Interactions among mycorrhizae, atmospheric CO₂ and soil N impact plant community composition

Nancy Collins Johnson,* Julie Wolf and George W. Koch
Departments of Environmental Sciences, Biological Sciences, and the Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86001-5694, USA
*Correspondence: E-mail: nancy.johnson@nau.edu

Abstract
We examined plant community responses to interactions between arbuscular mycorrhizal (AM) fungi and availability of atmospheric CO₂ and soil N. Communities of 14 plant species were grown in mesocosms containing living or killed AM fungal inoculum, ambient or elevated atmospheric CO₂ and low or enriched soil N. After one growing season, significantly different plant communities existed in the different treatments. Plant species richness was lowest in +N mesocosms and highest in +AM + CO₂ mesocosms. At ambient CO₂, AM fungi reduced richness but at elevated CO₂ they increased it. This was caused by changes in mortality rates of several C₃ forbs and may suggest that CO₂ enrichment ameliorates the carbon cost of some AM symbioses. Soil moisture was higher in +CO₂ mesocosms but +AM counteracted this effect. These results suggest that AM symbioses may be important mediators of plant community responses to anthropogenic CO₂ and N enrichment.

Keywords
Arbuscular mycorrhizae, CO₂ enrichment, community composition, evapotranspiration, grassland, mesocosm, mycotrophy, nitrogen eutrophication.


INTRODUCTION
Biotic communities are expected to respond to anthropogenic enrichment of atmospheric carbon dioxide (CO₂) and soil nitrogen (N); however, complex interactions among ecosystem components generate uncertainty about the nature of these responses. Arbuscular mycorrhizae are ubiquitous fungus–plant symbioses that enhance uptake of soil nutrients and water, protect plants from pathogens, and stimulate photosynthesis through enhanced sink strength for carbon (Smith & Read 1997; Wright et al. 1998). These associations help structure plant communities because arbuscular mycorrhizal (AM) fungi improve the fitness and productivity of some plant species more than others (Grime et al. 1987; Hartnett & Wilson 1999; Klironomos et al. 2000). Altered mycorrhizal function is predicted to influence plant community responses to CO₂ enrichment because AM fungi are obligate biotrophs and generate a substantial carbon sink for their host plant (Diaz 1996; Sanders 1996; Miller et al. 2002). In plants that are dependent upon mycorrhizae, the AM carbon sink has been shown to facilitate increased biomass production under elevated CO₂ (Gavito et al. 2000; Jifton et al. 2002). Arbuscular mycorrhizae may also mediate plant community responses to anthropogenic N enrichment because the species composition and mutualistic function of AM fungal communities are impacted by N fertilization (Johnson 1993; Egerton-Warburton & Allen 2000; Corkidi et al. 2002). Understanding the interactions between CO₂ and N availability and mycorrhizal function will help us better predict the responses of plant communities to the anticipated global enrichment of these resources.

Plant taxa vary in their responses to atmospheric CO₂ enrichment and mycorrhizae. Plant photosynthetic physiology is often a good predictor of responsiveness to both atmospheric CO₂ enrichment and mycorrhizae. C₃ plants have been shown to benefit more from CO₂ enrichment (Poorter et al. 1996; Reich et al. 2001) and less from mycorrhizae (Hetrick et al. 1990; Wilson & Hartnett 1998) than C₄ plants. Among species of C₃ and C₄ prairie grasses, there is evidence for an inverse relationship between plant responsiveness to CO₂ enrichment and mycorrhizal dependency (Reyes et al. 2002). Legumes have been shown to respond both positively and negatively to CO₂ enrichment (Körner et al. 1996). Most legumes benefit from AM colonization (Wilson & Hartnett 1998); however, the genus Lupinus is a notable exception because it often does not
form AM associations (O’Dell & Trappe 1992). Reich et al. (2001) found that grouping plants according to photosynthetic physiology, growth form (grass or forb), and N-fixation capability is useful but not sufficient to understand plant and ecosystem responses to elevated CO2 and N availability.

Both CO2 enrichment and mycorrhizae can indirectly influence soil moisture via effects on stomatal conductance. Soil moisture can increase under elevated atmospheric CO2 because of the commonly observed reduction in stomatal conductance, particularly in C3 species (Field et al. 1995). The increased soil moisture generated by elevated CO2 has been shown to increase rates of microbial metabolism and nutrient cycling (Hungate et al. 1997). Stomatal conductance and transpiration rates are generally higher in AM compared to non-AM plants, in both mesic and drought conditions (Auge 2000). Increased N availability typically stimulates plant growth, stomatal conductance, and whole-plant water use (Hunsaker et al. 2000). Because elevated CO2, AM fungi, and N availability have contrasting effects on plant growth, water use, and soil moisture, the interactive effects of these factors may have unexpected effects on plant community structure.

Species and genera of AM fungi vary in their responses to elevated CO2 (Klironomos et al. 1998) and N enrichment (Eom et al. 1999; Egerton-Warburton & Allen 2000). Field studies have shown that spore abundances of certain species of AM fungi increase while others decrease with elevated CO2 (Wolf et al. 2003). Also, CO2 enrichment has been shown to increase the density of extraradical mycelium of AM fungi under some plant communities but not under others (Rillig & Allen 1999; Rillig et al. 2000; Wolf 2001). In soils that are not severely phosphorus limited, anthropogenic N enrichment typically reduces species richness and changes the community composition in favour of fast growing, highly competitive plant (Berendse et al. 1993) and AM fungal species (Egerton-Warburton & Allen 2000). Enrichment of atmospheric CO2 and soil N can act synergistically on communities of plants and soil organisms (Klironomos et al. 1997; Schenk et al. 1997). However, the impact of simultaneous enrichment of both atmospheric CO2 and soil N on mycorrhizal function has not been well studied (Egerton-Warburton & Allen 2001).

AM associations are so ubiquitous in terrestrial ecosystems that it is difficult to find an experimental system without them in which their role in structuring plant communities can be assessed. Mesocosms provide a viable method to manipulate AM fungi and quantify their effects on community and ecosystem structure and function (Wilson & Hartnett 1997; Van der Heijden et al. 1998). This report describes plant community responses to enrichment of atmospheric CO2 and soil N in the presence and absence of AM fungi using mesocosms of prairie communities. This greenhouse study was designed to complement a Free Air CO2 Enrichment (FACE) experiment at Cedar Creek Minnesota, USA (Reich et al. 2001) in which AM associations were studied (Wolf 2001; Wolf et al. 2003), but not manipulated. Our study addressed the following questions: (1) Do AM associations mediate plant community responses to enrichment of atmospheric CO2 and soil N? (2) Do AM fungi impact C3 and C4 plants differently at elevated and ambient CO2? (3) Do AM fungi and availability of atmospheric CO2 interact to impact soil moisture?

**MATERIALS AND METHODS**

**Experimental design**

This study was conducted in 12 greenhouse chambers (2.5 m × 1.3 m × 1.5 m tall) at Northern Arizona University in Flagstaff Arizona, USA. Six chambers had ambient and six had elevated levels of atmospheric CO2 (set points of 450 and 688 p.p.m. respectively daylight hours only). At Flagstaff’s elevation, these CO2 levels are equivalent to 368 and 560 p.p.m. at sea level, which are the concentrations used at the Cedar Creek FACE experiment. Atmospheric CO2 level, presence or absence of AM fungi, and soil N availability were manipulated using a 2 × 2 factorial experiment replicated six times, for a total of 48 mesocosms. Each mesocosm (48 cm × 38 cm × 43 cm deep) was filled with approximately 61 L of soil and planted with 42 seedlings: three seedlings each of 14 plant species within five functional groups. The C4 grasses included: *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michaux) Nash, and *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths; C3 grasses included: *Agropyron repens* L., *Koeleria cristata* Pers, and *Poa pratensis* L.; C3 composites included: *Achillea millefolium* L., *Kleinitia baileyi* Hunter, and *Solidago rigida* L.; C3 legumes included: *Lupinus perennis* L., *Petalostemon villosum* Nutt.; putative non-mycotrophic C3 forbs included *Berteroa incana* L. and *Salvia kali* L. *Lupinus* is both a legume and a non-mycotrophic forb. These species co-occur at Cedar Creek and are common in mesic grasslands in North America.

Temperatures in the chambers varied diurnally and across the growing season ranging from 18 to 36 °C. During the first 2 weeks of the experiment, mesocosms were watered daily with water filtered through a charcoal cartridge. After 2 weeks, soil moisture content was measured three times per week using time domain reflectometry (TDR, Jones et al. 2002), and filtered water was added to each mesocosm in the quantity necessary to return the moisture level to 4.9% by mass. This target moisture level was equal to 75% of the estimated total water-holding capacity of the soil, and did not result in leakage from the mesocosm’s drainages. During

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weeks 3, 7, and 11, each +N mesocosm received 0.701 g of NH₄NO₃ dissolved in 500 mL of filtered water, which provided a seasonal total of 0.245 g total N per mesocosm. This level is equivalent to 4 g total N m⁻², the level used at the Cedar Creek FACE experiment. Because the mesocosms were never watered to above field capacity, this N can be assumed to have remained in the systems.

Soil, plants and fungi

Soil was collected adjacent to the FACE experiment at Cedar Creek Minnesota and transported to Flagstaff, AZ. Except for Salsola, seeds of the experimental species were acquired from the same sources that were used in the Cedar Creek FACE experiments (Reich et al. 2001). Salsola seeds were collected from a roadside near Flagstaff, AZ. Mesocosms were filled with a 1:3 mixture of Cedar Creek soil and silica sand that had been steam-sterilized (8 h on two consecutive days), and 2.30 g of Osmocote® slow release fertilizer (18-6-12 NPK) was scattered over the soil surface. Also, 0.127 g Ca(NO₃)₂·4H₂O, 2.51 g CaSO₄·2H₂O, 13.61 g MgSO₄, 0.023 g NaCl, 0.650 g H₂BO₃, 0.408 g MnCl₂·4H₂O, 0.053 g ZnSO₄·7H₂O, 0.015 g CaSO₄·5H₂O, and 0.0083 g FeEDTA were dissolved in 3 L of deionized water and mixed throughout the lower soil profile. The quantity of these amendments approximated the nutrient levels that would occur if the mesocosms were filled with 100% Cedar Creek soil. Mixed cultures of endemic Cedar Creek AM fungi were grown on leeks and celery using the methods of (Morton et al. 1993). Glomus aggregatum/intraradices, G. clarum, G. constrictum, Gigaspora gigantea, G. margarita, Acaulospora spinosa, A. scrobiculata, and A. tropicae present in the AM fungal inoculum. All of these species were observed in the field at the Cedar Creek FACE site (Wolf et al. 2003). Living spores, hyphae and fragments of colonized leek roots (16 g fresh weight per mesocosm) were added to the 24 + AM mesocosms and the same amount of killed (autoclaved) spores, hyphae and roots were added to the 24 − AM mesocosms. To equalize the microbial communities of the two treatments, each −AM mesocosm received 175 mL of a microbial slurry that had been rinsed from the +AM inoculum and filtered through a 20-µm sieve to remove AM fungal propagules. All 48 mesocosms received 250 mL of microbial slurry that was prepared by mixing 5 kg of fresh Cedar Creek soil with 20 L of deionized water and filtering it through a 20-µm sieve. Seedlings of each of the 14 species were grown in sterilized vermiculite for 1–8 weeks (depending upon their growth rates), at elevated or ambient CO₂, and were transplanted into mesocosms in corresponding CO₂ treatments. Plants were transplanted when their shoots were between 2.5 and 3.5 cm tall. Seedlings were planted into randomized positions on a 6 × 7 grid placed over the mesocosm surface. Each mesocosm was individually randomized to generate 48 unique planting patterns. Any seedlings that died within 3 weeks of transplantation were replanted. After that time, dead plants were not replaced. After 16 weeks, plant roots were collected from each mesocosm and checked for AM colonization. The +AM mesocosms had an average of 35% root length colonized and the −AM mesocosms had no colonization. There was no effect of CO₂ or N enrichment on the percentage of AM colonization. Low levels (ca. 2% root length colonized) of non-mycorrhizal fungi occurred with equal frequency across all treatments. The three legume species formed root nodules in all treatments. After 20 weeks, the plants had fully matured, many had produced flowers and seed, and all were beginning to senesce. Shoots of each plant were individually cut 3 cm above the soil surface, dried and weighed.

Statistical analyses

Total aboveground biomass, plant species richness and evenness, volume of water added per mesocosm and biomass of each of the 14 species were compared using ANOVA with the full model of all experimental treatments. This allowed us to test the main effects and interactions of: CO₂ level, N level, mycorrhizal status, and the random blocking effect of chamber nested within CO₂ level (no interactions tested). Mortality of individual plants within the functional groups was analysed by logistic regression of likelihood of mortality under the different treatments. ANOVA and logistic regression were performed using the JMP 4.0 statistical package (SAS 1997).

Plant communities within the different experimental treatments were compared with Multi-Response Permutation Procedure (MRPP; Mielke 1984) using PC-ORD (Version 4.14; McCune & Mefford 1999). This non-parametric resampling method accommodates the multivariate nature of community response data, and calculates the probability (P) that detected differences between treatment groups are due to random chance alone (Zimmerman et al. 1985). Shoot biomasses of conspecific plants within each mesocosm were summed to obtain total biomass per mesocosm for each of the 14 plant species. These specific biomasses were used to describe and compare plant communities under the experimental treatments.

The location of the air-cooling system generated a temperature gradient from the front to the back of the greenhouse. Therefore, MRPP analyses were run as a blocked design, with adjacent pairs of chambers (one ambient and one elevated chamber) as blocks. Median alignment of the blocks was used in all analyses. This removes between-block variation from the analysis, allowing treatment differences to be assessed independently from
spatial variation between chambers caused by the temperature gradient.

For all MRPPs, the chance-corrected within-group agreement \( A \) is presented. The value of \( A \) represents the degree of within-group homogeneity and is analogous to ‘effect size’. If all communities within each treatment-level group are identical, \( A \) takes a maximum value of 1; \( A = 0 \) when within-group heterogeneity equals that expected by random chance (i.e. no ‘effect’ of treatments). Values of \( A \) between 0.1 and 0.3 are often meaningful in ecological community data (McCune & Mefford 1999).

RESULTS

Across the 48 mesocosms, total aboveground biomass was not influenced by CO2 level, but it was significantly higher in mesocosms with enriched soil N (\( F = 38.1, P < 0.0001 \)), and in those with AM fungi present (\( F = 7.3, P = 0.011 \) Fig. 1). Mean plant species richness was significantly lower in mesocosms with high N (12 species) than with low N (13.2 species, \( F = 31.3, P < 0.0001 \)), and higher in mesocosms with elevated CO2 (13 species) than with ambient CO2 (12.2 species, \( F = 4.7, P = 0.05 \)). There was a significant interactive effect of AM \( \times \) CO2 on plant species richness (\( F = 16.4, P = 0.0003 \)); +AM mesocosms in elevated CO2 retained more plant species than the other treatments (Fig. 2a). Evenness of the communities was not significantly influenced by any of the experimental treatments. Mesocosms with different experimental treatments dried out at different rates. The presence of AM fungi increased evapotranspiration (\( F = 4.3, P = 0.05 \)) while elevated CO2 decreased it (\( F = 6.8, P = 0.03 \)). Compared to the other treatments, significantly less water was lost from the elevated CO2, –AM mesocosms (Fig. 2b). Enrichment of N strongly increased evapotranspiration (\( F = 81.6, P < 0.0001 \)), a mean of 33.6 L of water was added to the low N mesocosms and 41.1 L of water was added to the high N mesocosms.

![Figure 1](https://example.com/figure1.png)

**Figure 1** Total mean dry shoot biomass per mesocosm, ± one standard error (\( n = 48 \)). Open bars represent mesocosms with low soil N, hatched bars denote those with enriched N. Unshaded bars represent mesocosms grown under ambient CO2 (aCO2) and shaded bars denote those grown under elevated CO2 (eCO2). The left-hand side of each histogram shows non-mycorrhizal mesocosms (–AM) and the right-hand side shows mycorrhizal mesocosms (+AM). Total shoot biomass was significantly affected by the presence of AM fungi (\( P = 0.011 \)) and addition of N (\( P < 0.0001 \)).

![Figure 2](https://example.com/figure2.png)

**Figure 2** (a) Plant species richness and (b) total amount of water added to maintain uniform soil moisture in mesocosms under ambient (aCO2) or elevated (eCO2) CO2 and without (–AM) or with AM mycorrhizal fungi (+AM). Means ± one standard error are shown (\( n = 48 \)). The significance levels of relevant treatments and interactions, as detected by ANOVA, are listed for each response (\( ^{*} 0.10 \geq P > 0.05; ^{*}{*} 0.05 \geq P > 0.01; ^{*}{*}{*} 0.01 \geq P > 0.001; ^{*}{*}{*}{*} 0.001 \geq P \)). Addition of N uniformly decreased plant species richness and increased water usage (not shown).

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Plant community composition was influenced by CO$_2$ ($A = 0.18$, $P = 0.03$), and the two-way interactions: N × AM ($A = 0.25$, $P = 0.00009$), CO$_2$ × N ($A = 0.22$, $P = 0.0003$), and CO$_2$ × AM ($A = 0.18$, $P = 0.0007$; Fig. 5). Plant species responded individually to the experimental treatments. Aboveground biomass of two C$_3$ species responded positively to elevated CO$_2$; shoots of Koeleria and Achillea were significantly larger at high CO$_2$ (Fig. 4a and c). Nine of the 14 species responded significantly to N. Enrichment of soil N was associated with higher aboveground biomass of five species: Agropyron, Poa, Bouteloua, Salsola, and Berteroa (Fig. 4a, b and c), and lower biomass of four species: Andropogon, Solidago, Petalostemum, and Lespedeza (Fig. 4b–d). Eight species responded significantly to AM fungi. Five species had greater biomass in +AM mesocosms: Andropogon, Schizachyrium, Solidago, Lespedeza, and Salsola (Fig. 4b–e), and three species had greater biomass in −AM mesocosms: Poa, Achillea, and Lupinus (Fig. 4a, e and d). There was no Salsola mortality and almost no mortality among the C$_3$ and C$_4$ grasses; however, mortality was quite high among several of the forb species and rates varied with treatment. The likelihood of mortality of C$_3$ composites was significantly higher in mesocosms with high N ($P < 0.0001$), and significantly lower in +AM mesocosms at elevated CO$_2$ ($P = 0.027$, Fig. 5a). Mortality of mycorrhizal legumes (i.e. not including Lupinus) was significantly more likely in high N ($P < 0.0001$) and under elevated CO$_2$ ($P = 0.002$), and less likely in the presence of AM fungi ($P < 0.0001$, Fig. 5b). Mortality of the putative non-mycotrophic forb Berteroa plus the non-mycotrophic legume Lupinus was significantly less likely under elevated CO$_2$ ($P = 0.0001$), more likely in high N ($P = 0.047$), and more likely in the presence of AM fungi ($P = 0.020$, Fig. 5c).

**DISCUSSION**

Plant species composition in our experimental prairie communities diverged significantly within one growing season. Interactions among mycorrhizae and the availability of atmospheric CO$_2$ and soil N account for a significant amount of the variability in this divergence. As expected, many C$_3$ plants grew largest without AM fungi at elevated CO$_2$ and high N, while many C$_4$ grasses grew largest with AM fungi (e.g. Fig. 4a and b). However, some notable exceptions illustrate the shortcomings of the standard functional groups, and indicate that it may be impossible to distil the full diversity of prairie plant growth strategies into a few functional groups. Unexpectedly, Salsola was significantly larger in the presence of AM fungi (Fig. 4c). This is contrary to the findings of others (Allen et al. 1989; Johnson 1998) and we currently have no explanation for this result. The C$_3$ species Solidago and Lespedeza both grew largest in mesocosms with AM fungi at low soil N (Fig. 4c and d). This suggests that these two relatively slow growing prairie forbs require AM associations to establish as seedlings among faster growing members of the community. Nearly all of the species that grew significantly better in the presence of AM fungi also grew best at low soil N. This pattern suggests that mycotrophic plants compete less effectively at high soil N and/or that N fertilization has a detrimental effect on the maintenance of mutualistic AM associations. With the exception of the C$_4$ Bouteloua, all of the species that grew significantly larger with enriched soil N were C$_3$ species that also grew best at elevated CO$_2$. In summary, nitrophily was often associated with a positive response to elevated CO$_2$ and a negative response to AM fungi. These results suggest that plant growth rate (fast or slow) and mycorrhizal dependency (high or low) may be useful characteristics to consider when grouping plants according to their functional responses to resource enrichment (Diaz 1995).

Our findings support Reynolds’ (1996) suggestion that differences in species’ abilities to compete for potentially limiting resources can have large effects on community responses to elevated CO$_2$, and that root symbioses like AM fungi could mediate these responses. If our greenhouse mesocosms are an accurate proxy for real prairie communities, then we can predict that in the absence of mycorrhizae,
a world enriched with CO₂ and N should become dominated by fast growing C₃ nitrophilic plant species. However, CO₂ enrichment of systems with intact AM associations and/or low soil N are just as likely to be dominated with C₄ grasses and slow growing mycotrophic forbs. Interactions between AM fungi and soil moisture availability may further mediate
plant community responses to CO2 enrichment. We observed that elevated CO2 only generated higher soil moisture in the absence of AM fungi. This indirect abiotic impact of mycorrhizae is likely to be important, because C4 plants generally do better than C3 plants in dry soils.

Plant species richness was highest in mesocosms with elevated CO2, +AM fungi, and low soil N because mortality of many C3 forbs was lowest in this combination of treatments. This pattern cannot be explained by differences in soil moisture, because if water availability was a significant driver of mortality, then we would expect that the treatment combinations with the highest evapotranspiration would have the highest mortality rates. However, this was not the case. Except for the non-mycorrhizal forbs, mortality was consistently higher in the wetter elevated CO2, −AM treatment than in the drier elevated CO2, +AM treatment (Figs 2b and 5). It is possible that the carbon cost of AM associations is involved in this reversal, because CO2 enrichment can ameliorate AM-induced growth depressions (Gavito et al. 2000; Jifton et al. 2002). Thus, elevated CO2 may increase the mutualistic quality of some of the AM associations in our experimental community. Future studies that harvest both above and belowground biomass will test the hypothesis that CO2 enrichment increases the mutualistic value of AM associations for mycotrophic plant species.

Diaz et al. (1993) hypothesized that plants species that do not form mycorrhizal associations should benefit less from CO2 enrichment than mycotrophic plant species because they lack the belowground carbon sink necessary to prevent photosynthetic down-regulation or accumulation of carbohydrates in the rhizosphere. Our findings do not support this hypothesis; two of the non-mycorrhizal species in our community (Lupinus and Berteroa) had lower mortality under elevated CO2, and two strong mycotrophs (Schizachyrium and Lespedeza) grew best under ambient CO2. However, our findings do support the generalization that fast growing plants typically show the strongest growth response to elevated CO2 (Diaz 1995). All four of the species that grew best with enriched CO2 and N have relatively fast growth rates and two of them are classified as noxious weeds (USDA 2002).

**Synthesis**

Plant species responded individualistically to the presence of AM fungi and the availability of CO2 and N. Significantly different plant communities arose under different treatment combinations. As expected, fast growing C3 plants responded most positively to enriched atmospheric CO2 and soil N. However, the presence of AM fungi was deleterious to many of these C3 plants, and thus, mycorrhizae could reduce or eliminate the C3 advantage in CO2 and N enriched ecosystems. We found that at elevated CO2, the presence of AM fungi increased evapotranspiration rates to
levels equal to those found at ambient CO₂. Consequently, water balance is an indirect mechanism by which AM fungi may mediate plant community responses to CO₂ enrichment. Although our findings do not support the hypothesis that mycotrophic plant species benefit more from CO₂ enrichment than non-mycotrophic plant species, they do suggest that in some plant species elevated CO₂ can increase the net benefits of mycorrhizae by reducing their relative carbon cost. This was manifested in reduced mortality of several C₃ forbs when grown in the presence of AM fungi at elevated CO₂. Consequently, in our experimental system, plant species richness was greatest when AM fungi were present, soil N was low and atmospheric CO₂ was elevated. We conclude that mycorrhizae can be important mediators of plant community responses to atmospheric CO₂ enrichment, and that soil N further regulates these responses.

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