American Journal of Botany

American Journal of Botany 100(7): 1445–1457. 2013.

SPECIAL INVITED PAPER—GLOBAL BIOLOGICAL CHANGE

Fungal symbionts alter plant responses to global change[1]

Stephanie N. Kivlin[2,5], Sarah M. Emery[3], and Jennifer A. Rudgers[4]

[2]Section of Integrative Biology, University of Texas at Austin, Austin, Texas 78712 USA; [3]Biology Department, University of Louisville, Louisville, Kentucky 40292 USA; and [4]Department of Biology, University of New Mexico, Albuquerque, New Mexico 87048 USA

While direct plant responses to global change have been well characterized, indirect plant responses to global change, via altered species interactions, have received less attention. Here, we examined how plants associated with four classes of fungal symbionts (class I leaf endophytes [EF], arbuscular mycorrhizal fungi [AMF], ectomycorrhizal fungi [ECM], and dark septate endophytes [DSE]) responded to four global change factors (enriched CO_2, drought, N deposition, and warming). We performed a meta-analysis of 434 studies spanning 174 publications to search for generalizable trends in responses of plant–fungal symbioses to future environments. Specifically, we addressed the following questions: (1) Can fungal symbionts ameliorate responses of plants to global change? (2) Do fungal symbiont groups differ in the degree to which they modify plant response to global change? (3) Do particular global change factors affect plant–fungal symbioses more than others? In all global change scenarios, except elevated CO_2, fungal symbionts significantly altered plant responses to global change. In most cases, fungal symbionts increased plant biomass in response to global change. However, increased N deposition reduced the benefits of symbiosis. Of the global change factors we considered, drought and N deposition resulted in the strongest fungal mediation of plant responses. Our analysis highlighted gaps in current knowledge for responses of particular fungal groups and revealed the importance of considering not only the nonadditive effects of multiple global change factors, but also the interactive effects of multiple fungal symbioses. Our results show that considering plant–fungal symbioses is critical to predicting ecosystem response to global change.

Key words: arbuscular mycorrhizal fungi; class I endophytes; dark septate endophytes; ectomycorrhizal fungi; global change; plant biomass; symbiosis.

Global change is occurring at an unprecedented rate, with a 2–3°C increase in mean annual temperatures, shifts in precipitation location and frequency, and a 200% increase in atmospheric CO_2 predicted in some regions by the end of the 21st century (Soloman et al., 2007; Stott et al., 2010). Moreover, anthropogenic N deposition has doubled compared to preindustrial levels (Galloway et al., 2004) and is expected to increase another 2.5-fold over the next century (Lamarque et al., 2005). Predicting how terrestrial organisms will respond to these changes is crucial, as their responses can feedback to enhance or ameliorate global change (Melillo et al., 2002; Ciais et al., 2005). Understanding the responses of land plants is particularly important because plants not only control the flux of carbon into terrestrial systems but also store a large portion of terrestrial carbon (Schimel et al., 1995). Plants may respond to global change directly via altered physiology, fitness, or phenology and also indirectly through altered biotic interactions (Tylianakis et al., 2008; van der Putten et al., 2010).

[1]Manuscript received 21 October 2012; revision accepted 6 February 2013.

J.A.R. was supported by NSF DEB #1145588, #0949719 and #0918267. S.M.E. was supported by NSF DEB #0919093. S.N.K. was supported by NSF DEB #1119169. This manuscript was improved by comments from M. E. Afkhami, E. R. Worchel, L. P. Bell-Dereske, and A. Chung.

[5]Author for correspondence (e-mail: stephanie.kivlin@utexas.edu), phone: (512) 475-6479, fax: (512) 471-5858

doi:10.3732/ajb.1200558

Many studies have examined direct plant physiological responses to global change. For example, in a global meta-analysis, LeBauer and Treseder (2008) showed that N additions mimicking atmospheric deposition increased plant biomass across a variety of ecosystems. Similarly, a meta-analysis conducted by Curtis and Wang (1998) found that elevated atmospheric CO_2 concentrations caused a net increase in plant biomass. In contrast, drought conditions associated with climate change have generally reduced plant biomass (Ciais et al., 2005; Flanagan and Johnson, 2005). Global change factors also interact. For instance, plant responses to elevated temperature may depend on levels of soil moisture, with increased plant growth in mesic conditions and decreased growth in xeric conditions (Lin et al., 2010; Hoeppner and Dukes, 2012).

While these direct plant responses to global change have been well characterized, indirect plant responses to global change, via altered species interactions, have received less attention. In particular, plants commonly interact with a myriad of fungal symbionts that may influence their responses and feedbacks to global change. Belowground mycorrhizal fungi and dark septate endophytes (DSE) occur in the roots of up to 80% of terrestrial plant species (Smith and Read, 2008). Aboveground, plants interact with both vertically transmitted leaf endophytes (e.g., *Epichloë* and *Neotyphodium* spp., Clavicipitaceae, Ascomycota) and horizontally transmitted endophytes (diverse species, mainly Ascomycota) (Rodriguez et al., 2009). Both above- and belowground fungal symbionts can influence plant physiology (Elmi and West, 1995), population structure (Rudgers et al., 2012), community composition (van der Heijden et al., 1998; Clay and

Holah, 1999; Hartnett and Wilson, 1999), decomposition (Lemons et al., 2005), and nutrient cycling (van der Heijden et al., 2008). Above- and belowground fungal symbionts have each independently been shown to alter plant responses to global change factors including warming (Ju et al., 2006), altered precipitation (Augé, 2001), N deposition (Treseder, 2004), and increasing CO_2 concentrations (Treseder, 2004). Furthermore, the outcomes of plant–fungal symbioses can vary between mutualism and parasitism, producing context-dependent responses to global change (Johnson et al., 1997; Cheplick et al., 2000; Saikkonen et al., 2006; Johnson et al., 2010). However, the field has yet to arrive at a universally accepted theoretical or quantitative understanding of how plant–fungal symbioses will behave under global change.

Here, we examine responses of plants associated with four classes of fungal symbionts (class I leaf endophytes, arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and dark septate endophytes) to four global change factors (enriched CO_2, drought, N deposition, and warming) to search for generalizable trends in the responses of plant–fungal symbioses to future environments. Specifically, we addressed the following questions. (1) Can fungal symbionts ameliorate the response of plants to global change? (2) Do fungal symbiont groups differ in the degree to which they modify plant response to global change? (3) Do particular global change factors affect plant–fungal symbioses more than others?

BACKGROUND: BIOLOGY OF PLANT–FUNGAL SYMBIOSES UNDER GLOBAL CHANGE

***Leaf endophytes*—**Class I endophytes (EF) in the genus *Neotyphodium* along with its sexual teleomorph *Epichloë* occur systemically in an estimated 20–30% of grass species (Leuchtmann, 1992; Rudgers et al., 2009). These fungi can protect the plant host from herbivory (Rudgers and Clay, 2008), drought (Elmi and West, 1995; Schardl et al., 2004; Kannadan and Rudgers, 2008), and nutrient stress (Malinowski and Belesky, 1999). Because they produce N-rich alkaloid compounds as bioprotectants, EF may become costly at low nutrient levels (Cheplick et al., 1989). Class I endophytes vary in frequency over environmental gradients (e.g., Bazely et al., 2007; Granath et al., 2007), suggesting that their distributions are affected by climate. Indeed, EF presence has been reported to be higher in plants in drought-stressed relative to more mesic natural systems (Lewis et al., 1997; Leyronas and Raynal, 2001), but see (Cheplick et al., 2000; Rudgers and Swafford, 2009). They also have the potential to mediate plant responses to global change by altering plant population dynamics (Rudgers et al., 2012), community composition (Clay and Holah, 1999), succession (Rudgers et al., 2007), and even ecosystem level processes, such as aboveground productivity (Rudgers et al., 2004), decomposition (Lemons et al., 2005), and N or carbon pools in the soil (Franzluebbers et al., 1999; Franzluebbers and Hill, 2005).

***Arbuscular mycorrhizal fungi*—**Arbuscular mycorrhizal fungi (AMF) in the phylum Glomeromycota form symbioses with 80% of land plants (Smith and Read, 2008) and have a worldwide distribution (Öpik et al., 2010). They can receive up to 30% of a plant's photosynthates (Drigo et al., 2010) and in exchange provide plants with up to 80% of their required N or P (van der Heijden et al., 2008). In addition, AMF can enhance plant drought tolerance (Jakobsen and Rosendahl, 1990; Augé, 2001) and protect plants from pathogens (Sikes et al., 2009; Sikes et al., 2010). However, individual AMF isolates differ in their relative benefit to host plants, and these benefits can decrease in soils with high nutrient concentrations (Johnson et al., 1997; Hoeksema et al., 2010). AMF can have large impacts on ecosystems, as they can alter plant community composition (Hartnett and Wilson, 1999) and ecosystem-level nutrient cycling (van der Heijden et al., 2008).

***Ectomycorrhizal fungi*—**Ectomycorrhizal fungi (ECM) occur in up to 6000 plant species and are mainly widespread in coniferous tree species (Wang and Qui, 2006; Rinaldi et al., 2008; Smith and Read, 2008). ECM provide increased plant acquisition of both inorganic and organic soil nutrients and in return can receive up to 50% of plant photosynthate (Simard et al., 2002). In drought-prone ecosystems, ECM networks can redistribute water from deep soils to roots via hydraulic lift (Querejeta et al., 2007) and move water among roots of drought-stressed plant species (Egerton-Warburton et al., 2007). The ability of ECM to mediate host response to global change has mainly been observed in response to N deposition, CO_2 increases, and drought. For example, under high soil N concentrations, ECM can become parasitic to some plants relative to nonmycorrhizal controls (Jonsson et al., 2001), ostensibly because the plant is not receiving a fungal benefit under these conditions. Alternatively, under enriched atmospheric CO_2, ECM are often more beneficial to plant hosts because soil nutrients become increasingly limited (Choi et al., 2005). While few studies have manipulated ECM directly in natural plant communities, ECM can affect competition between plants (Booth and Hoeksema, 2009), primary productivity (Jonsson et al., 2001), and soil nutrient cycling (Chalot and Brun, 1998; Chapela et al., 2001).

***Dark septate endophytes*—**Dark septate endophytic fungi (DSE) occur in the roots of at least 600 plant species (Jumpponen and Trappe, 1998) and are mostly within the Ascomycota. These fungi have wide distributions and are especially abundant in alpine, arctic, and desert ecosystems (Read and Haselwandter, 1981; Jumpponen et al., 1998; Herrera et al., 2010; Porras-Alfaro and Bayman, 2011). The ecological function of most DSE is unknown, although they can improve plant growth (Newsham, 2010), potentially by accessing organic forms of N and P (Haselwandter and Read, 1982; Jumpponen et al., 1998) or soil moisture (Barrow, 2003). Despite the idea that nutrient-acquiring fungal symbionts may become less beneficial under N deposition (Johnson et al., 1997), a recent meta-analysis suggested that DSE benefits to plants did not vary with applications of inorganic N fertilizer (Newsham, 2010); however, they did increase plant biomass under additions of organic N fertilizer relative to control conditions. In addition, DSE are highly melanized, which may allow them to withstand extreme temperatures and drought and thereby increase plant growth under these conditions (Jumpponen and Trappe, 1998; Barrow, 2003). The role of DSE in influencing plant communities or ecosystem processes remains unresolved. However, differential growth rates of plant species with the same DSE have been described (Reininger et al., 2012), suggesting that DSE may alter the outcome of plant competition. Moreover, because DSE have the capacity to degrade organic N and P compounds (Jumpponen and Trappe, 1998) and provide them to their plant hosts (Usuki and Narisawa, 2007), they may also affect ecosystem-level nutrient and carbon cycling. Experiments in natural settings are needed before the ecological roles of DSE can be fully appreciated. Thus, the response of DSE to global change remains unclear.

***Predictions of plant response to global change*—**Using current knowledge of the biology of plant–fungal symbioses, we

generated expectations about how symbionts could modify plant response to global change factors. (1) We predicted that EF would increase plant biomass in response to all four factors we examined—warming (temperature), drought, atmospheric CO_2 concentration, and N deposition—because the most commonly observed endophyte benefits have been protection against drought and the most likely costs occur under low nutrient levels. (2) We expected that AMF and ECM would enhance plant biomass in response to warming, drought, and elevated atmospheric CO_2. Conversely, we hypothesized that AMF and ECM would have weak effects or even decrease plant biomass under N deposition because plants may gain few to no benefits from symbiont-assisted nutrient acquisition under high soil nutrient concentrations. (3) Hypotheses for DSE remain unclear, given the small number of experimental studies; if DSE primarily ameliorate water stress, then we should see positive effects on host plants under high temperatures and drought. However, if benefits include nutrient acquisition, these benefits would weaken under N deposition.

***Symbiont interactions*—**Plants simultaneously associate with many fungal symbionts in nature. However, few studies examine how interactions between multiple symbionts can affect plants under global change. Multiple plant–fungal symbioses within the same host can complicate the ability to predict plant responses to global change. Pairwise studies may underestimate the effects of fungal symbiosis if multiple fungi act synergistically to benefit hosts or may overestimate these effects if hosting multiple partners reduces the benefits of symbioses (e.g., via antagonistic interactions among the multiple fungi). In a recent meta-analysis, Larimer et al. (2010) indicated that concurrent colonization by both AMF and EF generally enhanced the growth of grass hosts. However, this relationship can be context dependent, as endophytes and AMF have been reported to have additive or synergistically beneficial effects on hosts (Novas et al., 2009; Larimer et al., 2012), no interaction (Chen et al., 2007), or antagonistic interactions (Chu-Chou et al., 1992; Müller, 2003; Omacini et al., 2006; Mack and Rudgers, 2008; Liu et al., 2011). Similarly, ECM and AMF may ameliorate negative effects of DSE (Reininger and Sieber, 2012) or have no interaction with DSE (Mandyam and Jumpponen, 2008). Overall, interactions among multiple symbionts can span the full range from negative to positive, depending on environmental and biotic mechanisms that are not yet fully resolved. Because only a few studies have manipulated multiple symbionts under global change, we were precluded from quantifying their effects on plant response to global change. Instead, we summarize the results from current studies and highlight topics in need of more research.

MATERIALS AND METHODS

Using meta-analysis, we quantified the effects of both above- and belowground plant–fungal symbioses on plant biomass under predicted global change scenarios. Studies were collected by performing a literature search in ISI Web of Science through July 2012 using the keywords of mycorrhiza* or endophyte AND stress, drought, warming, temperature, N, or CO_2. We screened the results to obtain studies that examined the response of plant biomass, both with and without a fungal symbiont, to at least one of the following global change factors: atmospheric CO_2 enrichment, drought stress, N deposition, and warming. We also collected studies from published meta-analyses (Hoeksema et al., 2010; Worchel et al., 2013). Furthermore, we only included studies that examined plant response to drought (not flooding), plant response to N addition in isolation (without fertilization by other elements), or plant response to warming (not cooling), as these treatments more closely mimic the most commonly predicted global change scenarios. In total, we examined 434 studies spanning 174 publications (Appendix S1, see Supplemental Data with the online version of this article). The majority of studies were conducted in the greenhouse ($N = 423$ studies; 97%).

***Data collection*—**We focused on plant biomass responses, as these data were reported in the majority of studies (in contrast to other measures such as seed production). When plant biomass was not reported ($N = 5$ studies from three publications), we collected other metrics of plant growth, such as plant height, leaf elongation rate, or tiller length (online Appendix S1). When available, means, sampling dispersion (standard error and/or standard deviation) and sample sizes were collected for each data point ($N = 185$ studies). Otherwise, we estimated the standard deviation as the mean divided by the square root of the sample size ($N = 249$) (Borenstein et al., 2009). We digitized data presented graphically using WebPlotDigitizer v. 2.4 (Rohatgi, 2011). Because data from the same study were not statistically independent (Gurevitch and Hedges, 1999), for each study, we only collected data from the longest time point and the most extreme manipulation. We included multiple data points from studies that compared effects of more than one class of fungal symbionts or multiple fungal taxa within a class of symbionts when such manipulations could occur independently.

To examine the influence of publication identity, in cases where multiple studies came from the same publication, we conducted an analysis including publication as a random effect on of the subset of data ($N = 336$ [or ~80%] of 434 total records analyzed) for which there were multiple records per study. Unfortunately, this analysis had greatly reduced sample sizes per fungal symbiont × global change factor combination, limiting our ability to test the original hypotheses (98 publications were included as a single record). In addition, 48% of the publications with more than one record were represented by only two records, which provided extremely low replication for estimating the variance explained by publication identity. In all but six publications, multiple records per publication reflected independent tests of different species of fungi and/or plants to the same global change factor.

As an alternative, and more robust, test of the importance of publication identity, we created a reduced data set in which each publication was represented by only a single record. We chose records at random from among the multiple records per study, except in the six publications where more than one fungal symbiont type and/or global change factor were examined. For this small subset, we chose the record that corresponded to least represented fungal symbiont type × global change factor combination in our overall data set, to maximize our coverage. This reduced data set had a total of 175 publications (1 record each). We applied the same analyses as for the full data set, and we report any cases where analysis of the full and reduced data sets diverged.

***Effect size metrics*—**We conducted an interaction meta-analysis following Hawkes and Sullivan (2001). We used two metrics for effect size. First, we calculated the log-response ratio (LRR), a standard metric for meta-analysis. The main effect of each global change manipulation was calculated as:

$$\mathrm{LRR}_{\text{global change}} = \left(\ln \bar{Y}_{t,s} + \ln \bar{Y}_{t,n}\right) - \left(\ln \bar{Y}_{c,s} + \ln \bar{Y}_{c,n}\right),$$

the main effect of having a fungal symbiont was calculated as:

$$\mathrm{LRR}_{\text{symbiont}} = \left(\ln \bar{Y}_{t,s} + \ln \bar{Y}_{c,s}\right) - \left(\ln \bar{Y}_{t,n} + \ln \bar{Y}_{c,n}\right),$$

and the interaction term was calculated as:

$$\mathrm{LRR}_{\text{interaction}} = \left(\ln \bar{Y}_{t,s} - \ln \bar{Y}_{c,s}\right) - \left(\ln \bar{Y}_{t,n} - \ln \bar{Y}_{c,n}\right),$$

where $\bar{Y}$ is the sample mean for t = treatment or c = control for the global change manipulation and s = symbiont or n = no symbiont. Second, we determined the relative interaction intensity metric:

$$\mathrm{RII} = \left(\bar{Y}_t - \bar{Y}_c\right) / \left(\bar{Y}_t + \bar{Y}_c\right)$$

and variance of RII following Armas et al. (2004). The RII is an improvement on LRR because it is bounded between −1 and 1 and symmetrical around zero; the LRR is unbounded and cannot be computed if the control group response variable is zero (Hedges et al., 1999; Armas et al., 2004). For RII, the main effect of each global change manipulation was calculated as:

$$\mathrm{RII}_{\text{global change}} = \frac{\left(\bar{Y}_{t,s} + \bar{Y}_{t,n}\right)}{\left(\bar{Y}_{t,s} + \bar{Y}_{t,n}\right)} - \frac{\left(\bar{Y}_{c,s} + \bar{Y}_{c,n}\right)}{\left(\bar{Y}_{c,s} + \bar{Y}_{c,n}\right)},$$

the main effect of having a fungal symbiont was calculated as:

$$\mathrm{RII}_{\text{symbiont}} = \frac{\left(\bar{Y}_{t,s} + \bar{Y}_{c,s}\right)}{\left(\bar{Y}_{t,s} + \bar{Y}_{c,s}\right)} - \frac{\left(\bar{Y}_{t,n} + \bar{Y}_{c,n}\right)}{\left(\bar{Y}_{t,n} + \bar{Y}_{c,n}\right)},$$

and the interaction term was calculated as:

$$\mathrm{RII}_{\text{interaction}} = \frac{\left(\bar{Y}_{t,s} - \bar{Y}_{t,n}\right)}{\left(\bar{Y}_{t,s} + \bar{Y}_{t,n}\right)} - \frac{\left(\bar{Y}_{c,s} - \bar{Y}_{c,n}\right)}{\left(\bar{Y}_{c,s} + \bar{Y}_{c,n}\right)}.$$

***Data analysis*—**Data were analyzed with weighted general linear models that included the fixed effects of symbiont type (EF, AMF, ECM, or DSE) and global change factor (enriched CO_2, drought, N deposition, and warming) (Proc MIXED, SAS v. 9.3, SAS Institute, Cary, North Carolina, USA) following Hoeksema et al. (2010). We could not test for a global change factor × symbiont type interaction because not all symbiont types were represented across all global change factors. Therefore, we decomposed the analysis by running a separate model for each global change factor; these models included the fixed effect of symbiont type. We only analyzed global change factors and symbiont groups with more than three comparisons. Response variables were the effect size metrics (RII and LRR) for (1) the magnitude of the global change effect, (2) the magnitude of the symbiont effect, and (3) the magnitude of the interaction between symbionts and global change. We weighted each effect size with the inverse of the pooled study variance, calculated as:

$$\mathrm{Vi} = \frac{s_{t,s}^2}{n_{t,s}\bar{Y}_{t,s}^2} + \frac{s_{t,n}^2}{n_{t,n}\bar{Y}_{t,n}^2} + \frac{s_{c,s}^2}{n_{c,s}\bar{Y}_{c,s}^2} + \frac{s_{c,n}^2}{n_{c,n}\bar{Y}_{c,n}^2},$$

with $\bar{Y}$= sample mean, n = sample size, and s = standard deviation. We did not observe any publication bias from a scatter plot of effect size vs. sample size. However, three records were excluded from the final analysis as extreme outliers due to the combination of their effect sizes and associated weights (two from Bunn et al. [2009], one from Corkidi et al. [2002], giving n = 432 records). Four records were excluded from the analysis of the reduced data set (Huang et al. [2011], Kannadan and Rudgers [2008], Sanchez-Blanco et al. [2004], Donoso et al. [2008], giving n = 171 records) due to outlier weights. In addition, because fewer than 10 studies examined the responses of ECM or DSE to some global change factors, we could not make quantitative comparisons of these groups for some factors, but we do present the general patterns. In all cases, analyses met assumptions of normality of residuals and homogeneity of variance. Overall, there was little divergence in results between the two effect size metrics, LRR and RII. Therefore, we focused our presentation on RII. RII is easier to visualize and assimilate the strength of the effect than LRR because the scale is confined between −1 and 1. However, we discuss all cases where LRR results differed from RII.

These analyses provided direct statistical tests of our questions. (1) Can fungal symbionts ameliorate the response of plants to global change? This would be confirmed by RII/LRR interaction effect sizes that are significantly greater than zero. Specifically, a significantly positive interaction effect size indicates that the presence of the symbiont minimized the effects of global change relative to symbiont-free plants. In contrast, a significantly negative interaction term indicates that the presence of the symbiont exacerbated the effect of the global change factor. (2) Do fungal symbiont groups differ in the degree to which they modify plant response to global change? This would be confirmed by a significant effect of symbiont type on the RII/LRR interaction effect. (3) Do particular global change factors affect plant–fungal symbioses more than others? This would be confirmed by a significant symbiont type effect on the RII/LRR interaction effect in models for individual global change factors.

RESULTS

Fungal symbionts altered the magnitude of plant response to global change for all factors we examined, except elevated CO_2. Studies on drought and N deposition showed the strongest influences of fungal symbionts on plant responses to global change, whereas studies on temperature showed weaker effects of symbionts on plant response to global change. These differences were evidenced by a significant effect of the identity of the global change factor on the magnitude of the interaction effect size ($F_{3,424}$ = 19.6, P < 0.0001). For both drought (mean RII [95% CI] = 0.09 [0.07, 0.10]) and N (−0.06 [−0.10, −0.01]), the interaction effect size was significantly different from zero, but symbionts had opposite effects on plant responses. Fungal symbionts ameliorated the negative effects of drought, as evidenced by a positive mean effect size, whereas fungal symbionts had not only weaker, but negative effects, on plant growth relative to symbiont-free conditions under N fertilization. Analysis of the reduced data set confirmed these results.

The type of global change factor ($F_{3,424}$ = 129.7, P < 0.0001) and the type of fungal symbiont ($F_{3,424}$ = 32.1, P < 0.0001) strongly affected the magnitude of the global change effect size, indicating that global change factors differed in how much they affected plant biomass, and that studies on different symbionts also varied in the overall magnitude of plant response to global change. Not surprisingly, plant response to drought was significantly negative overall (RII = −0.14), while responses to CO_2, N, and temperature were all positive and of similar magnitudes (RII = 0.10–0.15). Studies on plant-EF symbioses generally showed stronger net plant responses to global change factors (RII = 0.13) than did studies on other fungal symbionts (RII = 0.02–0.04) in the analysis of the full data set. However, when the data set was reduced to a single record per study, the significant effect of type of fungal symbiont on the global change effect size disappeared ($F_{3,164}$ = 1.39, P = 0.25), suggesting that the fungal effect in the full data set arose from unequal representation across publications.

The effect size for the presence of the symbiont (averaged over global change factors) varied among fungal symbiont types ($F_{3,424}$ = 10.9, P < 0.0001) and among studies on different global change factors ($F_{3,424}$ = 28.5, P < 0.0001). When averaged over all studies and global change factors, AMF and DSE had consistently positive effect sizes on plant biomass (both RII = 0.04), whereas ECM and EF effect sizes did not significantly differ from zero. Analysis of the reduced data set confirmed results from the full. These results suggest that ECM and EF may be more likely than the other symbionts to show context-dependency in response to global change. In the next section, we report plant responses to each global change driver in greater detail.

***Elevated CO_2*—**Studies on CO_2 enrichment spanned AMF, DSE, and ECM, but no CO_2 experiments on EF reported the response of host plant biomass to factorial manipulation of CO_2 and the endophyte, highlighting a gap in current research (Table 1). For the three fungal groups with adequate representation, presence of the symbiont did not alter the influence of CO_2 on host plant performance. That is, there were no interaction effects that significantly deviated from the null expectation (zero) (Fig. 1A). In addition, there were no differences among fungal groups in the magnitude of the interaction effect size ($F_{2,43}$ = 0.7, P = 0.935)—for all fungal groups, fungal presence had no effect on plant response to CO_2. Not surprisingly, elevated CO_2 caused a net increase in plant biomass

TABLE 1. Number of publications and studies for each fungal symbiont group and global change factor.

Factor	Total	Endophytic fungi	Arbuscular mycorrhizal fungi	Ectomycorrhizal fungi	Dark septate endophytes
A) Number of publications					
Elevated CO_2	26	2	16	10	1
Drought	116	24	79	11	3
N deposition	31	5	11	13	1
Warming	25	0	23	0	2
B) Number of studies					
Elevated CO_2	49	3	19	20	7
Drought	219	32	150	32	4
N deposition	81	5	16	59	1
Warming	90	0	69	0	21

("CO_2 effect", Fig. 1A), with similar magnitudes of effect size across plants hosting the three fungal groups ($F_{2,43} = 0.3$, $P = 0.777$). However, the effect size for fungal symbiont presence differed among fungal groups ("symbiont effect", Fig. 1A, $F_{2,43} = 3.4$, $P = 0.045$), with the strongest average benefit to hosts of AMF, a weaker benefit to hosts of DSE (with large variation around the mean), and no significant average benefit to hosts of ECM (Fig. 1A). Results for LRR and for the reduced data set (which lacked sufficient replication to test DSE) were identical to RII, with one exception: Neither showed any significant difference among fungal groups in the effect size for fungal symbiont presence on host biomass (LRR $F_{2,43} = 2.1$, $P = 0.136$; reduced data set $F_{2,18} = 0.1$, $P = 0.80$).

***Drought*—**Studies manipulating water availability had the best coverage across fungal groups, with some published work on all four types of symbionts, although the number of records for DSE studies was very low ($n = 4$, Table 1), and DSE studies could not be included in analysis of the reduced data set ($n = 2$). For all four fungal groups, presence of the symbiont reduced the negative effects of drought, as indicated by a significantly positive interaction effect term (Fig. 1B). There was no effect of fungal symbiont group on the magnitude of the interaction effect size ($F_{3,213} = 1.6$, $P = 0.197$), indicating that all groups effected similar levels of drought amelioration in host plants. As expected, all symbiont groups improved plant performance, with the strongest main effect size for DSE, and the weakest main effect for EF ("symbiont effect", Fig. 1B, fungal group: $F_{3,213} = 12.7$, $P < 0.0001$). Also, as expected, drought consistently reduced plant performance (negative effect sizes, "drought effect", Fig. 1B). For the full data set, the magnitude of the drought effect was strongest for studies on hosts of AMF and weakest for studies on hosts of EF ($F_{3,213} = 38.5$, $P < 0.0001$); in the reduced data set, there were no significant differences among fungal symbiont groups, although they followed the same rank order ($F_{2,92} = 0.2$, $P = 0.84$). Differences among fungal groups in the magnitude of the drought effect on host plants may simply reflect differences among fungal researchers in the choice of experimental design to manipulate drought or could indicate differences that reflect plant phylogeny (e.g., if different host species were often studied for different fungal groups). Analysis of LRR as an alternative effect size metric were consistent with RII, excepting that LRR did not show differences among fungal groups in the magnitude of the effect size for drought (consistent with reduced data set result).

***Nitrogen deposition*—**Studies manipulating N lacked coverage of DSE and had low replication for EF ($n = 5$ records, Table 1). Examination of the available data showed that plant response to N was weaker in the presence of symbionts than in their absence (i.e., significantly negative interaction effect sizes; Fig. 1C; interaction effect size compared across fungal groups: $F_{2,76} = 2.1$, $P = 0.126$). Only for EF was the interaction effect size positive, but it was not statistically significantly different from zero or from the interaction effect sizes for hosts of other fungal groups (Fig. 1C). As anticipated, N had positive effects on plant biomass/growth estimates, and there was no significant divergence among fungal groups in this effect size ("Nitrogen effect", $F_{2,77} = 1.5$, $P = 0.225$; Fig. 1C). Averaged across N treatments, AMF presence improved plant performance the most, followed by EF ("symbiont effect", Fig. 1C; fungal groups: $F_{2,77} = 9.1$, $P < 0.001$). Among the symbionts, only ECM had no significant overall effect on host plant performance (Fig. 1C), and in the analysis of the reduced data set, the effect of ECM was significantly negative (RII [95% CI] = –0.11 [–0.08 to –0.03]). This was the only difference in results between the reduced and full data sets. The only divergence in results for the LRR relative to the RII was that studies on host plants with AMF showed significantly larger net effect sizes for N addition ("nitrogen effect") compared to studies of ECM, which could simply reflect differences in methodologies among studies conducted on different fungal groups. In the one study that has manipulated N and DSE colonization, N addition increased plant biomass more in the presence of the DSE, *Phialocephala fortinii*, in N-poor soils (Jumpponen et al., 1998). Clearly, more research must be conducted in multiple ecosystems before generalizable responses of DSE to N deposition can be determined (see also Newsham, 2010).

***Warming*—**Sample sizes from published studies were only sufficient to examine the responses of AMF and DSE to temperature manipulations. For both fungal symbionts, plants were more sensitive to the benefits of temperature increases in the presence of the symbiont than in its absence, as indicated by positive interaction effect sizes (Fig. 1D). However, the interaction RII only significantly differed from zero for DSE (interaction effect size compared between fungal groups: $F_{1,88} = 8.3$, $P = 0.005$). Averaged over temperature treatments, DSE (unexpectedly) reduced plant performance, and the main effect of AMF presence was not significantly different from zero ("symbiont effect", Fig. 1D; fungal group: $F_{1,88} = 49.5$, $P < 0.0001$). The DSE studies were dominated by records from a single publication (Reininger et al., 2012), which manipulated the presence of different strains of the root endophyte, *Phialocephala fortinii* on two tree species, *Picea abies* and *Betula pendula*. This DSE appears to function as a parasite with respect to plant biomass. Higher temperatures reduced the parasitic effects of the fungus, thereby contributing to a positive interaction effect. Finally, elevated temperatures generally increased plant performance in studies on AMF, but we detected no average effect of temperature on plant growth across DSE treatments, reflecting the importance of DSE in mediating plant response to temperature ("temperature effect", Fig. 1D). The differences between AMF and DSE in the magnitude of the temperature effect were statistically significant ($F_{1,88} = 9.8$, $P = 0.002$). Results for LRR were qualitatively the same as for RII, although the P values for differences among fungal groups in both the temperature effect size and the interaction effect size were marginal ($P = 0.06$). Results from the reduced data set had too little coverage of DSE ($n = 2$ publications) to permit analysis. Effects of AMF in the

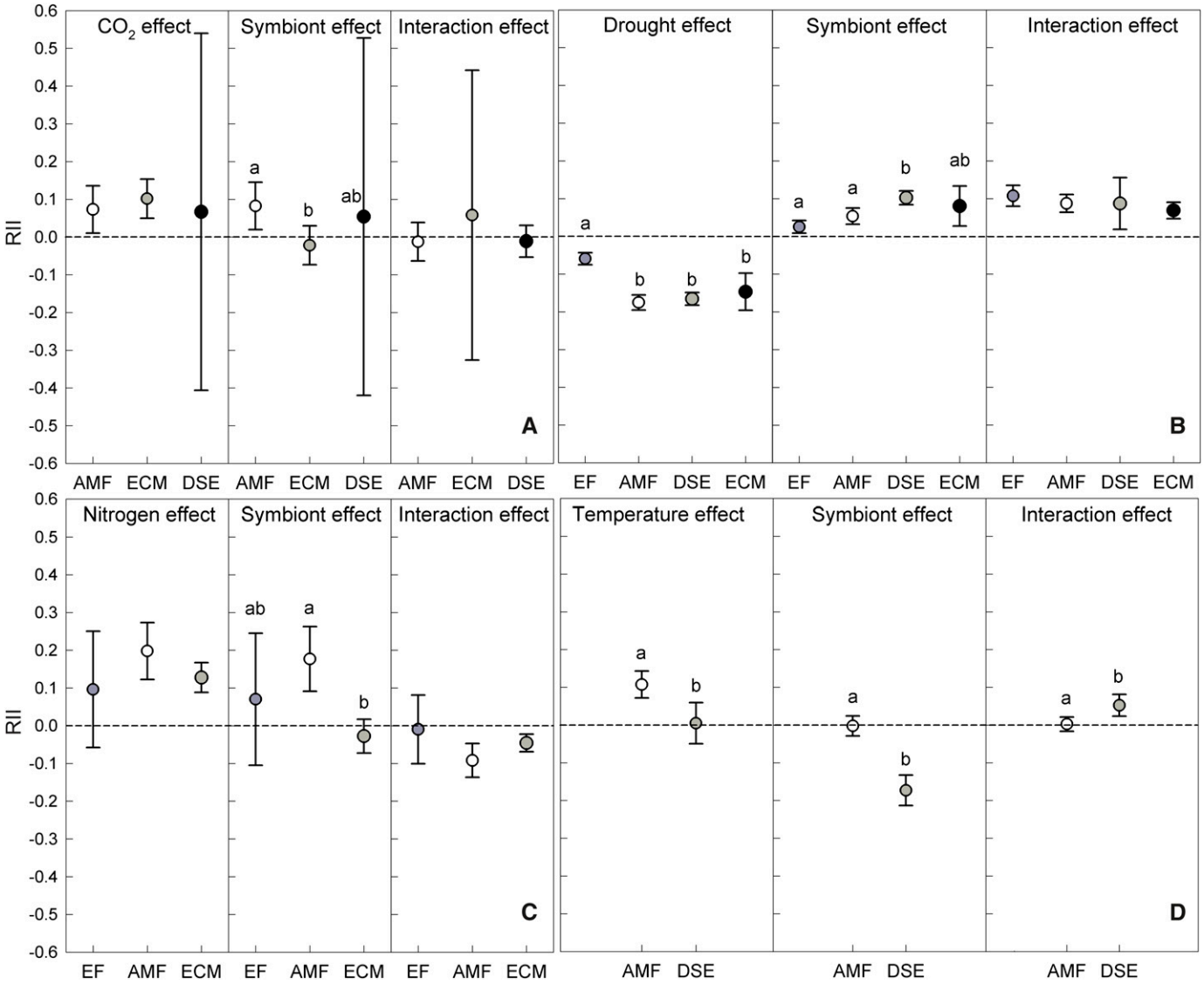

Fig. 1. Plant responses in presence and absence of fungal symbionts to (A) elevated CO_2, (B) drought, (C) N addition, (D) increased temperature. Effect sizes, calculated as the relative interaction intensity, RII, for plant responses to global change factors. In all panels, the "CO_2 effect" (or other global change factor) shows the net plant response to elevated CO_2 (averaged over the symbiont treatment) for studies on each fungal symbiont group. "Symbiont effect" shows the net plant response to the presence of a symbiont (averaged over the CO_2 treatment) for each fungal group. "Interaction effect" shows the magnitude of the interaction between symbiont presence and the CO_2 manipulation. Symbols show means and bars are 95% confidence intervals. Letters indicate significant differences among symbiont groups within an effect size metric as shown by post hoc Tukey honestly significant difference (HSD) tests.

reduced dataset ($n = 22$ publications) showed the same pattern as did analysis of the full dataset—only the AMF symbiont effect size on host plant biomass was significantly different from zero.

DISCUSSION

(1) Can fungal symbionts ameliorate the response of plants to global change?—In all global change scenarios that we examined, except elevated CO_2, at least one group of fungal symbionts significantly altered plant responses to global change. In most cases, fungal symbionts increased plant biomass, ameliorating the negative consequences of global change. The exception was symbiont effects under N deposition. Fungal symbioses are ubiquitous in natural systems (Leuchtmann, 1992; Jumpponen and Trappe, 1998; Smith and Read, 2008; Porras-Alfaro and Bayman, 2011). Therefore, individual plant responses to global change may often be mediated by fungal symbionts. Although the focus of our meta-analysis was on individual plant responses (because of the data currently available), the effects of plant–fungal symbioses may extend beyond individual plants, given the known influences of plant-fungal symbioses on plant population dynamics (Rudgers et al., 2012), community composition (Hartnett and Wilson, 1999), interactions with other trophic levels (Gehring and Whitham, 1994), and ecosystem-level nutrient cycling (van der Heijden et al., 2008). Considering the potentially large-scale impacts of fungal symbionts on plant communities in response to global change, it is critical to improve our

knowledge of how all plant-fungal symbioses respond to global change conditions.

Our meta-analysis revealed gaps in current research on the responses of plant–fungal symbioses to global change. Notably, the effects of mycorrhizal symbionts on plant growth are better understood than those of other fungal symbiont groups; most of the studies in our meta-analysis manipulated the presence of either AMF or ECM. For example, under elevated CO_2, only two publications manipulated EF and only one publication manipulated DSE, which precluded formal analysis of studies on these symbionts. Similarly, the effects of AMF and ECM on plant response to drought are well defined, while DSE have only been manipulated in three publications on three taxa (two on *Trichoderma* spp., one on *Sebacina*). Nitrogen fertilization experiments have also largely focused on AMF and ECM; only one publication manipulated DSE while five manipulated EF. Overall, few studies have examined plant biomass in response to manipulations of fungal symbionts under warmer temperatures. However, AMF have most often been manipulated in warming experiments, while ECM and EF effects on plant biomass have not, to our knowledge, been studied in this context. Overall, there is a paucity of data on the effects of all global change factors on symbioses between DSE and plants. DSE have only recently been characterized in detail (Porras-Alfaro and Bayman, 2011; Mandyam et al., 2012) and only for some ecosystems, so it is not surprising that DSE-plant symbioses have not received much attention in the context of global change. However, the roles of EF in plant response to global change have also not received much attention outside of drought manipulations. While, we focused on four groups of fungal symbionts, there are additional plant–fungal symbioses that we did not include. For example, horizontally transmitted leaf fungal endophytes (class II and class III endophytes, Rodriguez et al., 2009) are prevalent in natural systems and can confer plant tolerance to thermal stress (Redman et al., 2002), salinity (Rodriguez et al., 2008), and drought (Giauque and Hawkes, 2013). More studies manipulating EF, DSE and other horizontally transmitted endophytes under all global change scenarios would yield greater insight into how plants will respond to global change.

(2) Do fungal symbiont groups differ in the degree to which they modify plant response to global change?—All fungal symbionts (EF, AMF, ECM, and DSE) increased plant growth to a similar degree under drought (Fig. 1). For the other three factors of global change, different fungal groups distinctively altered plant growth responses to the different global change factors. DSE increased plant growth under warming (Reininger et al., 2012). Under N deposition, mycorrhizal symbionts (AMF and ECM) reduced the benefits of fertilization to plants. Most symbionts had average effect sizes that were positive, although in several cases, particularly for EF and ECM, these "symbiont effect sizes" were not significantly different from zero. These results emphasize that symbiont effects differ and are commonly context-dependent under treatments mimicking global change.

(3) Do particular global change factors affect plant–fungal symbioses more than others?—Plant–fungal responses varied strongly among the four factors of global change we examined. Drought and N deposition resulted in stronger fungal mediation of plant responses than did temperature, and studies of elevated CO_2 showed no effects of symbionts in modifying plant responses. However, more symbiont groups were manipulated under drought and N fertilization so this may skew our results. While it is not surprising that factors of global change varied in the strength of their effects on plant–fungal symbioses, our results are instructive in highlighting the contexts in which fungal symbionts may deserve the most attention. Specifically, current data suggest that studies on drought and N deposition could benefit the most from incorporating plant–fungal interactions into predictions of plant response.

Applying small-scale studies to natural ecosystems—Most studies in our meta-analysis were conducted within the greenhouse and therefore may not reflect responses in natural ecosystems for a variety of reasons. For example, in greenhouses plants are usually grown in isolation, while in natural systems both positive and negative species interactions (such as facilitation, herbivory, interspecific competition) can influence plant responses (Tilman, 1982; van der Putten, 2012). Additionally, plants in the greenhouse are typically grown with a limited number of fungal symbionts compared to the complex symbiont assemblages experienced in natural systems. Moreover, interactions between plants and microbial symbionts vary temporally (Kardol et al., 2006), with large shifts in fungal symbiont communities with succession (van der Putten et al., 1993) and time since invasion (Hawkes et al., 2006). Complex interactions between plants and fungal symbionts in natural systems may make it difficult to apply our meta-analysis results outside of the greenhouse.

In an effort to assess the applicability of the trends we observed to natural environments and field settings, we will discuss current understanding of plant and fungal responses to each global change factor gained from field observations and studies conducted outside of the greenhouse. While these studies did not include factorial manipulations of symbiont presence and global change factors, and thus, were not eligible for our meta-analysis, they provide some insight into the ability to scale up from small scale, manipulative studies. In addition, we address whether the *fungal* response to each global change driver tracks the same patterns observed for plants in our meta-analysis.

Elevated CO_2—Our meta-analysis showed that elevated atmospheric CO_2 concentrations increased plant biomass, regardless of the presence of fungal symbionts. The presence of fungal symbionts did not affect plant response to CO_2. Results from the field suggest that fungi may directly increase under elevated CO_2, but without influencing plant growth, which would explain the results of our meta-analysis. Specifically, a meta-analysis by Treseder (2004) demonstrated that, on average, elevated CO_2 increased extraradical AMF hyphal biomass (fungal biomass outside of the roots) by 36%. Soil fungal biomass and intraradical ECM biomass also have shown increases in response to elevated CO_2 (Alberton et al., 2005; Garcia et al., 2008). Because CO_2 enrichment creates progressive nutrient limitation in soils over time (Treseder and Allen, 2002), plant biomass and fungal biomass increases may be largely independent, with no effect of the fungi on the magnitude of plant response. Under nutrient limitation, fungal symbionts may become less beneficial as they can provide fewer soil resources in exchange for plant C. The responses of other types of plant–fungal symbioses to elevated CO_2 remain unresolved. Two studies suggest that EF may benefit plants under increased atmospheric CO_2. In a multiclimate change experiment, Brosi et al. (2011) showed that under enhanced CO_2 concentrations, a higher frequency of plants were colonized by EF than under ambient CO_2 conditions. Similarly, Marks and Clay (1990) observed an increased benefit of EF on

plant growth under elevated CO_2, but only when soil nutrients were not limiting. Because EF typically produce N-rich alkaloids that can deter herbivores, we expect any benefits under CO_2 to be highly dependent on the nutrient status of the soil (see also Cheplick et al., 1989; and nitrogen section later) and on whether elevated CO_2 intensifies herbivore pressure. Finally, for DSE, the one publication in our meta-analysis (several fungal species on Scot's pine, Alberton et al., 2010) suggests that this group will not affect plant response to CO_2, but more data are clearly needed.

Drought—Our meta-analysis showed that drought uniformly decreased plant biomass and the presence of any type of fungal symbiont significantly increased plant growth under drought, ameliorating the negative effects of this global change factor. Evidence from the natural distributions of fungal symbionts suggests that fungi may commonly increase plant tolerance to drought in natural ecosystems. For instance, EF frequency was higher in natural plant populations that experience frequent drought relative to populations in mesic areas (Lewis et al., 1997; Leyronas and Raynal, 2001). Likewise, the abundance of AMF is often inversely correlated with soil moisture (e.g., Hartnett and Wilson, 1999), suggesting that AMF benefit plants under drought. Moreover, DSE often occur in arid or semiarid ecosystems where they may provide drought tolerance to their hosts (Porras-Alfaro et al., 2008). Results from these natural patterns, combined with the experiments reviewed here suggest that both above- and belowground fungal symbionts may become more prevalent in ecosystems under the increased drought frequency predicted by climate change models.

Nitrogen deposition—Nitrogen fertilization increased plant growth, but generally decreased the benefit of symbionts in our meta-analysis. None of the symbionts we tested increased plant growth under N fertilization, and ECM and AMF actually decreased plant growth under high nitrogen. Similarly, a recent meta-analysis showed that N fertilization decreased plant growth relative to unfertilized plants when mycorrhizas were present, indicating this pattern may be quite general for mycorrhizal symbionts (Hoeksema et al., 2010). The direct effects of N deposition on the biomass of mycorrhizal fungi are well characterized. On average, N addition decreases AMF and ECM fungal biomass belowground by ~15% (Brandrud and Timmermann, 1998; Wallenda and Kottke, 1998; Nilsson and Wallander, 2003; Treseder, 2004). The mechanism driving these declines is likely that plants reduce investment in their nutritional fungal symbionts when plants can acquire N directly from soils (Johnson et al., 1997). However, this exact pattern of this response may depend on the overall level of nutrient limitation in the system. In very nutrient-poor systems such as the arctic tundra, N addition can actually increase ECM biomass, presumably by alleviating N limitation of the fungus itself (Clemmensen et al., 2006). In less nutrient-limited systems, even small increases in N may result in a shift from fungal mutualism to parasitism or abandonment of the fungus by the plant (Johnson et al., 2010). Because the general response for mycorrhizal symbioses seems to be a decrease in fungal biomass and increase in plant biomass under N fertilization, these symbioses may be degraded under future N deposition scenarios (see also Kiers et al., 2006).

In contrast to mycorrhizal symbioses, the response of EF to N is often context dependent, which may explain why EF did not show a net effect on the plant response to N fertilization in our meta-analysis. High levels of background soil N appear to confer more benefits of the endophyte to plants (possibly due to greater N-rich alkaloid production), while low levels of soil N tend to decrease the benefits of symbiosis (possibly due to the costs of alkaloid production) (e.g., Cheplick et al., 1989). Therefore, we predict that N deposition should increase the beneficial effects of EF if it increases alkaloid production or otherwise reduces the cost to the plant of hosting the endophyte. Unfortunately, too few data on DSE exist to make firm predictions about the effects of N deposition on these plant symbionts. However, some data suggest that the form of N (inorganic vs. organic) may affect DSE–plant symbioses (Newsham, 2010), although controlled experimental tests of this hypothesis are lacking.

Warming—Warming had little categorical effect on plant biomass overall, although plant biomass was enhanced for plants associated with DSE. Warming increases organismal metabolism (for both plants and fungi), often with correlated increases in growth. In fungal symbioses, an increase in metabolism can also result in higher rates of nutrient transfer to and C transfer from the plant host (Hawkes et al., 2008). All fungal symbionts are expected to increase metabolism in response to predicted levels of warming. Belowground symbionts, in particular, are expected to provide a larger net benefit to their hosts under warmer climates, as they have the potential to transfer more nutrients to their hosts. A long-term warming manipulation showed that ECM biomass and sequence abundance increased over time relative to control plots (Kirschbaum, 2000). However, these trends may be confounded by shifts in plant composition to an ECM dominated system or by temperature-induced changes in nutrient availability (Clemmensen et al., 2006; Deslippe et al., 2012). In other systems, ECM biomass decreased with warming (Chapin et al., 1995), so this response is not uniform across ecosystems, and more data are needed to identify the conditions under which ECM (as well as DSE and EF) will increase vs. decline under warming. For studies of AMF analyzed here, we did not find a significant overall modification of plant response to temperature. However, in nature, warming is often concurrent with decreases in soil moisture, which was not allowed to vary with warming in the studies in our meta-analysis. In natural systems, interactions between warming and drying may ultimately determine fungal symbiont responses (see next section). Since all of the symbionts we examined can provide increased drought avoidance in their plant hosts, they may be expected to increase plant biomass if warming creates drier conditions. More studies, including those that directly examine interactions among global change factors, should allow generalizable trends to be established for these other fungal symbiont groups.

Multiple global change factors—Global change will result in significant shifts in climate, N deposition, and atmospheric CO_2 concentrations simultaneously. When multiple global change factors are simultaneously manipulated, the results are often unpredictable (Allison and Treseder, 2008; Frey et al., 2008; Dieleman et al., 2012). For example, in a study manipulating moisture, temperature, and CO_2 concentration, Brosi et al. (2011) found that EF biomass responded the most to elevated CO_2; a result which is unanticipated from the findings in our meta-analysis. In the arctic, Clemmensen et al. (2006) discovered that warming and N fertilization independently and synergistically increased ECM biomass belowground. Predicting plant response to multiple global change factors will depend on

whether these drivers act additively, synergistically, or antagonistically. For example, if elevated CO_2 reduces any direct benefits of N deposition to plants, plant–fungal symbioses may become beneficial under the combination of high CO_2 and high N. Similarly, if climates become warmer and drier, plant benefits from all symbionts may increase. These interactions are difficult to predict as few studies have simultaneously examined plant–fungal symbioses in response to multiple global change factors.

Multiple fungal symbionts—Pairwise studies may underestimate the effects of fungal symbionts on hosts, if multiple symbionts interact synergistically to promote plant performance. Alternatively, pairwise studies could overestimate effects if there are fungal antagonisms that reduce the net benefit to hosts under conditions of global change. To date, only three studies have explicitly examined interactions between multiple fungal symbionts under global change scenarios. Lukac et al. (2003) found that increased CO_2 concentrations resulted in a 41–64% increase in plant root biomass for three species of *Populus*. However, this increase was positively correlated with both ECM and AMF colonization rates of roots for only one species (30% increase in AMF and 100% increase in ECM root colonization rates). For another species of *Populus*, AMF colonization increased by 37% with increased CO_2, while ECM did not increase, and the third species showed no increase in AMF or ECM colonization despite an increase in plant root biomass. This indicates that interactions between fungal symbionts under a changed climate may be plant-species-specific and nonadditive. The fungal symbionts were not directly manipulated; thus, it is not possible to assess whether they were directly responsible for the impact of elevated CO_2 on plant performance. Two other studies manipulating multiple symbionts, however, showed a lack of interaction between symbionts. In a greenhouse study manipulating CO_2, Chen et al. (2007) showed that AMF colonization did not differ between endophyte-colonized and endophyte-free tall fescue grass (*Lolium arundinaceum*) and, further, that CO_2 levels had no effect on these relationships. Mack and Rudgers (2008) manipulated N levels in a greenhouse study and found no interactive effect of N enrichment on the relationship between AMF and EF presence in tall fescue. In addition, plant performance was not altered by simultaneous colonization by both symbionts, but rather matched that of plants with EF alone. However, increased N levels were associated with higher endophyte densities in leaf tissues of plants with endophytes, and these densities correlated negatively with AMF colonization of the roots, suggesting a possibility for nonadditive effects. Similarly, Buyer et al. (2011) reported EF antagonism against AMF, with reduced levels of biomarkers for AMF and lower levels of glomalin (an AMF protein important for soil-binding and C sequestration) in the soil, but this study did not manipulate global change factors (Buyer et al., 2011). An observational study on AMF and DSE suggested that these two groups may respond to different suites of environmental conditions: While several conditions were correlated with AMF colonization (including soil P, rainfall, and sunlight hours), only relative humidity and sunlight hours correlated with DSE colonization (Lingfei et al., 2005). One additional observational study suggested interactive effects of fungal symbionts under changing environments. Lodge (1989) showed that AMF was most abundant in *Populus* and *Salix* at extremes of soil moisture (flooded or very dry), while ECM was most abundant in well-drained moist soils. This result could suggest competition between the two fungal symbionts, with AMF dominating under future climate scenarios.

The lack of research addressing multifungus interactions in plants is obvious from this review and others (e.g., Compant et al., 2010, Larimer et al., 2010). Few studies have examined multisymbiont interactions in general, let alone within the context of a changing environment. The published work to date shows contradictory patterns and suggests that the outcomes of multispecies plant–symbiont interactions may be highly species specific (i.e., Liu et al., 2011, Larimer et al., 2012). In at least in a few cases, fungal symbionts may not interact at all or may interact antagonistically, but have no net negative impact on their shared plant host (Chen et al., 2007; Mack and Rudgers, 2008). However, a meta-analysis by Larimer et al. (2010) found that in general, AMF and leaf endophytes have positive interactions within the same plant, while AMF and N-fixers have negative interactions, especially when N and P are limiting. An overarching framework for predicting when and in what direction interactions among symbionts will affect a shared host (or affect each other) would be useful for developing more refined predictions.

Larimer et al. (2012) offer the best suggestions thus far for making generalizations on multisymbiont interactions in plants. They proposed that the predictability of interactive effects will depend on the C cost of each symbiosis in each environment. For example, most symbionts act as carbon sinks. If we apply this framework to global change scenarios, we could assume that some global change factors alleviate C stress through increases in CO_2 and temperature, and these changes would facilitate positive interactions among symbionts (e.g., Chen et al., 2007), which feed back to have positive effects on plant growth. Alternatively, if global change creates more C stress, as is the case in N deposition scenarios, then competition between symbionts would be expected to become stronger and should result in suppression of one fungal partner or overall decreases in plant growth due to a switch to parasitic interactions. There is an obvious need for a better predictive framework for multisymbiont interactions, especially in a changing climate, as well as a need for many more experiments before strong generalizations can be made.

Future directions—Current understanding of how fungal symbionts influence plant response to global change could be enhanced in several ways. First, standardized methodologies, data collection strategies, and repositories could be employed to study the response of plants across ecosystems, global change factors and fungal symbionts. Second, the long-term effects of global change on plant–fungal symbioses are largely unknown. If the short-term trends that we described here are not consistent over long periods, then predictions for plant response to global change may be misleading. Third, the distributions of all fungal symbionts are not well described (see Opik et al., 2010, and Kivlin et al., 2011). A key step in applying the results of the current meta-analysis to natural systems will be to determine when fungal symbionts and plants co-occur, if these relationships are stable, and how these interactions may shift under future global change scenarios. For example, while most fungal symbionts seem to be widespread, phenological and habitat mismatches between fungal symbionts and their plant hosts may be common in future climates (e.g., Tylianakis et al., 2008; Pritchard, 2011). If climate affects plant and symbiont distributions in different ways, climate change could lead to symbiont losses, plant–fungal mismatches, and novel interactions with

no historical analogs (van der Putten, 2012). Finally, while here we considered interactions between fungal symbionts and plants, other organisms such as fungal plant pathogens and bacteria can also influence the response of plants to global change (Garrett et al., 2006; Tylianakis et al., 2008). Therefore, a whole plant microbiome approach may be necessary to determine how plants will respond to global change (sensu Porras-Alfaro and Bayman, 2011).

***Conclusions*—**Plants respond directly to global change, but plant response can also be influenced by interactions with other organisms. The interactions between fungal symbionts and plants in response to global change are crucial to understand, as plant–fungal symbioses can affect multiple aspects of natural systems; from individuals, to populations, communities and whole ecosystems. In our meta-analysis, plant responses to drought, N deposition and warming, significantly differed when symbionts were present. Moreover, different fungal symbionts differentially affected plant response and symbiont-mediated plant response differed between global change factors. Therefore, considering plant–fungal symbioses is critical to predicting ecosystem response to global change.

LITERATURE CITED

ALBERTON, O., T. KUYPER, AND A. GORISSEN. 2005. Taking mycocentrism seriously: Mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist* 167: 859–868.

ALBERTON, O., T. KUYPER, AND R. SUMMERBELL. 2010. Dark septate root endophytic fungi increase growth of Scots pine seedlings under elevated CO_2 through enhanced nitrogen use efficiency. *Plant and Soil* 328: 459–470.

ALLISON, S. D., AND K. K. TRESEDER. 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology* 14: 2898–2909.

ARMAS, C., R. ORDIALES, AND F. I. PUGNAIRE. 2004. Measuring plant interactions: A new comparative index. *Ecology* 85: 2682–2686.

AUGÉ, R. M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.

BARROW, J. R. 2003. Atypical morphology of dark septate fungal root endophytes of *Bouteloua* in arid southwestern USA rangelands. *Mycorrhiza* 13: 239–247.

BAZELY, D. R., J. P. BALL, M. VICARI, A. J. TANENTZAP, M. BÉRENGER, T. RAKOCEVIC, AND S. KOH. 2007. Broad-scale geographic patterns in the distribution of vertically-transmitted, asexual endophytes in four naturally-occurring grasses in Sweden. *Ecography* 30: 367–374.

BOOTH, M. G., AND J. D. HOEKSEMA. 2009. Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* 91: 2294–2302.

BORENSTEIN, M., L. HEDGES, J. HIGGINS, AND J. ROTHSTEIN. 2009. Introduction to meta-analysis. Wiley, West Sussex, UK.

BRANDRUD, T. E., AND V. TIMMERMANN. 1998. Ectomycorrhizal fungi in the NITREX site at Gårdsjön, Sweden; below and above-ground responses to experimentally-changed nitrogen inputs 1990–1995. *Forest Ecology and Management* 101: 207–214.

BROSI, G. B., R. L. MCCULLEY, L. P. BUSH, J. A. NELSON, A. T. CLASSEN, AND R. J. NORBY. 2011. Effects of multiple climate change factors on the tall fescue–fungal endophyte symbiosis: Infection frequency and tissue chemistry. *New Phytologist* 189: 797–805.

BUNN, R., Y. LEKBERG, AND C. ZABINSKI. 2009. Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants. *Ecology* 90: 1378–1388.

BUYER, J., D. ZUBERER, K. NICHOLS, AND A. FRANZLUEBBERS. 2011. Soil microbial community function, structure, and glomalin in response to tall fescue endophyte infection. *Plant and Soil* 339: 401–412.

CHALOT, M., AND A. BRUN. 1998. Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews* 22: 21–44.

CHAPELA, I. H., L. J. OSHER, T. R. HORTON, AND M. R. HENN. 2001. Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. *Soil Biology & Biochemistry* 33: 1733–1740.

CHAPIN, F. S., III, G. R. SHAVER, A. E. GIBLIN, K. J. NADELHOFFER, AND J. A. LAUNDRE. 1995. Responses of arctic tundra to experimental and observed changed in climate. *Ecology* 76: 694–711.

CHEN, X., C. TU, M. G. BURTON, D. M. WATSON, K. O. BURKEY, AND S. HU. 2007. Plant nitrogen acquisition and interactions under elevated carbon dioxide: Impact of endophytes and mycorrhizae. *Global Change Biology* 13: 1238–1249.

CHEPLICK, G. P., K. CLAY, AND S. MARKS. 1989. Interactions between infection by endophytic fungi and nutrient limitation in the grasses *Lolium perenne* and *Festuca arundinacea*. *New Phytologist* 111: 89–97.

CHEPLICK, G. P., A. PERERA, AND K. KOULOURIS. 2000. Effect of drought on the growth of *Lolium perenne* genotypes with and without fungal endophytes. *Functional Ecology* 14: 657–667.

CHOI, W.-J., S. X. CHANG, H. L. ALLEN, D. L. KELTING, AND H.-M. RO. 2005. Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. *Forest Ecology and Management* 213: 90–101.

CHU-CHOU, M., B. GUO, Z. Q. AN, J. W. HENDRIX, R. S. FERRISS, M. R. SIEGEL, C. T. DOUGHERTY, AND P. B. BURRUS. 1992. Suppression of mycorrhizal fungi in fescue by the *Acremonium coenophialum* endophyte. *Soil Biology & Biochemistry* 24: 633–637.

CIAIS, P., M. REICHSTEIN, N. VIOVY, A. GRANIER, J. OGEE, V. ALLARD, M. AUBINET, ET AL. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437: 529–533.

CLAY, K., AND J. HOLAH. 1999. Fungal endophyte symbiosis and plant diversity in successional fields. *Science* 285: 1742–1744.

CLEMMENSEN, K. E., A. MICHELSEN, S. JONASSON, AND G. R. SHAVER. 2006. Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. *New Phytologist* 171: 391–404.

COMPANT, S., M. G. A. VAN DER HEIJDEN, AND A. SESSITSCH. 2010. Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiology Ecology* 73: 197–214.

CORKIDI, L., D. L. ROWLAND, N. C. JOHNSON, AND E. B. ALLEN. 2002. Nitrogen fertilization alters the functioning of arbuscular mycorrhizas at two semiarid grasslands. *Plant and Soil* 240: 299–310.

CURTIS, P. S., AND X. WANG. 1998. A meta-analysis of elevated CO2; effects on woody plant mass, form, and physiology. *Oecologia* 113: 299–313.

DESLIPPE, J. R., M. HARTMANN, S. W. SIMARD, AND W. W. MOHN. 2012. Long-term warming alters the composition of Arctic soil microbial communities. *FEMS Microbiology Ecology* 82: 303–315.

DIELEMAN, W. I. J., S. VICCA, F. A. DIJKSTRA, F. HAGEDORN, M. J. HOVENDEN, K. S. LARSEN, ET AL. 2012. Simple additive effects are rare: A quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. *Global Change Biology* 18: 2681–2693.

DONOSO, E. P., R. O. BUSTAMANTE, M. CARU, AND H. M. NIEMEYER. 2008. Water deficit as a driver of the mutualistic relationship between the fungus *Trichoderma harzianum* and two wheat genotypes. *Applied and Environmental Microbiology* 74: 1412–1417.

DRIGO, B., A. S. PIJL, H. DUYTS, A. M. KIELAK, H. A. GAMPER, M. J. HOUTEKAMER, H. T. S. BOSCHKER, ET AL. 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO2. *Proceedings of the National Academy of Sciences, USA* 107: 10938–10942.

EGERTON-WARBURTON, L. M., J. I. QUEREJETA, AND M. F. ALLEN. 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *Journal of Experimental Botany* 58: 1473–1483.

ELMI, A. A., AND C. P. WEST. 1995. Endophyte infection effects on stomatal conductance, osmostic adjustment and drought. *New Phytologist* 131: 61–67.

FLANAGAN, L. B., AND B. G. JOHNSON. 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130: 237–253.

FRANZLUEBBERS, A. J., AND N. S. HILL. 2005. Soil carbon, nitrogen, and ergot alkaloids with short- and long-term exposure to endophyte-infected and endophyte-free tall fescue. *Soil Science Society of America Journal* 69: 404–412.

FRANZLUEBBERS, A. J., N. NAZIH, J. A. STUEDEMANN, J. J. FUHRMANN, H. H. SCHOMBERG, AND P. G. HARTEL. 1999. Soil carbon and nitrogen pools under low- and high-endophyte-infected tall fescue. *Soil Science Society of America Journal* 63: 1687–1694.

FREY, S. D., R. DRIJBER, H. SMITH, AND J. MELILLO. 2008. Microbial biomass, functional capacity, and community structure after 12 years of soil warming. *Soil Biology & Biochemistry* 40: 2904–2907.

GALLOWAY, J. N., F. J. DENTENER, D. G. CAPONE, E. W. BOYER, R. W. HOWARTH, S. P. SEITZINGER, G. P. ASNER, ET AL. 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70: 153–226.

GARCIA, M. O., T. OVASAPYAN, M. GREAS, AND K. K. TRESEDER. 2008. Mycorrhizal dynamics under elevated CO_2 and nitrogen fertilization in a warm temperate forest. *Plant and Soil* 303: 301–310.

GARRETT, K. A., S. P. DENDY, E. E. FRANK, M. N. ROUSE, AND S. E. TRAVERS. 2006. Climate change effects on plant disease: Genomes to ecosystems. *Annual Review of Phytopathology* 44: 489–509.

GEHRING, C. A., AND T. G. WHITHAM. 1994. Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. *Trends in Ecology & Evolution* 9: 251–255.

GIAUQUE, H., AND C. V. HAWKES. 2013. Climate affects symbiotic fungal endophyte diversity and performance. *American Journal of Botany* 100: 1435–1444.

GRANATH, G., M. VICARI, D. R. BAZELY, J. P. BALL, A. PUENTES, AND T. RAKOCEVIC. 2007. Variation in the abundance of fungal endophytes in fescue grasses along altitudinal and grazing gradients. *Ecography* 30: 422–430.

GUREVITCH, J., AND L. HEDGES. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80: 1142–1149.

HARTNETT, D. C., AND G. W. T. WILSON. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187–1195.

HASELWANDTER, K., AND D. J. READ. 1982. The significance of a root–fungus association in two *Carex* species of high-alpine plant communities. *Oecologia* 53: 352–354.

HAWKES, C. V., J. BELNAP, C. D'ANTONIO, AND M. K. FIRESTONE. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil* 281: 369–380.

HAWKES, C. V., I. P. HARTLEY, P. INESON, AND A. H. FITTER. 2008. Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. *Global Change Biology* 14: 1181–1190.

HAWKES, C. V., AND J. J. SULLIVAN. 2001. The impact of herbivory on plants in different resource conditions: A meta-analysis. *Ecology* 82: 2045–2058.

HEDGES, L. V., J. GUREVITCH, AND P. S. CURTIS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80: 1150–1156.

HERRERA, J., H. H. KHIDIR, D. M. EUDY, A. PORRAS-ALFARO, D. O. NATVIG, AND R. L. SINSABAUGH. 2010. Varition in root-associated fungal endophytes: Some taxonomic consistency at a transcontinental scale. *Mycologia* 102: 1012–1026.

HOEKSEMA, J. D., V. B. CHAUDHARY, C. A. GEHRING, N. C. JOHNSON, J. KARST, R. T. KOIDE, A. PRINGLE, ET AL. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13: 394–407.

HOEPPNER, S. S., AND J. S. DUKES. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology* 18: 1754–1768.

HUANG, Z., Z. R. ZOU, C. X. HE, Z. Q. HE, Z. B. ZHANG, AND J. M. LI. 2011. Physiological and photosynthetic responses of melon (*Cucumis melo* L.) seedlings to three *Glomus* species under water deficit. *Plant and Soil* 339: 391–399.

JAKOBSEN, I., AND L. ROSENDAHL. 1990. Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. *New Phytologist* 115: 77–83.

JOHNSON, N. C., J. H. GRAHAM, AND F. A. SMITH. 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist* 135: 575–585.

JOHNSON, N. C., G. W. T. WILSON, M. A. BOWKER, J. A. WILSON, AND R. M. MILLER. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences, USA* 107: 2093–2098.

JONSSON, L. M., M. C. NILSSON, D. A. WARDLE, AND O. ZACKRISSON. 2001. Context dependent effects of ectomycorrhizal species richness on tree seedling productivity. *Oikos* 93: 353–364.

JU, H. J., N. S. HILL, T. ABBOTT, AND K. T. INGRAM. 2006. Temperature influences on endophyte growth in tall fescue. *Crop Science* 46: 404–412.

JUMPPONEN, A., K. G. MATTSON, AND J. M. TRAPPE. 1998. Mycorrhizal functioning of *Phialocephala fortinii* with *Pinus contorta* on glacier forefront soil: Interactions with soil nitrogen and organic matter. *Mycorrhiza* 7: 261–265.

JUMPPONEN, A., AND J. M. TRAPPE. 1998. Dark septate endophytes: A review of facultative biotrophic root-colonizing fungi. *New Phytologist* 140: 295–310.

KANNADAN, S., AND J. A. RUDGERS. 2008. Endophyte symbiosis benefits a rare grass under low water availability. *Functional Ecology* 22: 706–713.

KARDOL, P., T. M. BEZEMER, AND W. H. D. PUTTEN. 2006. Temporal variation in plant–soil feedback controls succession. *Ecology Letters* 9: 1080–1088.

KIERS, E. T., R. A. ROUSSEAU, AND R. F. DENISON. 2006. Measured sanctions: Legume hosts detect quantitative variation in rhizobium cooperation and punish accordingly. *Evolutionary Ecology Research* 8: 1077–1086.

KIRSCHBAUM, M. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48: 21–51.

KIVLIN, S. N., C. V. HAWKES, AND K. K. TRESEDER. 2011. Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry* 43: 2294–2303.

LAMARQUE, J. F., J. T. KIEHL, G. P. BRASSEUR, T. BUTLER, P. CAMERON-SMITH, W. D. COLLINS, W. J. COLLINS, ET AL. 2005. Assessing future nitrogen deposition and carbon cycle feedback using a multimodel approach: Analysis of nitrogen deposition. *Journal of Geophysical Research: Atmospheres* 110

LARIMER, A. L., J. D. BEVER, AND K. CLAY. 2010. The interactive effects of plant microbial symbionts: A review and meta-analysis. *Symbiosis* 51: 139–148.

LARIMER, A. L., J. D. BEVER, AND K. CLAY. 2012. Consequences of simultaneous interactions of fungal endophytes and arbuscular mycorrhizal fungi with a shared host grass. *Oikos* 121: 2090–2096.

LEBAUER, D. S., AND K. K. TRESEDER. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally. *Ecology* 89: 371–379.

LEMONS, A., K. CLAY, AND J. A. RUDGERS. 2005. Connecting plant–microbial interactions above and belowground: A fungal endophyte affects decomposition. *Oecologia* 145: 595–604.

LEUCHTMANN, A. 1992. Systematics, distribution, and host specificity of grass endophytes. *Natural Toxins* 1: 150–162.

LEWIS, G. C., C. RAVEL, W. NAFFAA, C. ASTIER, AND G. CHARMET. 1997. Occurrence of *Acremonium* endophytes in wild populations of *Lolium* spp. in European countries and a relationship between level of infection and climate in France. *Annals of Applied Biology* 130: 227–238.

LEYRONAS, C., AND G. RAYNAL. 2001. Presence of *Neotyphodium*-like endophytes in European grasses. *Annals of Applied Biology* 139: 119–127.

LIN, D., J. XIA, AND S. WAN. 2010. Climate warming and biomass accumulation of terrestrial plants: A meta-analysis. *New Phytologist* 188: 187–198.

LINGFEI, L., Y. ANNA, AND Z. ZHIWEI. 2005. Seasonality of arbuscular mycorrhizal symbiosis and dark septate endophytes in a grassland site in southwest China. *FEMS Microbiology Ecology* 54: 367–373.

LIU, Q. H., A. J. PARSONS, H. XUE, K. FRASER, G. D. RYAN, J. A. NEWMAN, AND S. RASMUSSEN. 2011. Competition between foliar *Neotyphodium lolii* endophytes and mycorrhizal *Glomus* spp. fungi in *Lolium perenne* depends on resource supply and host carbohydrate content. *Functional Ecology* 25: 910–920.

LODGE, D. 1989. The influence of soil moisture and flooding on formation of VA-endo- and ectomycorrhizae in *Populus* and *Salix*. *Plant and Soil* 117: 243–253.

LUKAC, M., C. CALFAPIETRA, AND D. L. GODBOLD. 2003. Production, turnover and mycorrhizal colonization of root systems of three *Populus* species grown under elevated CO_2 (POPFACE). *Global Change Biology* 9: 838–848.

MACK, K. M. L., AND J. A. RUDGERS. 2008. Balancing multiple mutualists: Asymmetric interactions among plants, arbuscular mycorrhizal fungi, and fungal endophytes. *Oikos* 117: 310–320.

MALINOWSKI, D. P., AND D. P. BELESKY. 1999. *Neotyphodium coenophialum*–endophyte infection affects the ability of tall fescue to use sparingly available phosphorus. *Journal of Plant Nutrition* 22: 835–853.

MANDYAM, K., C. FOX, AND A. JUMPPONEN. 2012. Septate endophyte colonization and host responses of grasses and forbs native to a tallgrass prairie. *Mycorrhiza* 22: 109–119.

MANDYAM, K., AND A. JUMPPONEN. 2008. Seasonal and temporal dynamics of arbuscular mycorrhizal and dark septate endophytic fungi in a tallgrass prairie ecosystem are minimally affected by nitrogen enrichment. *Mycorrhiza* 18: 145–155.

MARKS, S., AND K. CLAY. 1990. Effects of CO_2 enrichment, nutrient addition, and fungal endophyte-infection on the growth of two grasses. *Oecologia* 84: 207–214.

MELILLO, J., P. STEUDLER, J. ABER, K. NEWKIRK, H. LUX, F. BOWLES, C. CATRICALA, ET AL. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298: 2173–2176.

MÜLLER, J. 2003. Artificial infection by endophytes affects growth and mycorrhizal colonisation of *Lolium perenne*. *Functional Plant Biology* 30: 419–424.

NEWSHAM, K. K. 2010. A meta-analysis of plant responses to dark septate root endophytes. *New Phytologist* 190: 783–793.

NILSSON, L., AND H. WALLANDER. 2003. Production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. *New Phytologist* 158: 409–416.

NOVAS, M. V., L. J. IANNONE, A. M. GODEAS, AND D. CABRAL. 2009. Positive association between mycorrhiza and foliar endophytes in *Poa bonariensis*, a native grass. *Mycological Progress* 8: 75–81.

OMACINI, M., T. EGGERS, M. BONKOWSKI, A. C. GANGE, AND T. H. JONES. 2006. Leaf endophytes affect mycorrhizal status and growth of co-infected and neighboring plants. *Functional Ecology* 20: 226–232.

ÖPIK, M., A. VANATOA, E. VANATOA, M. MOORA, J. DAVISON, J. M. KALWIJ, Ü. REIER, AND M. ZOBEL. 2010. The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist* 188: 223–241.

PORRAS-ALFARO, A., AND P. BAYMAN. 2011. Hidden fungi, emergent properties: Endophytes and microbiomes. *Annual Review of Phytopathology* 49: 291–315.

PORRAS-ALFARO, A., J. HERRERA, R. L. SINSABAUGH, K. J. ODENBACH, T. LOWREY, AND D. O. NATVIG. 2008. Novel root fungal consortium associated with a dominant desert grass. *Applied and Environmental Microbiology* 74: 2805–2813.

PRITCHARD, S. G. 2011. Soil organisms and global climate change. *Plant Pathology* 60: 82–99.

QUEREJETA, J. I., L. M. EGERTON-WARBURTON, AND M. F. ALLEN. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. *Soil Biology & Biochemistry* 39: 409–417.

READ, D., AND K. HASELWANDTER. 1981. Observations on the mycorrhizal status of some alpine plant communities. *The New Phytologist* 88: 341–352.

REDMAN, R. S., K. B. SHEEHAN, R. G. STOUT, R. J. RODRIGUEZ, AND J. M. HENSON. 2002. Thermotolerance generated by plant/fungal symbiosis. *Science* 298: 1581. doi:10.1126/science.1078055

REININGER, V., C. R. GRUNIG, AND T. N. SIEBER. 2012. Host species and strain combination determine growth reduction of spruce and birch seedlings colonized by root-associated dark septate endophytes. *Environmental Microbiology* 14: 1064–1076.

REININGER, V., AND T. N. SIEBER. 2012. Mycorrhiza reduces adverse effects of dark septate endophytes (DSE) on growth of conifers. *PLoS One* 7: e42865.

RINALDI, A. C., O. COMANDINI, AND T. W. KUYPER. 2008. Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fungal Diversity* 33: 1–45.

RODRIGUEZ, R. J., J. HENSON, E. VAN VOLKENBURGH, M. HOY, L. WRIGHT, F. BECKWITH, Y.-O. KIM, AND R. S. REDMAN. 2008. Stress tolerance in plants via habitat-adapted symbiosis. *ISME Journal* 2: 404–416.

RODRIGUEZ, R. J., J. F. WHITE JR., A. E. ARNOLD, AND R. S. REDMAN. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* 182: 314–330.

ROHATGI, A. 2011. WebPlotDigitizer, available at http://arohatgi.info/WebPlotDigitizer/. [accessed 15 September 2012].

RUDGERS, J. A., M. E. AFKHAMI, M. A. RUA, A. J. DAVITT, S. HAMMER, AND V. M. HUGUET. 2009. A fungus among us: Broad patterns of endophyte distribution in the grasses. *Ecology* 90: 1531–1539.

RUDGERS, J. A., AND K. CLAY. 2008. An invasive plant–fungal mutualism reduces arthropod diversity. *Ecology Letters* 11: 831–840.

RUDGERS, J. A., J. HOLAH, S. P. ORR, AND K. CLAY. 2007. Forest succession suppressed by an introduced plant–fungal symbiosis. *Ecology* 88: 18–25.

RUDGERS, J. A., J. M. KOSLOW, AND K. CLAY. 2004. Endophytic fungi alter relationships between diversity and ecosystem properties. *Ecology Letters* 7: 42–51.

RUDGERS, J. A., T. E. X. MILLER, S. M. ZIEGLER, AND K. D. CRAVEN. 2012. There are many ways to be a mutualist: Endophyte fungus reduces plant survival but increases population growth. *Ecology* 93: 565–574.

RUDGERS, J. A., AND A. L. SWAFFORD. 2009. Benefits of a fungal endophyte in *Elymus virginicus* decline under drought stress. *Basic and Applied Ecology* 10: 43–51.

SAIKKONEN, K., P. LEHTONEN, M. HELANDER, J. KORICHEVA, AND S. H. FAETH. 2006. Model systems in ecology: Dissecting the endophyte–grass literature. *Trends in Plant Science* 11: 428–433.

SÁNCHEZ-BLANCO, M. J., T. FERRÁNDEZ, M. A. MORALES, A. MORTE, AND J. J. ALARCÓN. 2004. Variations in water status, gas exchange, and growth in Rosmarinus officinalis plants infected with Glomus deserticola under drought conditions. *Journal of Plant Physiology* 161: 675–682.

SCHARDL, C., A. LEUCHTMANN, AND M. J. SPIERING. 2004. Symbioses of grasses with seedbornce fungal endophytes. *Annual Review of Plant Biology* 55: 315–340.

SCHIMEL, D., I. ENTING, M. HEIMANN, T. WRIGLEY, D. RAYNAUD, D. ALVES, U. SIEGENTHALER, ET AL. 1995. CO_2 and the carbon cycle. *In* Climate change 1994: Radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios, 39–71. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

SIKES, B. A., K. COTTENIE, AND J. N. KLIRONOMOS. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* 97: 1274–1280.

SIKES, B. A., J. R. POWELL, AND M. C. RILLIG. 2010. Deciphering the relative contributions of multiple functions within plant–microbe symbioses. *Ecology* 91: 1591–1597.

SIMARD, S., M. JONES, D. DURALL, E. VAN DER HEIJDEN, AND I. SANDERS. 2002. Carbon and nutrient fluxes within and between mycorrhizal plants. *Mycorrhizal Ecology* 157: 34–74.

SMITH, S. E., AND D. J. READ. 2008. Mycorrhizal symbiosis, 3rd ed. Academic Press, New York, New York, USA.

SOLOMAN, S., D. QIN, M. MANNING, Z. CHEN, M. MARQUIS, K. B. AVERYT, M. TIGNOR, AND H. L. MILLER. 2007. Climate Change 2007: The physical science basis. Cambridge University Press, Cambridge, UK.

STOTT, P. A., N. P. GILLETT, G. C. HEGERL, D. J. KAROLY, D. A. STONE, X. ZHANG, AND F. ZWIERS. 2010. Detection and attribution of climate

change: A regional perspective. *Wiley Interdisciplinary Reviews: Climate Change* 1: 192–211.

TILMAN, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

TRESEDER, K., AND M. ALLEN. 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: A model and field test. *New Phytologist* 155: 507–515.

TRESEDER, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytologist* 164: 347–355.

TYLIANAKIS, J. M., R. K. DIDHAM, J. BASCOMPTE, AND D. A. WARDLE. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351–1363.

USUKI, F., AND K. NARISAWA. 2007. A mutualistic symbiosis between a dark septate endophytic fungus, *Heteroconium chaetospira*, and a nonmycorrhizal plant, Chinese cabbage. *Mycologia* 99: 175–184.

VAN DER HEIJDEN, M. G. A., R. D. BARDGETT, AND N. M. VAN STRAALEN. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11: 296–310.

VAN DER HEIJDEN, M. G. A., T. BOLLER, A. WIEMKEN, AND I. R. SANDERS. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79: 2082–2091.

VAN DER PUTTEN, W. H. 2012. Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution and Systematics* 43: 365–383.

VAN DER PUTTEN, W. H., M. MACEL, AND M. E. VISSER. 2010. Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 365: 2025–2034.

VAN DER PUTTEN, W. H., C. VAN DIJK, AND B. A. M. PETERS. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362: 53–56.

WALLENDA, T., AND I. KOTTKE. 1998. Nitrogen deposition and ectomycorrhizas. *New Phytologist* 139: 169–187.

WANG, B., AND Y. L. QUI. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16: 299–363.

WORCHEL, E. R., H. E. GIAUQUE, AND S. N. KIVLIN. 2013. Fungal symbionts alter plant drought response. *Microbial Ecology* 65: 671-678.