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The influence of arbuscular mycorrhizae and light on Wisconsin (USA) sand savanna understories 1

Plant community composition

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Abstract To explain the complex community composition found in Wisconsin (USA) oak savannas, we investigated potentially interacting effects of light gradients and arbuscular mycorrhizal fungi (AMF) on community composition in the greenhouse, using a fully randomized block experimental design. We used plant species, soil, and AMF from a remnant sand savanna in setting up the experiment, using two light and five AMF treatments. Eleven plant species were seeded into 80 microcosms, and they were grown together for 20 weeks. Plant numbers and biomass were measured, and Simpson's index was calculated for both. Data were analyzed using ANOVA and nonparametric ANOVA. We found significant light effects on biomass and on numbers of four species. There were no treatment effects on Simpson's index, and only *Schizachyrium* numbers showed a significant AMF effect. These findings are consistent with results from other studies of the sand savanna, and, collectively, these data suggest that plant community composition in this species-rich savanna is not strongly influenced by arbuscular mycorrhizae. This is a novel finding with important implications for understanding interactions between plant and AMF diversity in wild communities.

Keywords Arbuscular mycorrhizal fungi (AMF) · Oak savanna · Microcosm · Light gradient · Nonparametric MANOVA (NPMANOVA)

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Introduction

Research has shown that arbuscular mycorrhizal fungi (AMF) can potentially either decrease plant community diversity (Hartnett and Wilson 1999, 2002; Marler et al. 1999) or increase it (Grime et al. 1987; van der Heijden et al. 1998; van der Heijden 2002). In this study, we examine the influence of AMF under light regimes in microcosms modeled on a Wisconsin (USA) oak savanna.

Oak savannas are probably the most species-rich and most endangered plant communities in Wisconsin. They are extraordinarily floristically diverse for American midwestern plant communities; one survey found 417 plant species (22% of the Wisconsin flora) in 722 m^2 surveyed across 12 remnant savannas (Leach and Givnish 1999). Unfortunately, due to fire suppression and agricultural conversion, most oak savannas are isolated fragments only a few acres in size. Understanding what factors create and maintain oak savanna diversity is thus critical for their preservation and restoration.

Studies of Wisconsin oak savannas (Leach and Givnish 1996, 1999; Meisel et al. 2002) have shown that the composition of the understory is strongly correlated with two gradients: a soil gradient, corresponding to soil texture and nutrients, and a light gradient, generated by the high variability of light, from deep shade under the canopy to full sun in adjacent openings. One effect of the light gradient is that grasses and legumes tend to be more common in well-lit areas, whereas broad-leaved forbs tend to dominate in the shade (Leach and Givnish 1999).

The light gradient suggests a way that AMF may affect community composition; under different rates of photosynthesis, plant–AMF interactions may change. The idea that plant–AMF interactions may change under different rates of photosynthesis has been examined extensively by physiologists (e.g., Diederichs 1982; Borges and Chaney 1993; Saito and Kato 1994; Skalova and Vosatka 1998; Facelli et al. 1999; see review in Smith and Read 1997). However, the potential for interacting light and AMF effects on plant community composition has been essentially unexplored by ecologists.

In this study, we tested the effects of light and AMF on community composition in greenhouse microcosms, using plants, AMF, and soil native to a sand savanna in central Wisconsin that contains 129 plant species (Leach and Givnish 1999). The goal of our study was to evaluate the effects of light and AMF treatments, and any Light×AMF interaction effect, on community composition (measured by species number, biomass, and Simpson's diversity index) and on individual species within the savanna (measured by biomass and numbers of plants). The null hypothesis was no effect of any treatment. Our expectation was that grasses and legumes would grow larger in high light, whereas forbs would do better in low light, as seen in savannas. AMF treatment responses would run the gamut: our study included putatively obligate mycorrhizal species (which should grow larger in the presence of AMF), facultatively mycorrhizal species (which would show at best a weak AMF effect), and a nonmycorrhizal weed (which should show less growth under AMF treatments). (Benjamin et al. 1989; Hetrick et al. 1991, 1992; Newsham et al. 1995).

Context plays a key factor in understanding this study. This study was one of three undertaken roughly simultaneously, the other two being a study of the effects of light and AMF on plant competition (Landis et al. 2005) and a field study of three plant and AMF community relationships in three oak savannas (Landis et al. 2004), one of which served as the model and material source for this experiment and its companion. Thus, an additional goal of this study was to determine whether the microcosm data were consistent with field data. This last question proved critical in understanding the results of this experiment.

Methods

Experimental setup Eleven species of plants were used in the experiment, including two C_4 grasses, two C_3 grasses, five forbs, one legume, one nonnative weed, and one shrub (Table 1). Seeds for six species were collected from Upper Tarr Creek, a sand savanna at Ft. McCoy, WI (lat 44°0′N, long 90°39′W), a site used for savanna research (Leach and Givnish 1999; Landis et al. 2004). The other five species also occur at the Tarr Creek site but they were not producing seed in harvestable quantities. Seeds for these species were purchased from Prairie Moon Nursery (Winona, MN). All seeds were stratified or pretreated as necessary, following directions from Prairie Moon. The number of seeds sown (Table 1) was intended to produce one to five plants of each species per pot, based on germination rates from pilot studies (unpublished data). Establishment rates were estimated by dividing the total number of plants at the end of the experiment by the number of seeds sown. Frequency was calculated as the percentage of pots (out of 80) that contained at least one member of the species (Table 1).

The experiment ran from June to October 2002 at the Walnut Street Greenhouses of the University of Wisconsin–Madison. For this experiment, all plants were grown in a soil mix of three parts #2 silica sand to two parts sieved Upper Tarr Creek soil, thoroughly mixed and autoclaved for 90 min. The resulting mix had a pH of 5.9 and contained 3,000 mg/kg organic matter, 200 mg/kg Kjeldahl N, 14 mg/kg P, 30 mg/kg K, 255 mg/kg Ca, and 75 mg/kg Mg (tested at the University of Wisconsin Soils Testing Laboratory, Madison, WI, USA). Upper Tarr Creek soil is over 90% fine silica sand; although mixing in more sand did decrease nutrient concentrations to a small degree (based on data from Leach and Givnish 1999; Landis et al. 2004), the soil mix was very similar to field soil.

Experiments were conducted in new Classic 1200 pots (27 cm diameter, 10.8 L capacity). Pretreated seeds were sown in two complete blocks, the first started June 7, 2002, and the second, June 21, 2002. The plants were grown for 20 weeks, and each block was harvested within 2 days of experiment termination. To avoid the effects of uneven light within the greenhouse, we moved the pots to different benches every 2 weeks, reshuffling neighbors

Table 1 Species planted in microcosms

Species	Functional group	Source	Seeds per pot	Planted	Establishment	Frequency
Amorpha canescens Pursh.	Legume	PM	5	1 cm	0.098	0.61
Asclepias syriaca L.	Forb	TC	10	1 cm	0.123	0.74
Elymus riparius Wieg.	C_3 grass	TC	5	1 cm	0.410	0.79
Galium boreale L.	Forb	PM	20	Surface	0.004	0.06
Koeleria macrantha (Ledeb.) Schult.	C_3 grass	PM	10	1 cm	0.029	0.20
Monarda fistulosa L.	Forb	PM	10	1 cm	0.360	0.91
Rubus occidentalis L.	Shrub	TC	10	1 cm	0.008	0.06
Rumex acetosella L.	Exotic	TC	17	Surface	0.155	0.51
Schizachyrium scoparium (Michx.) Nash	C_4 grass	TC	10	1 cm	0.389	1.00
Sorghastrum nutans (L.) Nash	C_4 grass	TC	10	1 cm	0.285	0.80
Viola pedata L.	Forb	PM	20	Surface	0.013	0.19

Each species is classified into a functional group, and details about seed source, numbers of seeds sown, and depth of planting are listed by species. Establishment per pot is the total number of plant divided by the number of seeds planted. Frequency is the proportion of pots (out of 80) in which at least one individual grew

PM Prairie Moon, *TC* Tarr Creek

such that every pot rotated through the greenhouse at least twice over the course of the experiment. Every pot received roughly 1 L of dH_2O every 2 days (daily in hot weather) from clean watering cans dedicated to the experiment. The pots were hand-watered to minimize splashing and associated AMF movement among the pots. Every week, the pots received 1 l of a 500-mg/L N solution of Plant Marvel 25-0-25 (NPK)+minors fertilizer in dH_2O in place of water, so that phosphorus was the only limiting nutrient.

Two light treatments were created by tenting half the space with 50% shade cloth, leaving the other half uncovered, and pots were assigned randomly to each treatment. Decagon Accupar ceptometer readings (11 A.M.–2 P.M., July 15, 2002) showed that mean photosynthetically active radiation (PAR) values were 30% of outside light for unshaded treatments, 17% of outside light for shaded treatments, and within the range of values measured at Upper Tarr Creek (Landis et al. 2004 and unpublished data). Percentages are given rather than numbers, as light inputs obviously varied over the 20 weeks of the experiment. Supplemental lighting was used after September 21, 2002, to maintain a 12-h light period and delay senescence.

The AMF species used for this experiment, *Glomus claroideum* Schenck and Smith and *G. mosseae* (Nicol. and Gerd.) Gerd. and Trappe, were cultured in the greenhouse in sand, using either *Sorghum sudanense* or *Schizachyrium scoparium* as hosts. Both AMF species were cultured from Upper Tarr Creek, but insufficient quantities of *G. mosseae* were grown from that source. Because of this, we used *G. mosseae* spores cultured from the Sugar River savanna, a restored sand savanna near Mt. Horeb, WI.

We set up five mycorrhizal treatments: (1) inoculation with *Glomus claroideum*, (2) inoculation with *G. mosseae*, (3) inoculation with both *G. claroideum* and *G. mosseae*, (4) a negative control, and (5) a wild control. Two weeks after planting, inoculation was applied to 28 shallow holes bored by hand in a regular pattern (a 4×4 grid in the center with points spaced roughly 4 cm apart, surrounded by 12 evenly spaced points in a circle 1 cm in from the edge). For treatments (1) and (2), each hole received 1 ml of water containing 80–150 spores/ml via syringe. For treatment (3), each hole received 80–150 spores of each AMF species. The negative control received dH_2O. In treatment (5), the holes received 2 ml of inoculum.

To obtain material for the wild control, we wet-sieved soil from Upper Tarr Creek following standard protocols (Daniels and Skipper 1982; Brundrett et al. 1996). We resuspended material from both the 100- and 38-μm sieves in 100 ml dH_2O and inoculated each pot with 10 ml of this mixture. The wild control was used to test the realism of the experiment. Substantial differences between this treatment and others would point to problems with the experiment. Examination of 100 g of the wild soil indicated the presence of a variety of soil mesofauna (oligochaetes, nematodes, etc.), plus four live spores of *G. mosseae*.

In addition, all pots received 70 ml of general soil inoculum from the wash water of the 38-μm sieve used to prepare the wild control. A common technique in AMF microcosm studies (e.g., van der Heijden et al. 1998), this inoculation was designed to introduce the rest of the Tarr Creek soil microbiota (bacteria, other fungi, nematodes, etc.) into the pots so that the soil community would be more realistic. Examination of soil samples from half the negative controls revealed no evidence of AMF contamination from this inoculum.

Plants were harvested 20 weeks after planting. The root balls were washed clean of soil, the shoots were counted and separated from the root ball, and all were dried for at least 24 h at 50°C before being weighed separately. Most pots were somewhat rootbound, and disentangling all of them would have prevented timely harvest. Thus, the root balls in 16 pots (20% of experiment) were separated and weighed by species, and these data were used to estimate the root weights by species in the other 64 pots. We regressed root weight on shoot weight by species in the 16 pots and used these regression equations (linear, quadratic, or power, depending on best fit) to create allometric equations (data and equations available on request). These equations were used to estimate both absolute and proportional root weights in the other 72 pots based on measured shoot weights. We then calculated the proportional shoot weight per species. By plugging these values into the allometric equations, we were able to apportion the root mass of each pot into root mass by species. The sum of the measured shoot mass and the estimated root mass per species was used in the analyses.

Data analysis

Experimental setup The effects of light level, AMF treatment, and Light×AMF interactions were analyzed using either ANOVA (S-Plus version 6) or nonparametric MANOVA (NPMANOVA) (Anderson 2003) depending on data distributions. The ANOVA used a fix-effects balanced model, and individual treatments were compared using Tukey's Honestly Significant Difference (HSD) tests with 95% confidence intervals. NPMANOVA is similar to parametric MANOVA, except that the test statistic F is generated by permutation (Anderson 2001; McArdle and Anderson 2001). Here, the permutation test was based on 5,000 permutations of a matrix of Euclidean distances among all samples in the untransformed data set. The comparisons of differences in AMF treatment effects within each light level were calculated using a posteriori t tests with 5,000 replicates of the same distance matrix.

At the microcosm level, we tested for treatment and interaction effects on pot weight and numbers of species per pot using ANOVA. As measures of community composition, the weights and numbers of species per pot were tested using NPMANOVA. To test the prediction that grasses and legumes would be heavier in the unshaded treatments and forbs would be heavier in the shade, we tested the difference between grass and legume vs forb weights under all treatments and combinations using NPMANOVA. Another community composition measure, Simpson's index of diversity ($1-\sum p^2$), where p is the sample proportion per species, was also calculated using

the weights and number of plants per species per microcosm. Treatment effects on both Simpson's indices were tested using NPMANOVA. For the seven most abundant species, treatment effects on the species weight and number of plants per microcosm were tested using NPMA NOVA.

Results

The plants did not germinate evenly (Table 1). Only *Schizachyrium* established in all microcosms, and although *Elymus* had a higher per seed establishment rate, it occurred in fewer microcosms. At the other end of the scale, *Galium*, *Koeleria*, *Viola*, and *Rubus* occurred in fewer than 20% of the microcosms, with per seed establishment rates in three cases below 1%. There was a mean of 5.9 (±1.2) species per microcosm, less than half the species planted established in half the microcosms. This uneven distribution undoubtedly played a role in determining the results that follow.

Microcosm properties were significantly affected only by light treatments (Table 2). Mean microcosm biomass was significantly 1.5 times higher in unshaded pots. Two community composition variables were significantly larger in unshaded rather than shaded treatments: dry biomass (64.9 vs. 49.4±3.1 g) and numbers of plants per species per microcosm (1.5±2.3 vs. 1.3±1.9 plants per species per microcosm). Grasses and legumes were significantly heavier than forbs in unshaded microcosms (19.2±4.6 g), whereas forbs were heavier than grasses and legumes in shaded microcosms (10.4±4.6 g). However, the Simpson's indices for these values showed no treatment effect, nor were the numbers of species per microcosm significantly affected by any treatment.

Rumex, *Schizachyrium*, and *Sorghastrum* were significantly heavier in the unshaded microcosms, whereas only *Asclepias* was significantly heavier in the shade (Table 2, Fig. 1). Overall, there were significantly more plants of *Amorpha* and *Rumex* in the unshaded microcosms and more *Asclepias* plants in shaded microcosms. Mycorrhizal treatments had much weaker effects. Only *Schizachyrium* numbers showed a significant AMF treatment effect due to the large number of plants per microcosm in the unshaded *G. mosseae* treatment. *Schizachyrium* numbers and *Amorpha* biomass showed significant Light×AMF interaction effects. The *Schizachyrium* effects are described earlier, and *Amorpha* was significantly heavier in unshaded treatments in the double AMF treatment and in the negative control.

Discussion

In this experiment, light treatment had significant effects, especially on weight measurements. Four species were significantly affected by the light treatment, including both C_4 grasses and *Asclepias*, one of the largest forbs. This resulted in forbs dominating the shaded treatment and C_4 grasses the unshaded treatment, matching our initial hypothesis and mirroring data from Upper Tarr Creek (Leach and Givnish 1999; Landis et al. 2004).

Table 2 Results of analysis of variance (ANOVA, MANOVA, and NPMANOVA) on microcosm properties and the weights of individual species per microcosms that were subjected to two light treatments (light or shade) and five AMF treatments (see text for details)

	Light, $F_{1,70}$	AMF, $F_{4,70}$	Light×AMF, $F_{4,70}$
Microcosm properties			
Microcosm dry biomass	****(U>S)	NS	NS
Number of species per microcosm	NS	NS	NS
Dry biomass per species per microcosm	****(U>S)	NS	NS
Number of plants per species per microcosm	*	NS	NS
Grass weight—forb weight per microcosm	****(U>S)	NS	NS
Simpson's index (weight)	NS	NS	NS
Simpson's index (number of plants)	NS	NS	NS
Plant species dry biomass per microcosm			
Amorpha canescens	NS	NS	*(U×Neg, cl+mo>rest)
Asclepias syriaca	*(S>U)	NS	NS
Elymus riparius	NS	NS	NS
Monarda fistulosa	NS	NS	NS
Rumex acetosella	***(U>S)	NS	NS
Schizachyrium scoparium	****(U>S)	NS	NS
Sorghastrum nutans	****(U>S)	NS	NS
Plant species numbers per microcosm			
Amorpha canescens	*(U>S)	NS	NS
Asclepias syriaca	*(S>U)	NS	NS
Elymus riparius	NS	NS	NS
Monarda fistulosa	NS	NS	NS
Rumex acetosella	*(U>S)	NS	NS
Schizachyrium scoparium	NS	***(G mo>rest)	*(U×G mo>rest)
Sorghastrum nutans	NS	NS	NS

The *F* statistic subscripts show factor *df* and residual *df*. Asterisks and NS indicate probability levels. The letter codes in parentheses show which treatments significantly differ from others, following the codes in the footnotes
NS Not significant, *U* unshaded, *S* shaded, *G mo* G. mosseae, *cl+mo* both AMF species, *Neg* negative control, *rest* all others
*$p<0.05$; **$p<0.01$; ***$p<0.005$; ****$p<0.001$

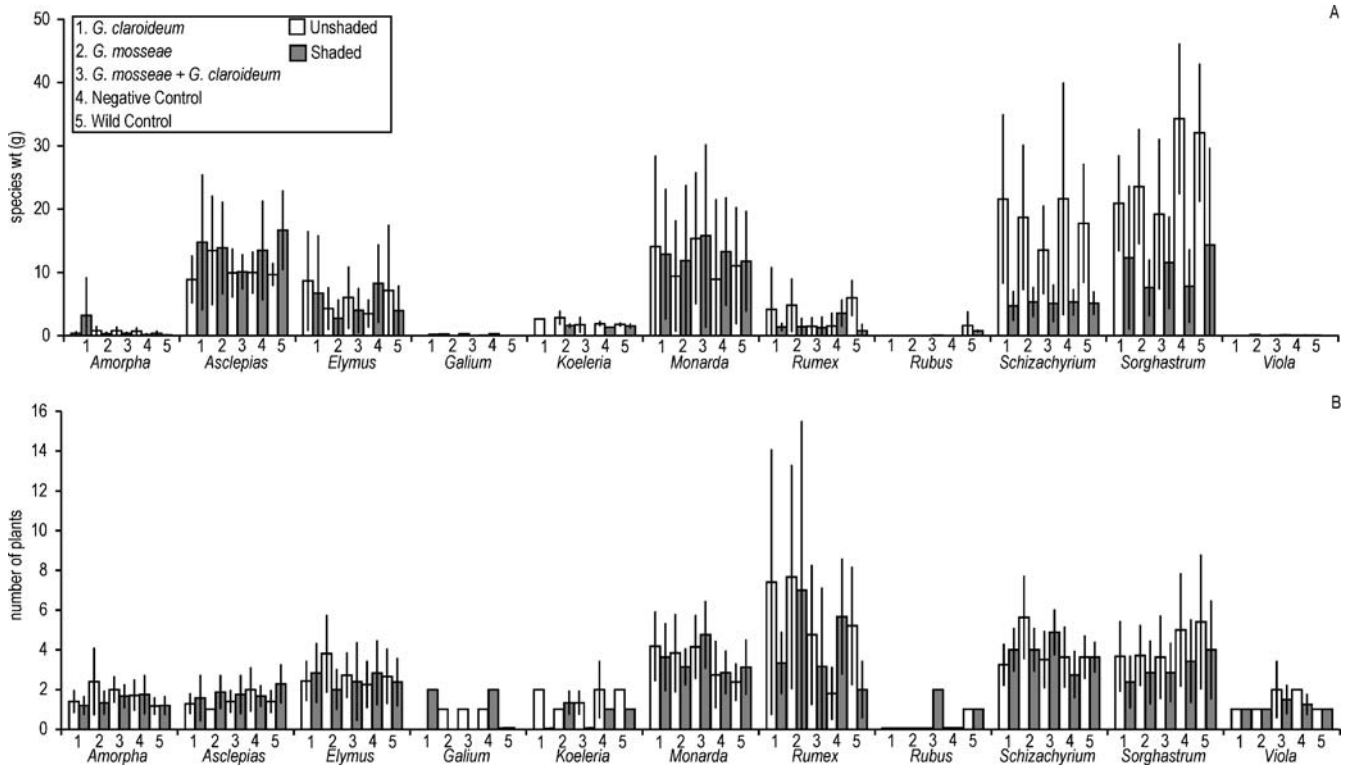

Fig. 1 Mean weights (**a**) and numbers of plants per microcosm (**b**) per species per microcosm (g) arranged by species. For each species, results are ordered 1–5 for treatments (following codes in **a**). Within each numbered treatment, *bars* are coded for *unshaded* or *shaded* (as shown in legend). The graphs show means (±1 SD) for treatments

Conversely, the AMF treatments had less effect. Only *Schizachyrium* numbers were highly significantly affected by AMF treatment. *Schizachyrium* numbers and *Amorpha* biomass showed significant Light×AMF interaction effects. As might be expected, the effects differed between the species (van der Heijden et al. 1998; Klironomos 2003). These results only partially match our hypotheses. *Amorpha*, *Schizachyrium*, and *Sorghastrum* were expected to respond strongly to AMF; none of these showed significant biomass responses, and *Sorghastrum* showed no response at all.

In the results shown, there is no relation between plant diversity and the number of AMF species in the treatment. This was confirmed by regression analysis, ordination using nonmetric multidimensional scaling (McCune and Mefford 1999), and mycorrhizal dependency (Plenchette et al. 1983) (analyses not shown). In all cases, there was no significant correlation between microcosm weights, microcosm diversity, plant numbers, and AMF treatment.

Two issues complicate the interpretation. One is that species establishment in the microcosms was uneven. Prairie (and by extension, savanna) plants are well known for having unpredictable germination rates (Packard and Mutel 1997). Whereas we attempted to insure more uniform germination rates by pretreating the seeds and using a germination study to estimate the numbers of seeds needed, we were unsuccessful in obtaining uniform germination. This was frustrating, but because these are polymorphic wild species rather than highly selected cultivars, it was not abnormal.

Under these circumstances, it was quite interesting that the number of plant species that did establish in the microcosms (5.9±1.2) was entirely consistent with the numbers of species per sample found at Upper Tarr Creek (Landis et al. 2004). This could be coincidence, but given that the experiment was designed to examine AMF effects on microcosm richness, it should not be dismissed out of hand. If the microcosms were accurately mimicking the savanna, we would expect such numbers. The only way to achieve them would be if almost half the plant species failed to establish on average.

A second, bigger problem is that we largely succeeded in proving our null hypothesis that AMF had no effect on plant community properties. Whereas this does suggest that our AMF inoculation protocol failed, it should be noted that the companion study (Landis et al. 2005) used the same soil, the same inocula, four of the same plant species from the same seed sources, and grew in the same greenhouse at largely the same time and with the same care. That study did show significant AMF effects, and it is difficult to believe that the fungi failed to establish in this one. Ideally, we would have liked to measure root colonization rates. Unfortunately, the logistics of handling the three studies simultaneously precluded such measurements, as there were neither the personnel nor the laboratory space to handle such work.

Moreover, the survey of Upper Tarr Creek found 1.8 AMF species per sample on average (Landis et al. 2004), and 18 months of Benomyl application in experimental plots at Upper Tarr Creek failed to produce a measurable effect on plant community composition (unpublished study). This is the opposite of what we would expect if AMF played a major role in plant community composition there (e.g., Hartnett and Wilson 1999, 2002).

The suggestion here is that although this study reports negative AMF results, these results are entirely congruent with results from the field. This is important because the Upper Tarr Creek savanna contains over 100 plant species (Leach and Givnish 1999), and this is the first case of a nutrient-poor, species-rich plant community where AMF do not appear to play a role in plant community composition. Although proving this negative relationship was not a goal of this study, these results are important enough to mycorrhizal ecology that they deserve attention.

Wisconsin oak savannas may be a system where plant and AMF interactions vary across an environmental gradient. The other savannas surveyed do contain many AMF species, and overall, we found a positive correlation between plant and AMF species richness and community composition (Landis et al. 2004). These endangered communities appear to be a good system in which to study the ways in which plant and AMF communities influence each other and the ways in which environmental gradients influence the interaction.

In the field, the gradient was correlated both with soil texture and with Kjeldahl N, from sandy, low-N soils to high clay, high-N soils. Inasmuch as nitrogen was supplied ad libitum in this experiment, here we suggest that the soil texture gradient may be the major factor. A hypothesis for how soil texture influenced plant–AMF interactions is explored in the companion paper (Landis et al. 2005).

In conclusion, this microcosm experiment showed that of the two treatments, light showed significant effects on community composition, numbers of plants, and biomass. Significant mycorrhizal effects were noted only for *Schizachyrium* numbers and *Amorpha* biomass. Although the microcosms were an artificial collection of species, the numbers of plant species established in each pot was similar to that found in Upper Tarr Creek, the system from which soil, seeds, and fungi had in part been taken. This study, along with other work from the same system, suggests that AMF are not a strong influence on community composition at Upper Tarr Creek despite the high plant diversity found there.

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References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46

Anderson MJ (2003) NPMANOVA: a FORTRAN computer program for non-parametric multivariate analysis of variance (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, Auckland, NZ

Benjamin PK, Anderson RC, Liberta AE (1989) Vesicular–arbuscular mycorrhizal ecology of little bluestem across a prairie-forest gradient. Can J Bot 67:2678–2685

Borges RG, Chaney WR (1993) Solar irradiance and the development of endomycorrhizal green ash seedlings. Tree Physiol 13:227–238

Brundrett M, Bougher N, Dell B, Grove T, Malajczuk N (1996) Working with mycorrhizas in forestry and agriculture. ACIAR, Canberra, Australia

Daniels BA, Skipper HD (1982) Methods for the recovery and quantitative estimation of propagules from soil. In: Schenck NC (ed) Methods and principles of mycorrhizal research. APS, St. Paul, MN, pp 29–35

Diederichs C (1982) Influence of light on the efficacy of vesicular–arbuscular mycorrhiza in tropical and sub-tropical plants. 1. Effect of light-intensity under greenhouse conditions. Angew Bot 56:325–333

Facelli E, Facelli JM, Smith SE, McLaughlin MJ (1999) Interactive effects of arbuscular mycorrhizal symbiosis, intraspecific competition and resource availability on *Trifolium subterraneum* cv. Mt. Barker. New Phytol 141:535–547

Grime JP, Mackey JML, Hillier SH, Read DJ (1987) Floristic diversity in a model system using experimental microcosms. Nature 328:420–422

Hartnett DC, Wilson GWT (1999) Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80: 1187–1195

Hartnett DC, Wilson GWT (2002) The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. Plant Soil 244:319–331

Hetrick BAD, Wilson GWT, Leslie JF (1991) Root architecture of warm-season and cool-season grasses: relationship to mycorrhizal dependence. Can J Bot 69:112–118

Hetrick BAD, Wilson GWT, Todd TC (1992) Relationships of mycorrhizal symbiosis, rooting strategy, and phenology among tallgrass prairie forbs. Can J Bot 70:1521–1528

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorhizal fungi. Ecology 84:2292–2301

Landis FC, Gargas A, Givnish TJ (2004) Relationships among arbuscular mycorrhizal fungi, vascular plants, and environmental conditions in oak savannas. New Phytol 164:493–504

Landis FC, Gargas A, Givnish TJ (2005) The influence of arbuscular mycorrhizae and light on Wisconsin (USA) sand savanna understories 2. Plant competition. Mycorrhiza DOI 10.1007/s00572-005-0366-1

Leach MK, Givnish TJ (1996) Ecological determinants of species loss in remnant prairies. Science 273:1555–1558

Leach MK, Givnish TJ (1999) Gradients in the composition, structure and diversity of remnant oak savannas in southern Wisconsin. Ecol Monogr 69:353–374

Marler MJ, Zabinski CA, Callaway RM (1999) Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80:1180–1186

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data. MjM Software Design, Gleneden Beach, OR

Meisel J, Trushenski N, Weiher E (2002) A gradient analysis of oak savanna community composition in western Wisconsin. J Torrey Bot Soc 129:115–124

Newsham KK, Watkinson AR, West HM, Fitter AH (1995) Symbiotic fungi determine plant community structure-changes in a lichen-rich community induced by fungicide application. Funct Ecol 9:442–447

Packard S, Mutel CF (1997) The tallgrass restoration handbook. Society for Ecological Restoration, Washington, DC

Plenchette C, Fortin JA, Furlan V (1983) Growth response of several plant species to mycorrhiza in a soil of moderate P-fertility. I. Mycorrhizal dependency under field conditions. Plant Soil 70: 199–209

Saito M, Kato T (1994) Effects of low temperature and shade on relationships between nodulation, vesicular–arbuscular mycorrhizal infection, and shoot growth of soybeans. Biol Fertil Soils 17:206–211

Skalova H, Vosatka M (1998) Growth response of three *Festuca rubra* clones to light quality and arbuscular mycorrhiza. Folia Geobot 33:159–169

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic, London

van der Heijden MGA (2002) Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search of underlying mechanisms and general principles. In: van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin Heidelberg New York, pp 243–265

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boiler T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72