results (Table S1). In the second model type, the species-based model, we analysed the data without regard to a priori groupings of species into successional status categories by identifying plant species, along with the experimental manipulations and all interactions, as fixed effects.

Total biomass was transformed as the natural log of 1 + biomass, and the proportion of biomass below-ground was logit-transformed to meet the assumption of normality. The interaction between initial height and species identity was included in all models to account for variation in seedling size at planting. Block was also identified as a random effect in all analyses. All analyses were performed in R *v4.3.2* (R Core Team, 2023) using *lme4 v1.1-35.1* (Bates et al., 2015) and reportedly converged. We reported the estimated marginal means from our models using *emmeans v1.10.1* (Lenth, 2024). Mycorrhizal response (MR) is calculated as the natural log ratio of plant mass when grown with and without AM fungi. We used the back-transformed estimated marginal means to estimate the biomass and calculate the MR of each species or successional status category in different treatments for statistical tests. To calculate the response of the logit-transformed proportion of total biomass below-ground (PB) to variables like AM fungi and P level, we calculated the difference between the estimated marginal means of PB in different treatments. To calculate the relationship between MR and logit-transformed percent root colonization as well as between species MR and responsiveness to P (using estimated marginal means), we performed simple linear regressions. When visually inspecting the PB of individual plant species, we noted greater variance between early successional species means than between late successional species means. We tested whether there was a difference in median value of PB between early and late successional species using the non-parametric Wilcoxon-Mann–Whitney test. Finally, where successional status effects were significant, we test whether the differences in successional status are robust by controlling for phylogenetic non-independence among species using phylogenetic linear models on the estimated marginal means using *caper v1.0.3* (Orme et al., 2023). We constructed a phylogenetic tree for our species using *V.PhyloMaker2 v0.1.0* (Jin, 2024).

3 | RESULTS

3.1 | Effects on plant biomass

There were similar trends across both models incorporating successional status and species identity (Table 2; Table S2). In general, plants inoculated with AM fungi grew larger than those in sterile soil ($F_{1,14.96} = 42.93$, $p < 0.001$; Table 2). Species differed in their MR ($F_{16,523.2} = 12.51$, $p < 0.001$; Table S2; Figure 2); yet across all 17 plant species and environmental conditions, we found that late successional species responded more positively to AM fungi overall ($F_{1,14.96} = 3.90$, $p = 0.067$; Table 2; Figure 2); this finding was upheld in a test accounting for phylogenetic non-independence ($F_{1,15} = 17.29$, $p < 0.001$). This result was particularly consistent in below-ground biomass ($F_{1,14.95} = 4.80$, $p = 0.045$; Table S3). Upon analysis, we found that MR was also positively correlated with percent root colonization across environments among the species for which we were able to collect this data ($F_{1,46} = 4.32$, $p < 0.05$, $R^2 = 0.07$; Figure S1).

As expected, plants fertilized with P also grew larger than those in unfertilized soil ($F_{1,15.02} = 42.03$, $p < 0.001$; Table 2; Figure 3a). MR decreased in plants with high soil P levels ($F_{1,15.16} = 28.06$, $p < 0.001$; Table 2; Figure 3d) regardless of successional status differences; this finding was consistent even while plant species varied in how much P fertilization affected MR ($F_{16,523.17} = 1.71$, $p = 0.042$; Table S2; Figure 3e). The MR of some species, therefore, is more plastic than others in the context of soil P levels, and successional status may not capture this variation, counter to our expectation.

Plant species varied in their growth response to P fertilization ($F_{16,523.15} = 3.40$, $p < 0.001$; Table S2; Figure 3c), with late successional species tending to be more responsive to soil P than early successional species ($F_{1,15.02} = 3.11$, $p = 0.097$; Table 2; Figure 2b). In fact, testing across the estimated marginal means of each species, responsiveness to P positively correlated to MR ($F_{1,15} = 6.17$, $p < 0.05$; $R^2 = 0.24$; Figure S2). This was counter to our original hypothesis that late successional plants that tend to have higher MR would be less responsive to P in sterile soil. There was little evidence for an impact of water on plant biomass or MR (Tables 2 and S2). However, there was a non-significant interaction between successional status, AM fungi and water levels in below-ground biomass ($F_{1,598.48} = 3.47$, $p = 0.067$; Table S3), a pattern that reflected allocation patterns.

TABLE 2 ANOVA table for the response of total biomass and proportion of biomass below-ground in the successional status-based mixed model.

Fixed effects							
		Log(1 + Total biomass)			**Logit(proportion of Total biomass below-ground)**		
	NumDF	**DenDF**	***F*-value**	**Pr(>*F*)**	**DenDF**	***F*-value**	**Pr(>*F*)**
AMF	1	15.0	42.93	**<0.001**	15.0	5.08	**0.040**
P	1	15.0	42.03	**<0.001**	15.0	0.18	0.678
Water	1	588.5	0.49	0.483	56.7	0.36	0.553
Successional Status (SS)	1	12.7	0.13	0.727	14.0	1.09	0.313
Height1:Species	17	55.2	13.17	**<0.001**	201.2	2.17	**0.006**
AMF:P	1	15.2	28.06	**<0.001**	15.2	0.04	0.853
AMF:Water	1	599.0	1.50	0.222	59.2	5.31	**0.025**
P:Water	1	585.6	0.17	0.683	56.1	3.46	*0.068*
AMF:SS	1	15.0	3.90	*0.067*	15.0	<0.01	0.975
P:SS	1	15.0	3.11	*0.098*	15.0	<0.01	0.992
Water:SS	1	588.4	1.16	0.28	56.7	3.48	*0.067*
AMF:P:Water	1	589.7	0.36	0.550	567.0	0.32	0.577
AMF:P:SS	1	15.2	0.65	0.432	15.2	0.29	0.600
AMF:Water:SS	1	598.9	1.72	0.190	59.2	6.16	**0.016**
P:Water:SS	1	585.7	0.08	0.783	56.1	4.42	**0.040**
AMF:P:Water:SS	1	589.8	0.31	0.580	56.9	1.21	0.275
Random effects							
	Groups	σ^2	σ	**Pr(>Chisq)**	σ^2	σ	**Pr(>Chisq)**
SS:Sp	17	0.0359	0.1894	0.126	0.2170	0.4658	**0.001**
AMF:SS:Sp	34	0.0262	0.1619	**<0.001**	0.0484	0.2199	**<0.001**
P:SS:Sp	34	0.0036	0.0604	0.301	0.0109	0.1043	0.194
Water:SS:Sp	34	0.0000	0.0000	1.000	0.0000	0.0000	1.000
AMF:P:SS:Sp	68	0.0047	0.0688	*0.064*	0.0034	0.0583	0.662
AMF:Water:SS:Sp	68	0.0000	0.0000	1.000	0.0000	0.0000	1.000
P:Water:SS:Sp	68	0.0000	0.0000	0.999	0.0000	0.0000	1.000
AMF:P:Water:SS:Sp	136	0.0000	0.0000	1.000	0.0123	0.1110	0.110
Block	5	0.0009	0.0293	**0.050**	0.0015	0.0384	*0.100*
Residual		0.0542	0.2328		0.1123	0.3351	

Note: Boldface *p*-values indicate a significant response ($p < 0.05$), and italics indicate that $0.10 > p\text{-value} > 0.05$. 'SS' refers to 'successional status'.

3.2 | Effects on plant below-ground allocation

There was a lot of variation in allocation to roots due to species identity ($F_{16,523.23} = 4.78$, $p < 0.001$; Table S2; Figure S3a) as expected due to the variety of growth forms of our plants, but successional status did not consistently impact plant below-ground biomass allocation. However, visual inspection of Figure S3a shows a clear clustering of late successional species with high allocation below-ground and high variation in below-ground allocation of early successional species. Non-parametric tests reveal that the median below-ground allocation of late successional plant species was greater than that of early successional species' (Wilcoxon-Mann–Whitney $W_x = 53$, $n_1 = 8$, $n_2 = 9$, $p = 0.037$ two-tailed), consistent with late successional species allocating greater resources to below-ground perennial storage structures. On average, plants inoculated with AM fungi had a greater proportion of their biomass below-ground ($F_{1,14.99} = 5.08$, $p = 0.040$; Table 2) though this varied by species ($F_{16,523.11} = 9.65$, $p < 0.001$; Table S2; Figure S3b).

Plant biomass allocation below-ground responded to an interaction between P and water levels in a way that was species-specific ($F_{16,522.93} = 2.61$, $p < 0.001$; Table S2; Figure 4b), and successional status was a useful way to describe this variation. While early successional plants' below-ground allocation in response to P addition remained relatively unchanged or slightly elevated in high water, late successional plants' below-ground allocation tended to respond

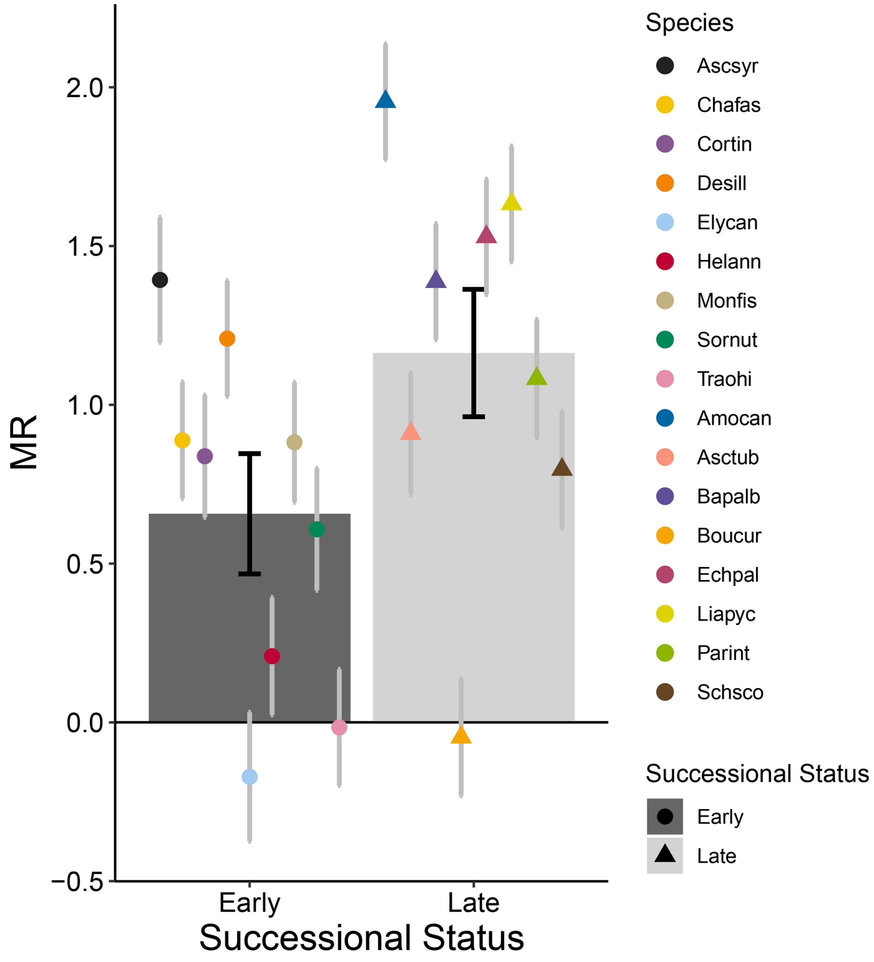

FIGURE 2 Successional status and species differences in mycorrhizal response. The bar heights and points designate estimated marginal means of successional status groups and individual species, respectively, from their respective models. The bars around these means represent the standard error. Positive mycorrhizal responsiveness (MR) values indicate that plants grew larger with arbuscular mycorrhizal fungi and vice versa. MR tended to differ by both successional status ($p=0.067$) and species identity ($p<0.001$). Species codes are composed of the first three letters of the genus and species names.

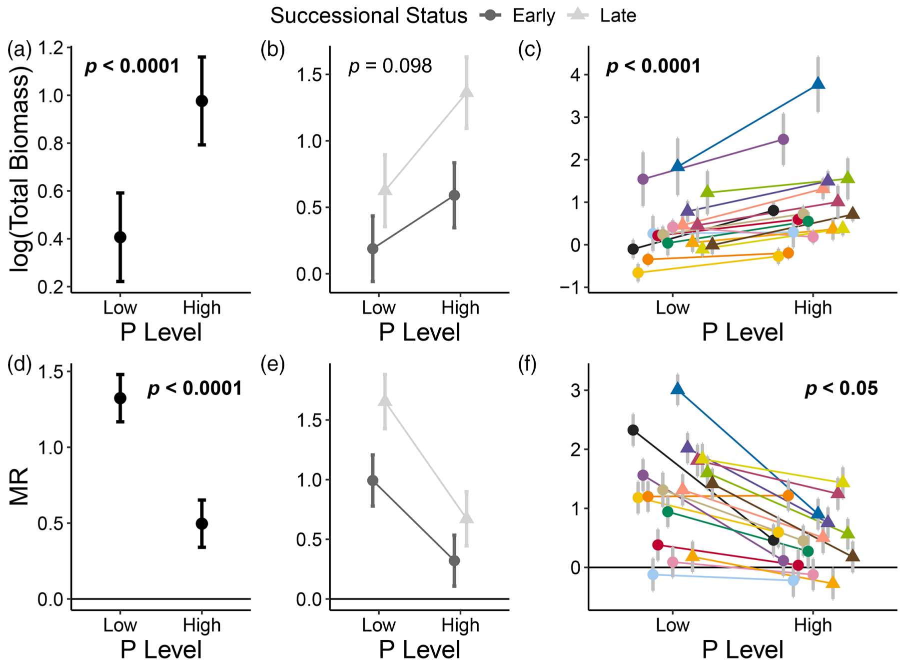

FIGURE 3 Plant biomass and mycorrhizal responsiveness (MR) under different P levels. Graphs (a)–(c) display the total plant biomass response to P (a) across all plants, (b) by successional status and (c) by species. Similarly, graphs (d)–(f) display plant MR in different P conditions (d) across all plants, (e) by successional status and (f) by species. Individual points represent estimated marginal means and standard errors calculated by (a, b, d, e) the successional status-based or (c, f) the species-based model.

negatively to P addition in high water treatments ($F_{1,56.06}=4.42$, $p=0.040$; Table 2; Figure 4a).

Additionally, there was a significant interaction between inoculation with AM fungi, successional status and water levels ($F_{1,59.2}=6.16$, $p=0.016$; Table 2; Figure 5a); this finding was upheld in a test accounting for phylogenetic non-independence ($F_{1,15}=30.09$, $p<0.001$). In the low water treatment, belowground allocation of late successional plants showed an increased

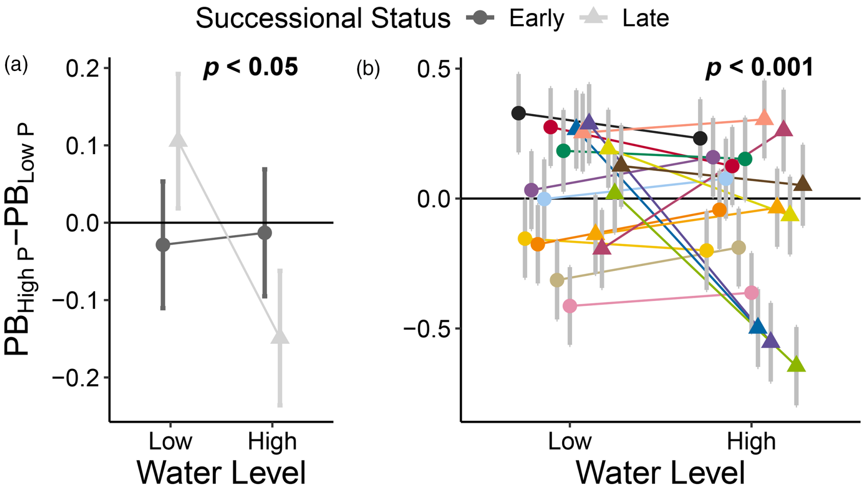

FIGURE 4 Logit-transformed proportion of biomass below-ground (PB) in response to P under different water regimes. The graphs display the log ratio of plant species' PB with and without added P in different water conditions (a) by successional status and (b) by species. Individual points represent estimated marginal means and standard errors calculated by (a) the successional status-based or (b) the species-based model.

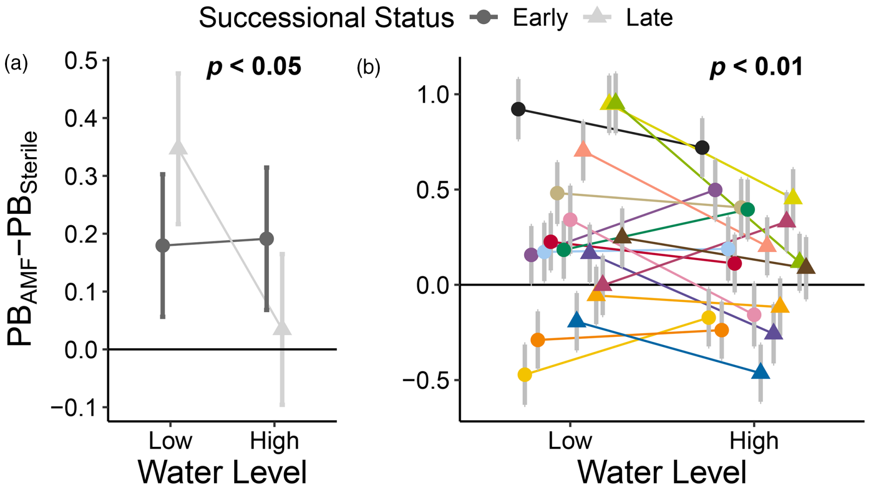

FIGURE 5 Logit-transformed proportion of biomass below-ground (PB) in response to arbuscular mycorrhizal (AM) fungi under different water regimes. Graphs (a) and (b) display the difference of plant species' PB with and without AM fungi in different water conditions (a) by successional status and (b) by species. Individual points represent estimated marginal means and standard errors calculated by (a) the successional status-based or (b) the species-based model.

responsiveness to AM fungi while we saw little difference in the responsiveness of early successional plants between water treatments. This successional status difference in below-ground allocation in response to AM fungi and water levels described variation among species in their response to these same variables ($F_{16,523.1} = 2.33$, $p < 0.01$; Table S2; Figure 5b). Therefore, early successional plants showed little difference in their below-ground allocation response to either P or AM fungi between water treatments, while late successional plants reduced below-ground allocation response to both variables in wetter conditions. This result ran counter to our hypothesis (adapted to focus on the responsiveness of below-ground allocation to AM fungi rather than biomass) in which we would expect the early successional plants' responsiveness to be more plastic.

Plant biomass below-ground allocation with and without AM fungi under different P levels also varied according to species ($F_{16,523.04} = 1.7982$, $p = 0.028$; Table S2), similar to the previous model with total biomass as the response variable. In general, it appears that P addition lowered the magnitude of the below-ground allocation response to inoculation with AM fungi regardless of whether the response was positive or negative (Figure 6). This pattern can be illustrated as a negative correlation between the difference in below-ground allocation with and without AM fungi in high versus low P and the difference in below-ground allocation with and without AM fungi under low P conditions (Figure 6).

4 | DISCUSSION

Most studies of the context-dependence of growth benefits from AM fungi focus on individual plant species (e.g. Corrêa et al., 2014; Johnson et al., 2015; Qu et al., 2021) or have tried to generalize across species with meta-analyses (Hoeksema et al., 2010, 2018); we have tested for generality in responses across plant species in the tallgrass prairie ecosystem known to vary in their overall growth response to mycorrhizal fungi. In doing so, we found that plants generally grew larger with AM fungi and that, across all species, growth response to inoculation declines with P fertilization. We also find high variation between plant species in overall response to mycorrhizal fungi and in the context dependence of mycorrhizal response. Some of this variation maps onto successional status as we predicted. For instance, late successional plant species have more positive responses to mycorrhizal fungi than early successional species, and this generally holds true across variation in soil P. While this result suggests that the role of AM fungal successional processes may be robust to environmental changes in the Anthropocene, patterns

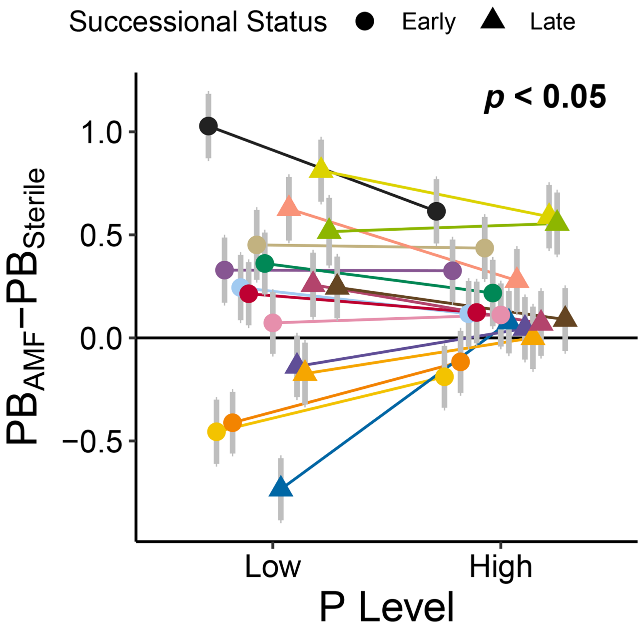

FIGURE 6 Species logit-transformed proportion of biomass below-ground (PB) in response to arbuscular mycorrhizal (AM) fungi under different P regimes. The graph displays the log ratio of plant species' PB with and without AM fungi in different P conditions. Individual points represent estimated marginal means and standard errors calculated by the species-based model.

of biomass allocation paint a more nuanced picture of the potential changes in plant-AM fungi interactions in a changing environment.

4.1 | Context dependence of plant response to AM fungi is partially predicted by stoichiometry

We find that growth benefits from mycorrhizal fungi declined with increasing P, and that this result was consistent across all plant species regardless of successional status. While this result was expected from basic stoichiometry, as increasing soil P decreases the need for AM fungi (Johnson, 2010), it is notable in that it was not obscured by the high variation in overall responsiveness of the plant species included. This variance between plant species was thought to be a reason for a consistent response to P fertilization not being detected in a major meta-analysis of mycorrhizal response, where recent evolutionary history explained more of this variation (Hoeksema et al., 2018); this finding was key to the development of our hypothesis that successional status could explain the variance in plant species responsiveness in different environmental conditions. Our study held other environmental dimensions constant while manipulating soil P concentration, suggesting that the limitation of inference of the previous meta-analyses (Hoeksema et al., 2010, 2018) likely stemmed from the challenges of assembling data from published papers on the many dimensions of the environment that can impact mycorrhizal response that were performed in different environmental conditions such as background soil nutrient and light levels. Our results provide strong support for the context-dependence of plant-AM fungi interactions being governed in part by stoichiometric expectations (Johnson, 2010), even while identifying that the strength of this reduction varies by species.

Plant allocation response to AM fungi does not so clearly follow physiological expectations. One might expect that plants with AM fungi would have reduced need for direct resource acquisition via roots, which would lead to reduced allocation to roots when inoculated with AM fungi and increased above-ground allocation to capture light. This expectation was upheld in a meta-analysis of root-shoot ratios (Veresoglou et al., 2012). We, however, do not find support for this generalization; a few plant species decreased below-ground allocation when inoculated with AM fungi as expected from physiology, but most plant species increased their proportional allocation below-ground. We suggest that part of the difference in our findings is due to the function of roots and other below-ground plant structures in both resource acquisition and storage. This is particularly true for perennial prairie plant species, which are uniformly fire-adapted and invest all perennial storage below-ground. For such perennial plant species, increased investment below-ground can in part be explained by greater perennial storage with AM fungi—that is it is a reflection of fitness benefits from AM fungi. We note that the previous meta-analysis (Veresoglou et al., 2012) finding reduction on allocation to roots was dominated by annual crop species, which would not have significant below-ground storage.

While overall below-ground allocation did not respond to P or water manipulation individually, both environmental manipulations were involved in significant high order interactions, indicating complex patterns of context dependence. The context dependence of plant allocation response to AM fungi can best be understood in light of the dual functions of below-ground biomass in both acquiring and storing resources. We observed, for example, a reduction in interspecific variation in mycorrhizal influence on below-ground allocation with soil P fertilization (Figure 6). This pattern makes sense as resulting from two processes. Plants that increase allocation to storage when inoculated with AM fungi (and hence have positive allocation responses) would be expected to moderate that response with P fertilization because of stoichiometrically reduced overall benefits of AM fungi. While plants that reduce allocation to roots for resource uptake when inoculated with AM fungi (and hence have negative allocation responses), would be expected to moderate that response within P fertilization because of the reduced contribution of AM fungi to P uptake.

The interactions of below-ground allocation with water are best understood in the context of plant successional status, with late successional plants having both high below-ground allocation (Figure S3a) and high biomass responsiveness to AM fungi (Figure 2). In low water environments, late successional plants derive greatest benefits from AM fungi, because their overall biomass and the proportion of that biomass allocated to storage increased. In high water environments, late successional plants still increased overall biomass with AM fungi (which was not dependent on water), but less of this biomass was allocated to below-ground storage (Figure 5a). This suggests that the fitness benefits of AM fungi were greatest for late successional prairie plant species in low water conditions, consistent with observations of a keystone plant species along the natural precipitation gradient in the United States Midwest (Schultz et al., 2001). In support of this interpretation and in support of AM fungi primarily providing P (Smith & Read, 2008), we find that P fertilization increases below-ground allocation of late successional species in low water conditions, but decreases allocation below-ground in high water (Figure 4b). In contrast, early successional plant species did not show variation in AM fungi or P fertilization influence on below-ground allocation with watering treatment (Figures 4b and 5a, respectively). Because of these complexities associated with the dual function of roots in perennial plants, future studies of biomass allocation responses to AM fungi including information about root biomass going towards storage and acquisition of nutrients would, while difficult, be essential to further interpret these relationships.

4.2 | Successional status and environmental dependence of AM fungal benefits: Implications for AM fungi influence on plant community structure

We found that late successional species tended to receive greater growth benefits from AM fungi (mycorrhizal responsiveness or MR) than early successional species, and that this generally holds true when testing across variation in plant species within successional status category and when testing MR across variation in soil P and watering conditions. This affirms that patterns seen in previous studies (Bauer et al., 2018; Koziol & Bever, 2015) can hold across environments. We note that we also observed that species designated as late successional also had overall greater allocation below-ground, consistent with both expectations for late successional, fire-adapted prairie plants, and previous observations (Bauer et al., 2018; Koziol & Bever, 2015). We also found that late successional plants tended to have greater responses to P fertilizer than early successional species, suggesting that late successional species may be more reliant on AM fungi for P uptake in low P soils. Together this suggests that beneficial AM fungi can differentially advantage late successional plant species, potentially leading to a positive feedback accelerating community change (Koziol & Bever, 2019), and that AM fungi are likely to contribute to successional species turnover even in a changing environment.

However, our results also suggest that the role of AM fungi may change in changing environments, as we do observe significant changes in plant-AM fungi interactions with environment. Most notably, to the extent that below-ground allocations positively reflect fitness in long-lived prairie plants, then the benefit that late successional plants receive from AM fungi are differentially diminished with high soil P and high water availability. Our results connect with observations that sustained P fertilization differentially inhibits highly responsive late successional prairie plant species (Wang et al., 2022). Moreover, the sensitivity of mycorrhizal growth response to P fertilization varies among plant species, suggesting potential changes in AM fungi mediated plant community changes that are independent of our current understanding of AM fungi's role in plant succession.

AM fungi have been identified as playing critical roles in structuring plant communities, but understanding how this role may be altered in a changing environment remains a major challenge. On the one hand we find that most plants benefit from AM fungi regardless of environment, perhaps indicating a sustained role of AM fungi in terrestrial productivity. However, that AM fungal benefit declined with P fertilization, suggesting a more limited role in eutrophic environments. From a community perspective, we have evidence suggesting resilience of the contemporary role of AM fungi in plant succession, as late successional species benefited more in terms of biomass from AM fungi regardless of environmental context. However, we also observed from mycorrhizal influence on below-ground allocation that fitness effects of AM fungi on late successional species are differentially negatively impacted in high soil P and high water, suggesting a fragility of the contemporary role of AM fungi in succession. This may also explain conflicting findings in grassland restoration experiments, where AM fungi have been found to be both effective (Zhang & Feng, 2021) and ineffective (Collins & Foster, 2009) at buffering biodiversity loss due to increases in P and/or N. Given the increased likelihood of drought in a large percentage of grasslands (Dai, 2013), our results also suggest that late successional plant species are likely to continue to differentially benefit from AM fungi with climate change. Further work is necessary to evaluate whether inferences drawn here are manifest in field settings, in a wider variety and range of soil resources, and under designs specifically testing drought conditions (versus altered water regimes as we have done). Moreover, the net impact of AM fungi is also dependent upon fungal response to environmental perturbations, and much work remains to evaluate this.

Altogether, our research supports the idea that AM fungi are important drivers of plant community dynamics like succession, and that this role may shift under different environmental contexts like those associated with anthropogenic change. While more research must be done to build a predictive framework of plant mycorrhizal response under different resource contexts, AM fungi are likely to continue to be critical to supporting plant biodiversity, conservation and grassland restoration.

AUTHOR CONTRIBUTIONS

Reb L. Bryant and James D. Bever both contributed to the conception, design and data analysis of the experiment and writing of the manuscript. Reb L. Bryant also collected the data.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data for this paper are available through the Environmental Data Initiative Data Repository at https://doi.org/10.6073/pasta/98baac520b49aa691c1afa9eb29ade1b (Bryant & Bever, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: ANOVA table for the response of total biomass and proportion of biomass belowground in the coefficient of conservatism (CC)-based mixed model.

Table S2: ANOVA table for the response of total biomass and proportion of biomass belowground in the species-based model.

Table S3: ANOVA table for the response of above- and belowground biomass in the successional status-based mixed model.

Figure S1: Species mycorrhizal responsiveness (MR) versus percent root colonization by arbuscular mycorrhizal (AM) fungi.

Figure S2: Species MR versus responsiveness to P.

Figure S3: Logit-transformed proportion of biomass belowground (PB) of plants in general and in response to AM fungi.

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