PLANT MICROBE INTERACTIONS

# Fungal Symbionts Alter Plant Drought Response

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**Abstract** Grassland productivity is often primarily limited by water availability, and therefore, grasslands may be especially sensitive to climate change. Fungal symbionts can mediate plant drought response by enhancing drought tolerance and avoidance, but these effects have not been quantified across grass species. We performed a factorial meta-analysis of previously published studies to determine how arbuscular mycorrhizal (AM) fungi and endophytic fungal symbionts affect growth of grasses under drought. We then examined how the effect of fungal symbionts on plant growth was influenced by biotic (plant photosynthetic pathway) and abiotic (level of drought) factors. We also measured the phylogenetic signal of fungal symbionts on grass growth under control and drought conditions. Under drought conditions, grasses colonized by AM fungi grew larger than those without mycorrhizal symbionts. The increased growth of grasses conferred from fungal symbionts was greatest at the lowest soil moisture levels. Furthermore, under both drought and control conditions, C3 grasses colonized by AM fungi grew larger than C3 grasses without symbionts, but the biomass of C4 grasses was not affected by AM fungi. Endophytes did not increase plant biomass overall under any treatment. However, there was a phylogenetically conserved increase in plant biomass in grasses colonized by endophytes. Grasses and their fungal symbionts seem to interact within a context-dependent symbiosis, varying with biotic and abiotic conditions. Because plant–

fungal symbioses significantly alter plant drought response, including these responses could improve our ability to predict grassland functioning under global change.

## Introduction

Plant productivity is primarily limited by water availability in many ecosystems [1]. Climate change may exacerbate water limitation as models predict an increase in the intensity and frequency of droughts [2]. Plants respond to drought via three mechanisms: (1) by altering their phenology, (2) by avoiding water deficits through reduced evapotranspiration and increased root-to-shoot ratios, and (3) by tolerating water limitation by increasing cellular osmolite concentrations to improve water uptake [3]. In addition to the above-mentioned direct plant responses to drought, fungal symbionts can enhance plant drought avoidance and tolerance strategies [4, 5].

Plant species predominantly associate with arbuscular mycorrhizal (AM) fungi belowground and endophytes aboveground [6, 7]. These two classes of fungal symbionts can alter how plants respond to drought and thus have the potential to ameliorate or intensify the effects of climate change. Arbuscular mycorrhizal fungi can promote drought avoidance by producing hyphae with access to small soil pores, expanding belowground water uptake surface area [4]. Similarly, fungal leaf endophytes can influence both plant drought avoidance by controlling stomatal conductance [5, 8] and drought tolerance by influencing osmotic adjustment [9].

However, the beneficial effect of fungal symbionts can become detrimental to plant growth under drought. For example, the benefits on host growth from AM fungi can decrease under extremely low water availability as drier soil

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conditions can inhibit the flow of phosphorus from AM fungi to plants [10]. Aboveground, endophytes may negatively affect plant biomass during drought, ostensibly because they can incur a metabolic drain on plant carbon and nutrients without increasing plant drought tolerance [11]. Endophytes can also contribute to larger rates of water loss in plants by increasing leaf conductance under drought stress [12].

The direction of plant–fungal symbioses is often dependent on biotic and abiotic factors, with the same fungal taxa conferring different costs or benefits under different conditions. For instance, under drought conditions, the relative benefit from a fungal symbiont may be different depending on the photosynthetic pathway of the host plant. Plants with C4 physiology have greater water use efficiency and stomatal conductance than C3 species; therefore, they may rely less on fungal symbionts for water acquisition [13, 14]. In addition to plant photosynthetic pathway, soil nutrient concentrations can dictate the interaction between a plant host and its fungal symbionts. For example, a beneficial fungal symbiont can become parasitic when nutrient availability is not limiting [15]. Moreover, AM fungi and endophytes can differ in their benefit to host plants under similar abiotic conditions. For example, benefits from AM fungi often increase under low soil nutrient concentrations [16] as AM fungi can acquire limiting resources from the soil, while benefits from endophytes may decrease under the same conditions as aboveground symbionts only acquire nitrogen from the host plant. While plant–fungal symbioses often range from mutualism to parasitism dependent on soil nutrient conditions, it is not clear if the same continuum exists in response to soil moisture.

We used a meta-analysis of previously published studies to quantify the relative strength and direction of plant biomass responses to both AM fungi and endophytes under a range of drought conditions. We focused on plant–fungal symbioses in grasslands, as grassland productivity is primarily limited by water availability, and grasslands are thus expected to be sensitive to altered precipitation [17–19]. In previous qualitative reviews, grasses appear to have variable responses to fungal symbionts under drought and control conditions [4, 20]. In order to explain the variability observed between studies, we also examined how the effect of fungal symbionts on plant biomass was influenced by plant physiology, and evolutionary history. We addressed several questions with our meta-analysis: (1) Does the presence of a fungal symbiont affect the growth of grasses (Poaceae) under drought? (2) Does the magnitude and direction of the effect differ between AM fungi and endophytes? (3) Are there environmental conditions or plant characteristics that influence this effect? (4) Is the effect of fungal symbionts on growth of plant species phylogenetically conserved?

## Methods

### Data Collection

We obtained our data from several different sources. First, we conducted an ISI Web of Science [21] search with the keywords mycorrhiza* OR endophyte AND drought for the time period September 2011 to July 2012. For the studies collected via this search, we further included relevant papers from the literature-cited sections. We similarly collected all of the appropriate publications from the previous review by Augé [4]. Finally, all papers obtained above were subject to reverse search via ISI Web of Science to find any newer publications in which they had been cited. Each paper was then screened for inclusion as described below.

All studies included in our meta-analysis compared the effect of fungal symbiont status (present versus absent) on the growth of grasses under drought and control conditions. For inclusion, we created five requirements. First, the plant was a member of the Poaceae family (grasses). Second, the presence of at least one fungal symbiont was manipulated, regardless of the method of inoculation or resulting colonization rate. Though we had no criteria on the class of fungal symbionts to include in our study, only Clavicipitaceous endophytes and AM fungi were manipulated often enough to be compared quantitatively. This excluded all horizontally transmitted leaf fungal endophytes from our study. Third, water levels were manipulated with a drought and a control condition for both the symbiotic and nonsymbiotic treatments. We termed a drought treatment as any intentional reduction in soil moisture and control conditions as maintaining soil moisture at field capacity or watering daily. To account for hierarchical dependencies, we only included the most severe level of drought in our dataset. Fourth, plant size or growth rate was measured. We chose biomass as the response variable of drought tolerance because drought stress often significantly affects biomass [22] and biomass is correlated with plant productivity, competitive ability, and fitness [23]. We prioritized total biomass, followed by shoot biomass, root biomass, or elongation rate. If there was more than one measurement of biomass over time, we only recorded biomass measured from the final date. Finally, we allowed studies to differ in their level of fertilization, location (greenhouse, growth chamber or field), duration of pre-growth (growth before drought was initiated) and soil type into our meta-analysis. However, within a study, we only included studies that did not alter these factors concomitantly with drought. These variables could be sources of heterogeneity between studies.

For each study, we recorded the following biomass means: $\overline{Y}_{df}$, $\overline{Y}_{dn}$, $\overline{Y}_{cf}$, and $\overline{Y}_{cn}$, where $\overline{Y}$ = sample mean, d = drought, c = control, f = fungus, and n = no fungus. All reported measures of variation were transformed to standard deviation.

If a measure of variance was not provided, we estimated standard deviation as the mean divided by the square root of the sample size, as in Borenstein et al. [24]. If data were reported in graphical form, means and error terms were extracted using WebPlotDigitizer [25].

Though we followed strict inclusion criteria, there are limitations to our dataset. In particular, the use of sample size to estimate variance in 62 of the comparisons can cause an overestimation of the within-study variance. Overestimating the within-study variance could lead to biases in the overall effect size, in which weights based on the sampling error will be more negatively biased compared to weights using sample sizes [26]. We quantified the potential bias in our study by calculating Rosenthal's failsafe number (i.e., the number of studies necessary to negate the reported effect size) [27] (Table 1). We also included a small set of studies where the same control was used for different fungal species treatments (n=25 comparisons). This creates nonindependence of effect-size estimates, which results in an underestimate of the standard deviation of the mean effect [28].

Effect Size Calculations

In order to address if the presence of a fungal symbiont affected the growth of grasses under drought, we calculated an individual effect size from each study for the response of plant biomass to drought ($L_{drought}$), fungus ($L_{fungus}$), and their interaction ($L_{interaction}$). We used a response ratio because it gives a standardized measurement of the proportion change in plant biomass from the control treatment relative to the fungal-drought treatment. Effect sizes were calculated using the following calculations:

$$L_{drought} = \left(\ln\left(\overline{Y}_{dn}\right) + \ln\left(\overline{Y}_{df}\right)\right) - \left(\ln\left(\overline{Y}_{cn}\right) + \ln\left(\overline{Y}_{cf}\right)\right)$$
$$L_{fungus} = \left(\ln\left(\overline{Y}_{cf}\right) + \ln\left(\overline{Y}_{df}\right)\right) - \left(\ln\left(\overline{Y}_{cn}\right) + \ln\left(\overline{Y}_{dn}\right)\right)$$
$$L_{interaction} = \left(\ln\left(\overline{Y}_{df}\right) - \ln\left(\overline{Y}_{dn}\right)\right) - \left(\ln\left(\overline{Y}_{cf}\right) - \ln\left(\overline{Y}_{cn}\right)\right)$$

The response of plant biomass to drought, fungus, and their interaction is reflected in the sign of the effect size. For example, a negative effect size for $L_{drought}$ indicates that plants are smaller under drought treatments than under control watering conditions, while a negative effect size for $L_{fungus}$ indicates that a fungal symbiont decreases plant biomass. However, we are most interested in $L_{interaction}$, which addresses under which conditions (drought or control) the plant receives a greater benefit from associating with fungal symbionts. The interaction term can be divided into two components: $\left(\ln\left(\overline{Y}_{df}\right) - \ln\left(\overline{Y}_{dn}\right)\right)$ and $\left(\ln\left(\overline{Y}_{cf}\right) - \ln\left(\overline{Y}_{cn}\right)\right)$. The first term measures the effect of a fungal symbiont on plant biomass under drought conditions. A positive value indicates that the fungus decreases the effect of drought on plant biomass, while a negative value indicates that the fungus is detrimental to plant growth under a drought. The second term measures the effect of a fungal symbiont under control conditions. The first term is sufficient in addressing whether a fungal symbiont confers drought tolerance in grasses. However, by subtracting

**Table 1** Meta-analysis summary with number of studies, number of data points (comparisons), mean effect size (effect size) ± 95 % CI, degree of heterogeneity (Q), and fail safe number for each meta-analysis calculation

| Variable | Studies | Comparisons | Effect size | Q value | Fail safe |
|---|---|---|---|---|---|
| All | | | | | |
| Drought | 51 | 86 | −0.72 (±0.14) | 1,122 | 584 |
| Fungus | 51 | 86 | 0.07 (±0.10) | 517 | 36 |
| Interaction | 51 | 86 | 0.08 (±0.08) | 256 | 12 |
| AM fungi | | | | | |
| Drought | 30 | 57 | −0.78 (±0.16) | 138 | 1,880 |
| Fungus | 30 | 57 | 0.17 (±0.21) | 240 | 9 |
| Interaction | 30 | 57 | 0.16 (±0.09) | 14 | 32 |
| Endophyte | | | | | |
| Drought | 21 | 29 | −0.61 (±0.22) | 926 | 273 |
| Fungus | 21 | 29 | 0.04 (±0.14) | 255 | 0 |
| Interaction | 21 | 29 | 0.11 (±0.18) | 242 | 0 |
| C3 | | | | | |
| Drought | 37 | 54 | −0.69 (±0.28) | 972 | 190 |
| Fungus | 37 | 54 | 0.24 (±0.24) | 266 | 26 |
| Interaction | 37 | 54 | 0.42 (±0.32) | 245 | 0 |
| C4 | | | | | |
| Drought | 14 | 32 | −0.84 (±0.19) | 83 | 820 |
| Fungus | 14 | 32 | 0.09 (±0.31) | 262 | 0 |
| Interaction | 14 | 32 | 0.11 (±0.12) | 45 | 0 |

these values, we are able to determine if the relative benefit of fungal symbionts changes under different watering conditions. If $L_{interaction}$ is positive, a fungal symbiont provides greater benefit to grasses under drought stress. If $L_{interaction}$ is negative, a fungal symbiont is more beneficial to grasses under controlled conditions. Individual study variances were calculated using the following calculation:

$$V_i = \frac{\sigma_{df}^2}{n_{df}\overline{Y}_{df}^2} + \frac{\sigma_{dn}^2}{n_{dn}\overline{Y}_{dn}^2} + \frac{\sigma_{cf}^2}{n_{cf}\overline{Y}_{cf}^2} + \frac{\sigma_{cn}^2}{n_{cn}\overline{Y}_{cn}^2}$$

Where $\overline{Y}$ = sample mean, $n$ = sample size, and $\sigma$ = standard deviation. To account for unequal study variances, we assigned weights to each effect size as the inverse of the overall study variance [28].

To quantify the strength and direction of plant–fungal interactions in grasses under drought, we used all comparisons in our dataset ($n=86$) to calculate the three mean effect sizes: the response of plant biomass to drought, fungus, and their interaction. Mean effect sizes were calculated as the sum of the individual study effect sizes divided by the sum of their weights. We calculated the mean variance as the inverse of the sum of the study weights plus tau (an estimate of between-study variance) [24]. Since each study independently manipulated either AM fungi or endophytes, we examined the mean effects of each symbiont separately.

Statistics

In order to assess how plant characteristics influence plant response to fungal symbionts, we performed a post hoc random effects model of within-group variances for the effects of plant photosynthetic pathway (C3 or C4) and fungal type (AM fungi or endophyte) [28]. Briefly, the difference between the weighted within-group variance ($Q_{within}$) and the weighted overall variance ($Q$) was compared to a chi-squared distribution. Groups were considered significantly different if within-group variance was significantly lower than the overall variance (i.e., between-group variance was large) at $P<0.05$.

To understand if soil moisture influenced the mean effect sizes, we performed a random effects meta-regression [29]. Soil moisture can be measured many ways, so we separately regressed weighted effect sizes of each study against the continuous variables of drought duration, percent reduction in water level between the control and drought treatments, and soil moisture levels (in megapascal). All data were normally distributed and homoscedastic. All statistics were conducted in SPSS v. 17.

Phylogenetic Signal

In order to evaluate if the effect of fungal symbionts on the growth of plant species is phylogenetically conserved, we calculated weighted mean effect sizes ($L^*_{drought}$, $L^*_{fungus}$, and $L^*_{interaction}$) for each plant species. We then used each effect size as trait values to identify phylogenetic signals in Phylocom using the AOT module [30]. AOT compares the branch length shared between species to the distribution of trait values to determine if variables are significantly clustered on a phylogeny. We created separate alignments using the complete ITS gene for grass species containing either endophytes or AM fungi in SATé [31]. We created phylogenies for each alignment with bootstrap values using RAxML BlackBox [32]. We based the grass phylogenies on the ITS region because it is sufficiently variable to distinguish among species, was the only gene consistently available for the majority of our grass species, and has been used to successfully create grass species phylogenies [33]. The resulting topologies were very similar to existing phylogenies based on multiple gene regions [13].

## Results

Overall, our dataset contained 86 comparisons from 51 different studies (Tables 1 and S1). For AM fungi, there were 57 comparisons from 30 studies, and for endophytes, we included 29 comparisons from 13 studies.

Effects of Fungal Symbionts on the Growth of Grasses

Arbuscular mycorrhizal fungi categorically increased the growth of grasses under drought conditions, but not under control conditions (Fig. 1, Table 1). Endophytes tended to increase plant biomass under drought conditions, but this effect was extremely variable so there was no significant overall effect (Fig. 1, Table 1). Similarly, endophytes had no overall effect on the growth of grasses under control conditions (Fig. 1, Table 1). Because the effect of endophytes on plant growth under drought conditions was so variable, the effects of AM fungi and endophytes on the growth of grasses under drought were not significantly different from each other based on pairwise comparisons (Table 2). Finally, as expected, grass biomass was smaller under all drought conditions compared to control conditions, regardless of the presence of fungal symbionts (Table 1).

Plant Photosynthetic Pathway

We only examined the effect of AM fungal symbionts in C3 versus C4 grasses, as all of the endophyte symbioses in this study were with C3 grasses. The biomass of both C3 and C4 grasses decreased under drought (Fig. 2, Table 1). Under both control and drought conditions, AM fungi increased biomass of C3 grasses, while the biomass of C4 grasses did not change when colonized with AM fungi (Fig. 2, Table 1).
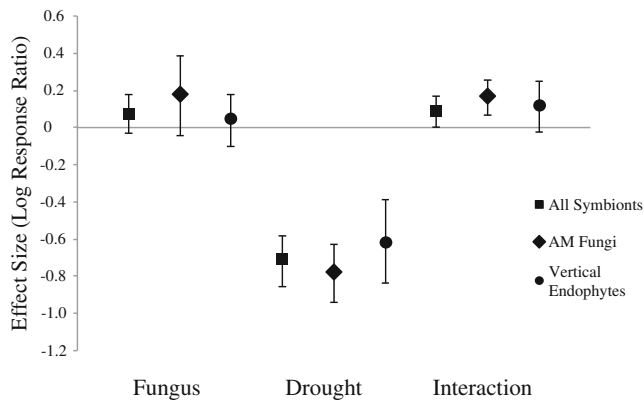
Fig. 1 Log response ratios for grasses associating with AM fungi and endophyte symbionts. $L_{fungus}$ represents the difference between the biomass of grasses associating with a fungus to grasses without a fungus. $L_{drought}$ represents the difference between the biomass of grasses under drought versus control conditions. $L_{interaction}$ represents the difference between the biomass of grasses associating with a fungus under drought conditions to grasses associating with a fungus under control conditions. There is a significant positive response to the interaction of drought and all fungi and drought and AM fungi. *Error bars* represent ±95 % CI

### Drought Treatment Characteristics

Plant biomass was lower under lower soil moistures ($r^2$=0.34, $P$=0.01). Plants also experienced the largest growth benefits of fungal symbionts under the lowest soil moistures ($r^2$=0.26, $P$=0.02). Effect sizes did not vary with the duration of drought or the percent reduction of water levels in drought compared to control treatment.

### Phylogenetic Signal

Closely related grass species had more similar biomass responses than distantly related species when associated with endophytes (variance contrast=0.04, $P$=0.01; Fig. 3a), but plant response to the interaction of drought and associating with an endophyte was not phylogenetically conserved (variance contrast=0.38, $P$=0.25; Fig. 3b). Grasses within the genus *Elymus* grew largest when
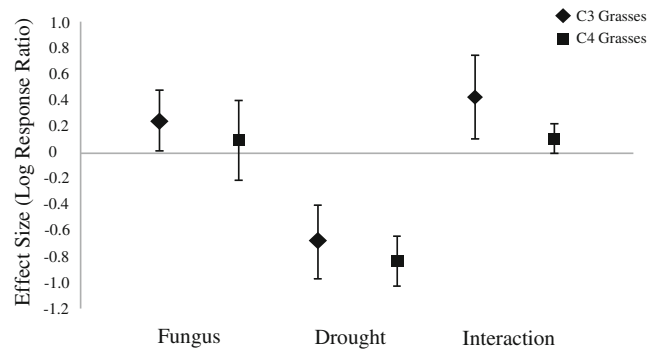


Fig. 2 Log response ratios for C3 and C4 grasses associating with AM fungi. We only examined the effect of AM fungal symbionts in C3 versus C4 grasses, as all of the endophyte symbioses in this study were with C3 grasses. The effect of AM fungi on grass biomass is significantly positive for C3 grasses under a drought and under control water levels. The effect on C4 grasses is insignificant. *Error bars* represent ±95 % CI

associated with endophyte symbionts (*Elymus virginicus* $L_{endophyte}$=0.76±0.33, *Elymus dahuricus* $L_{endophyte}$=0.92±0.25) while most other grass species (with the exception of *Festuca arundinacea*) either decreased in biomass or remained unchanged when associated with an endophyte. When AM fungi were present, both plant biomass (variance contrast=0.40, $P$=0.54; Fig. 3c) and plant drought response (variance contrast=0.37, $P$=0.50; Fig. 3d) were not significantly phylogenetically conserved.

### Discussion

Only AM fungi categorically influenced the growth of grasses under drought, although endophytes had a similar trend. The outcome of grass–fungal interactions under drought was context dependent, however, with three factors playing important roles. First, fungal symbionts increased plant biomass more as water limitation increased. Second, plant photosynthetic pathway affected the AM fungal–plant symbiosis, with C3 grasses receiving a greater benefit from associating with AM fungi than C4 grasses under both control and drought conditions. Finally, while endophytes had little effect on plant biomass overall, we detected a significant phylogenetic signal for biomass in response to endophyte presence. As fungal symbionts significantly affect plant growth under both drought and mesic conditions, including plant–fungal symbioses will improve our understanding of grassland response to climate change.

Soil moisture levels greatly affected the outcome of grass–fungal interactions in our study, with increasing plant benefit from fungal symbionts under lower soil moistures. However, several data points from studies with exceptionally low soil moistures may have influenced our trends. Nevertheless, AM fungi and endophytes may be more

| Variable | df | $Q_B^*$ |
|---|---|---|
| Fungus | | |
| $L_{fungus}$ | 1 | 0.01 |
| $L_{drought}$ | 1 | *58.62* |
| $L_{interaction}$ | 1 | *3.09$^{-5}$* |
| Plant photosynthetic pathway | | |
| $L_{fungus}$ | 1 | *5.94* |
| $L_{drought}$ | 1 | 1.62 |
| $L_{interaction}$ | 1 | 0.00 |

Table 2 Heterogeneity ($Q_B^*$) results for weighted $L_{interaction}$ effect size in comparison of plant photosynthetic pathway (C3 or C4) and fungal type (AM fungus or endophyte)

Significant $P$ values are in italics

**Fig. 3** Phylogeny of grasses with endophyte associations (*a* and *b*) and AM fungal associations (*c* and *d*) with the average $L_{fungus}$ effect size for each species. Endophytes had a significant phylogenetically conserved effect on plant biomass (*a*), but the interaction effect between endophytes and plants under drought was not phylogenetically conserved (*b*). Arbuscular mycorrhizal fungi did not have a phylogenetic signal on plant biomass under control conditions (*c*) or under drought (*d*). *Error bars* represent ±95 % CI. The phylogenies are rooted with the *Joinvillea plicata* outgroup and base pair changes per unit branch length are noted below each phylogeny. Bootstrap values are noted next to every bifurcation
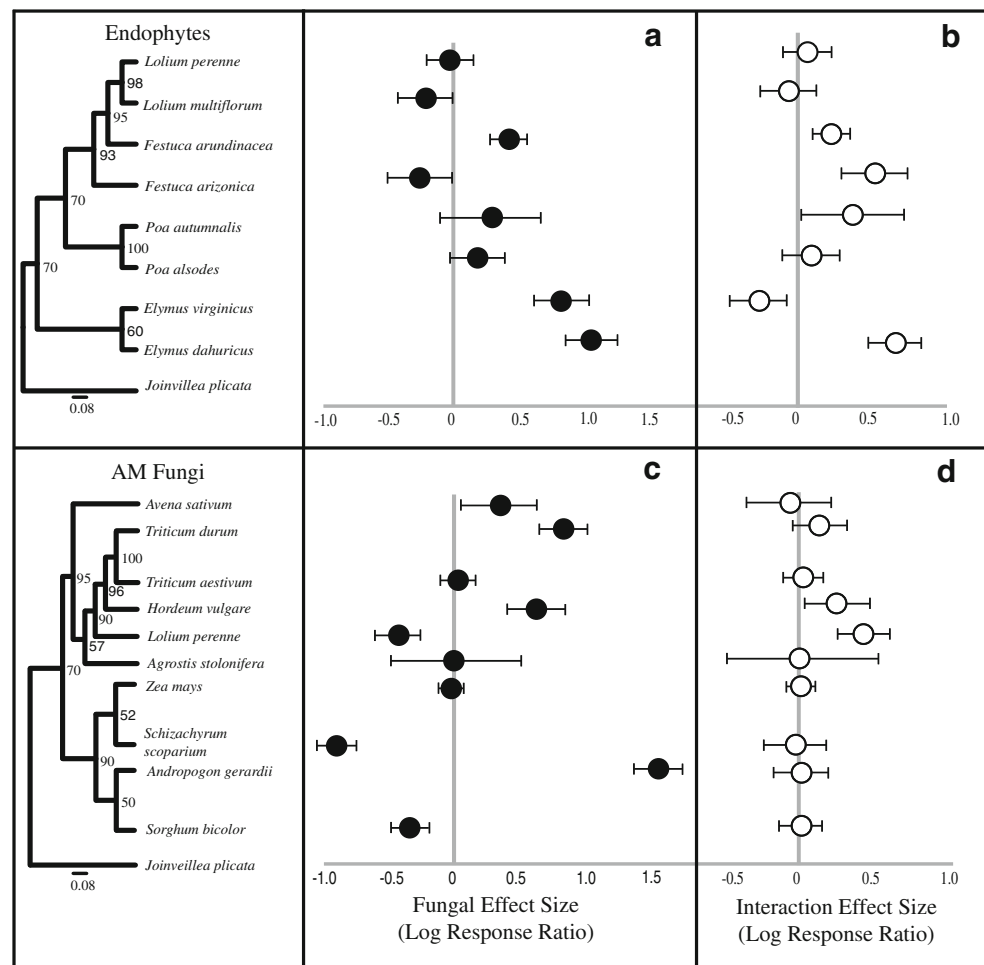


beneficial under extreme environmental water limitation. Fungal symbionts often increase plant tolerance in extreme environments [34–36]. For example, in extremely warm soils in Yellowstone National Park, both AM fungi and leaf endophytes increase thermal tolerance of their host plants. Similarly, AM fungal symbioses are often most beneficial to their hosts under low soil nutrient concentrations [16]. Therefore, the shift between mutualism, amensalism, and parasitism of plant–fungal symbioses may depend on not only soil nutrients and temperature, as previously documented, but also on soil moisture.

Despite the consistent influence of AM fungi on plant drought tolerance, the magnitude of this effect was dependent on plant photosynthetic pathway [37]. The C3 grasses benefitted more than C4 grasses from associating with AM fungi under drought and well-watered conditions. Improved C3 grass biomass in the presence of AM fungi likely reflects intrinsically lower water use efficiencies in C3 than in C4 grasses [14, 38]. This result initially seems counterintuitive, as C4 grasses often receive more of a growth benefit from AM fungi under field conditions [16, 39, 40]. Under field conditions, however, plant communities may be structured

by competition for limiting soil nutrients, while in these greenhouse studies, nutrients were not limiting, but water availability was low. Therefore, C4 grasses may receive the most benefit from AM fungi via increased nutrient acquisition, while C3 grasses may receive greater benefits from AM fungi through water acquisition.

The phylogenetic signal observed among grass species in their growth response to Clavicipitaceous endophytes suggests that these interactions are shaped by their long evolutionary history, dating to approximately 80 million years ago [41]. Endophytes in our study are mostly vertically transmitted, so their distributions are congruent with those of their plant host. Moreover, endophyte fitness is dependent on their host's fitness. This life history favors plant–fungal coevolution and predisposes endophytes to evolve highly beneficial and species-specific mutualisms [41]. In our study, grasses in the *Elymus* genus received the most benefit from their endophyte symbionts. This effect may be common, as other studies have observed similar trends [42]. Nevertheless, since the majority of the studies in this meta-analysis were conducted on commercial grasses grown in the greenhouse, caution must be applied when comparing

our results to natural systems. Indeed, endophytes are more common in drought-prone areas [43], suggesting that they may provide plant benefits under drought in natural systems that were not captured in our meta-analysis. Endophytes may also be beneficial in other respects (i.e., herbivory tolerance, nutrient acquisition), which may also explain why endophytes affected plant biomass, but not under drought stress.

Arbuscular mycorrhizal fungi are horizontally transmitted and are rarely host specific [7], which may explain the lack of phylogenetic signal between plant biomass and AM fungi that we observed. Instead, AM fungal composition often shifts among broad plant biomes or climatic regions [44, 45]. The relative effect on plant drought tolerance by AM fungi could therefore be explained by environmental sorting of AM fungal taxa or AM fungal adaptation to environmental conditions. Indeed, AM fungi may be more adapted to environmental conditions rather than their host plant [46]. Similarly, composition of horizontally transmitted leaf endophytes is less likely to be affected by plant hosts and more by environmental filtering [47], but we were unable to quantify this effect, due to the lack of empirical data. Nevertheless, the fungal symbiont mode of transmission may explain whether the benefits of plant–fungal symbioses are mainly host or environment dependent.

While we focused on how grass drought responses were affected individually by AM fungi or endophytes, grasses are typically colonized by both symbionts simultaneously in natural systems. Such tripartite interactions may affect plant drought response in positive or negative ways. A meta-analysis by Larimer et al. [20] observed an increase in plant growth from the interaction between AM fungi and endophytes. However, in some cases, endophytes can reduce the benefit of AM fungi in grasses [48]. Additionally, we quantified plant biomass to capture drought responses from fungal symbionts. However, in response to herbivory, endophytes can decrease individual plant biomass and fitness while increasing population growth [49]. Thus, fungal symbionts may increase plant drought response through means other than increased plant productivity.

Fungal symbionts may have disproportionate effects on grassland ecosystems under drought. Fungi are key regulators of plant physiology, fitness, community structure, and ecosystem dynamics [50–52]. By increasing the productivity of their plant host, fungal symbionts can shift community composition to those plant species that receive the largest benefits from them [50]. With individual plant biomass being a large determinant of plant survival during a drought [53], the ability of fungal symbionts to increase or maintain plant biomass in a drought may play an important role in structuring grassland communities. Because AM fungal associations are so prevalent in grasslands [7], grass–fungal mutualisms have the potential to modify plant physiology, competition, and community composition on a large scale.

Moreover, because AM fungi intercept carbon from aboveground and regulate nutrient fluxes from belowground, these symbioses have the potential to affect soil nutrient and carbon cycling at the ecosystem level under drought [54]. A greater understanding of plant–fungal interactions under drought may therefore lead us to a better appreciation of whole ecosystem response to climate change.

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