Mycorrhiza (2005) 15: 555–562
DOI 10.1007/s00572-005-0366-1

ORIGINAL PAPER

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The influence of arbuscular mycorrhizae and light on Wisconsin (USA) sand savanna understories 2. Plant competition

Received: 14 July 2004 / Accepted: 1 April 2005 / Published online: 16 June 2005
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Abstract Wisconsin (USA) oak savannas are endangered plant communities that have remarkably high plant species diversity. To investigate factors underlying this richness, we experimentally investigated the potentially interacting effects of light gradients and arbuscular mycorrhizal fungi (AMF) on plant competition in the greenhouse, using a fully randomized block design. We used four plant species, soil, and AMF from a remnant sand savanna, under two light and five AMF treatments. Plants were grown four per pot under two competition treatments (either one or four species per pot) for 20 weeks. Using ANOVA, we found that all species showed significant treatment effects on total and shoot biomass, primarily due to differences in competition and light, less to AMF. However, effects were the opposite of predictions. Putatively mycorrhizal plants showed neutral to negative responses to AMF, and a nonmycorrhizal species outcompeted AMF species in infected pots. We concluded that our experimental setup of small pots, sandy soil, and long growing period had induced parasitism by the AMF on susceptible hosts. This unexpected result is consistent with field data from the sand savanna, and may help explain how nonmycorrhizal plants can compete successfully with AMF species in established, species-rich communities.

Keywords Arbuscular mycorrhizal fungi (AMF) · Oak savannas · Plant competition · Light gradient · Parasitic mycorrhizal fungi

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Introduction

Arbuscular mycorrhizal fungi (AMF, phylum Glomeromycota) have been shown to affect plant competition positively and negatively, within and among species (e.g., Fitter 1977; Eissenstat and Newman 1990; Goodwin 1992; Hamel et al. 1992; Hartnett et al. 1993; Anderson et al. 1994; Hetrick et al. 1994; Moora and Zobel 1996; Marler et al. 1999; Kytoviita et al. 2003; van der Heijden et al. 2003). Inasmuch as AMF fungi obtain most or all of their carbohydrates from their photosynthetic partners (Smith and Read 1997), we examined the effects of AMF on plant competition under two different light regimes to determine if there was an interaction between light and AMF on plant competitive interactions.

Our experimental system was derived from Wisconsin oak savannas, which are probably the most species rich and most endangered plant communities in Wisconsin (Leach and Givnish 1999). Most savanna plant species are potentially arbuscular mycorrhizal, making savannas a good system for studying effects of AMF on plant diversity (Landis et al. 2004; Landis et al. 2005). Studies of Wisconsin oak savannas have shown that understory composition is correlated in part with a light gradient, generated by the high variability of light, from deep shade under tree canopies to full sun in adjacent openings (Leach and Givnish 1999; Meisel et al. 2002). 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).

In this research, we focused on the effects of AMF and light on plant competition to see if effects on competition might help explain patterns of plant distribution seen in savannas. To do this, we chose two high-light species (a C_4 grass and a legume), one low-light forb, and one nonmycorrhizal weedy forb. These four plant species were grown under five mycorrhizal treatments and two light regimes. To test competitive effects, all species were grown in single-species pots and in mixed-species pots in a fully replicated 2×2×5 factorial design. We hypothesized that if AMF promoted diversity, then they would ameliorate be-

tween-plant competition, and we were interested in finding any evidence of Light×AMF interaction effects on competition. In addition, we hypothesized that the grass and legume would do best in high light and be most positively affected by AMF treatments, that the forb would do best in low light, and that the nonmycorrhizal weed would be negatively affected by the presence of AMF. The results were almost exactly the opposite of our predictions.

Methods

Experimental setup The experimental setup mimicked the Upper Tarr Creek sand savanna at Fort McCoy, WI (latitude 44°0′N, longitude 90°39′W); the experiment was conducted in the Walnut Street Greenhouses of the University of Wisconsin–Madison, roughly 185 km from Tarr Creek. We used four species found at Upper Tarr Creek: (1) the native mycorrhizal legume *Amorpha canescens* Pursh., (2) the native mint *Monarda fistulosa* L., (3) the exotic, nonmycorrhizal *Rumex acetosella* L., and (4) the native C_4 grass *Schizachyrium scoparium* (Michx.) Nash. Seeds for *Rumex* and *Schizachyrium* were collected from Upper Tarr Creek in summer 2001, whereas *Amorpha* and *Monarda* seeds were purchased from Prairie Moon Nursery (Winona, MN). All seeds were stratified or pretreated as necessary, following directions from Prairie Moon Nursery. We germinated the seeds in flats before treatment, then transplanted equivalently sized seedlings for the experiment. Plants were grown in a soil mix of three parts #2 silica sand to two parts sieved soil from the Upper Tarr Creek, thoroughly mixed and steam autoclaved for 90 min. Because Upper Tarr Creek soil is over 90% silica sand (Leach and Givnish 1999; Landis et al. 2004), adding sand made little difference in soil chemistry. The characteristics of this soil mix are discussed in the accompanying paper (Landis et al. 2005). Experiments were conducted using autoclaved, standard, 15-cm clay pots, and each pot was planted with four seedlings of similar size in a diamond pattern equidistant from edge and center.

The experimental design had two competition treatments, two light treatments, and five mycorrhizal treatments in a randomized block design, with nine replicate pots per block, for 450 pots containing 1,800 plants. Plantings were carried out in nine complete replicates, each planted on a separate day, starting May 23, 2002, and ending June 5, 2002. Pots were harvested 20 weeks later by replicate.

Plants were exposed to either intraspecific or interspecific competition. In monocultures (to test intraspecific competition), four plants of the same species were planted in 90 pots per species. In polycultures (to test interspecific competition), one plant of each of the four species was planted into the pot, in random order, in 90 pots total. Light and shade treatments were randomly assigned after this planting.

The two light treatments were shaded and unshaded. The shaded treatment was created by tenting half of the

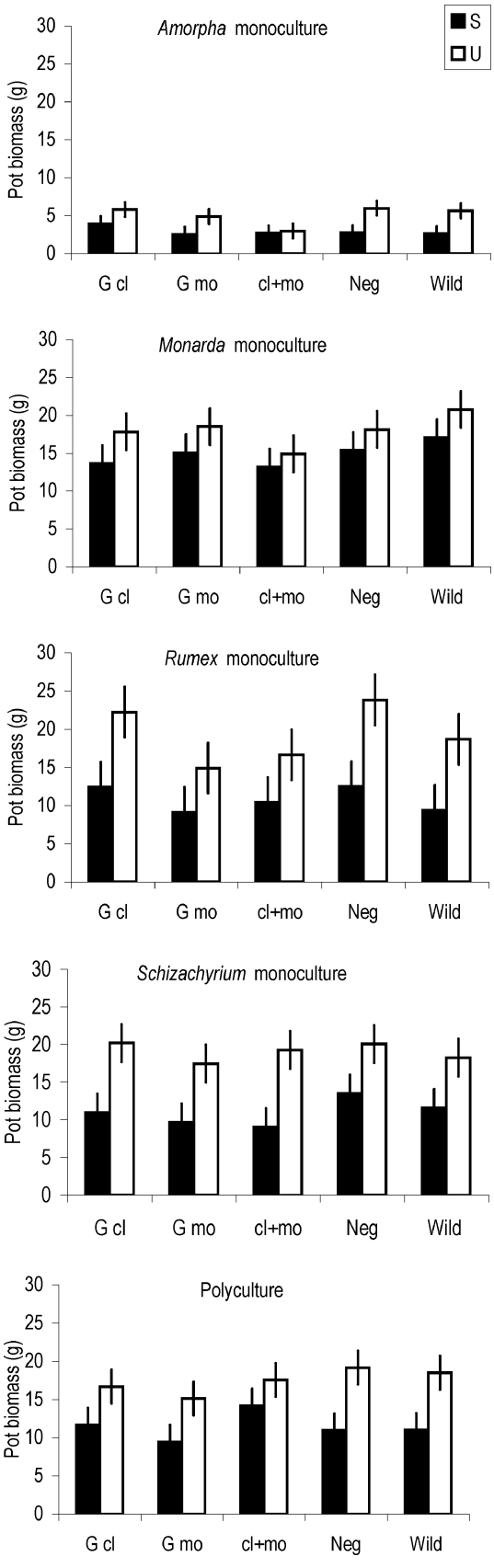

Fig. 1 Pot dry biomass. Mean dry biomass (±SD) in grams per microcosm is shown. The codes follow those in Table 1

bench space with 50% shade cloth, and the light characteristics of this treatment are described elsewhere (Landis et al. 2005). Supplemental lighting was used after September 21 to maintain a 12-h light period and delay senescence.

We set up five mycorrhizal treatments: (1) inoculation with *Glomus claroideum* Schenck and Smith, (2) inoculation with *G. mosseae* (Nicol. and Gerd.) Gerd. and Trappe, (3) inoculation with both species, (4) a negative control, and (5) a wild control. Aside from the inoculation protocol described below, these treatments are identical to those described in the accompanying paper (Landis et al. 2005). For treatments (1) and (2), each plant in a pot received 1 mL dH_2O containing 80–150 spores/mL, injected into a hole within 1 cm of the plant. For treatment (3), each plant received 80–150 spores of each AMF species in 2 mL dH_2O. The negative control (4) received dH_2O only, and the wild control (5) received 10 mL of solution. The wild control was used to test the realism of the experiment, as in the accompanying paper (Landis et al. 2005).

Each pot also received 10 mL of general soil inoculum from the wash water of the 38-μm sieve used to prepare the wild control. This inoculation was designed to introduce other elements of the Tarr Creek soil microbiota (bacteria, other fungi, nematodes, etc.) into the pots, so that the soil community in the pots would better resemble that at Tarr Creek (e.g., van der Heijden et al. 1998b). This raised the possibility of AMF contamination, but checks of the soil from nine negative controls revealed no signs of fresh or even viable spores after 20 weeks, so we concluded that contamination was not an issue.

Every pot received roughly 150 mL of dH_2O every 2 days (more frequently in hot weather). Every week, pots received 150 mL of 500 mg/L N solution of Plant Marvel 25-0-25 (NPK) + minors fertilizer in dH_2O in place of water. To control for the heterogenous light environment within the greenhouse, every 2 weeks, we moved pots to different benches, reshuffling neighbors.

R. acetosella root sprouts (Klimes and Klimesova 1999) and, over the experiment, secondary rosettes sprouted in many pots. It was not possible to connect the new ramets with their parent plants, so we clipped out every root sprout every 2 weeks. *Rumex* biomass data should be regarded as a systematic underestimate.

After 20 weeks, the plant replicates were harvested in the order planted. After unpotting, root balls were washed clean of soil, the shoots were separated from the root ball, and all were dried separately for at least 24 h at 50°C before being weighed separately. We had planned to disentangle the roots of each plant, but by the end of the experiment, most pots (with the exception of about half the *Amorpha*) were rootbound and the individual plants' roots were inseparable. Thus, we generated data on total pot biomass and individual shoot weights.

Data analysis The experiment contained three treatments: competition (monoculture vs polyculture), light (light vs shade), and AMF (*G. claroideum*, *G. mosseae*, both species, or the two controls). We tested the effects of these treatments, individually and interacting, on three measures: pot dry biomass, shoot weight, and what we termed first difference in shoot weight (described next). To test for treatment and interaction effects, we used ANOVA (S-Plus version 6).

Dry pot biomass provided the baseline against which we assessed differences in weight among plants; we would expect to see greater biomass differences between plants in pots with greater total biomass. We analyzed total pot biomass against light, AMF, and Light×AMF, using fixed-effects ANOVA, and compared individual treatments with Tukey's HSD tests with 95% confidence intervals. The competition treatments were analyzed separately: monocultural *Amorpha*, *Monarda*, *Rumex*, *Schizachyrium*, and polycultural pots (all species together).

To analyze shoot biomass, we used ANOVA models with a fixed-effect, split-plot design, the plants being grouped within pots, on the assumption that a plant's neighbors affected its growth through competition. The results were then tested with a Tukey's HSD test with 95% confidence intervals to determine which combinations of treatments differed significantly within the ANOVA. We analyzed shoot biomass for each species separately, using two different ANOVA models. First, to test for the effects of monoculture vs polyculture competition, we analyzed all data, with competition, light, and AMF treatments. These data were unbalanced due to the different numbers of plants per species in the monoculture and polyculture treatments (360 pots vs 90 pots). To compensate for the unbalanced design, we tested using type III sums of squares.

Table 1 Pot weight ANOVA and Tukey's test results

Pot weight	*Amorpha*	*Monarda*	*Rumex*	*Schizachyrium*	Polyculture
Light	****U>S	**U>S	****U>S	****U>S	****U>S
AMF	*G cl>cl+mo	n.s.	n.s.	n.s.	n.s.
Light×AMF	n.s.	n.s.	n.s.	n.s.	n.s.

Asterisks or n.s. indicate probabilities for ANOVA results The letter codes show the results of Tukey's HSD comparisons of all treatment combinations (interaction terms were not tested). Only treatment combination terms that are significant at $p<0.05$ are shown. For light, there were only two treatments. For AMF, there were five treatments. The pairs of AMF treatments are the *only* ones that were significant under Tukey's test. The other three treatments were not significantly different from either of the ones shown in the table
U Unshaded, *S* shaded, *G cl G. claroideum*, *cl + mo* both AMF species, *n.s.* not significant
*$p<0.05$; **$p<0.01$; ****$p<0.001$

Second, monoculture and polyculture treatments per species were analyzed separately, to examine light, AMF, and Light×AMF effects within the competition treatments. These ANOVA tests had a balanced design, and were thus tested with type I sums of squares.

Finally, to measure treatment effects on competition, we calculated variation in shoot weight within pots. This is conceptually straightforward: if treatments ameliorate competition among plants, plant weights should be closer to the pot mean. To determine within-pot variation, we calculated "proportional first differences," which are simply the difference between individual shoot and mean shoot weights per pot divided by mean shoot weight per pot. We used proportional first difference rather than variance for three reasons. First, analyzing variance per pot would have decreased the sample from 1,800 plants to 450 pots, radically decreasing analysis sensitivity. Since ANOVA is notoriously sensitive to sample size, using first differences allows us to compare weights and differences among plants with the same ANOVA design. Second, metrics such as proportional difference have been used in other studies of competition (Facelli et al. 1999). Third and most important, we were interested in plant responses to interspecific competition, and assessing that in terms of variance in weight per pot in polycultures is conceptually problematic. Proportional differences were analyzed using the ANOVA models described for shoot biomass.

Results

As expected, all unshaded pots produced significantly more biomass than did the shaded pots (Fig. 1, Table 1). Ratios of unshaded to shaded mean dry weights per pot ranged from 1.2 for *Monarda* to 1.74–1.76 for the other three monocultures, and 1.52 for the polyculture pots.

The legume *Amorpha* showed significant responses to competition, light, and AMF treatments. Plants grown in monocultures were on average four times heavier than plants in the polyculture pots (Fig. 2, Table 2). Conversely, first differences in polyculture shoot weights were 1.6 times higher (i.e., more variable) than monoculture shoot weights (Fig. 3, Table 3).

Light treatments had no significant overall effects on *Amorpha*. However, plants grown in unshaded monocultures were almost twice as heavy as shade monoculture plants (Fig. 2), whereas plants grown in shaded polycultures were almost twice as heavy as those grown in unshaded pots, leading to a significant Competition×Light effect (Table 2). In polycultures, unshaded plants were significantly 6% more variable than shaded plants (Fig. 3, Table 3), an effect due to the differences between shaded and unshaded plants treated with *G. mosseae*.

Amorpha showed significant AMF treatment effects. In general, plants inoculated with AMF were the same size or

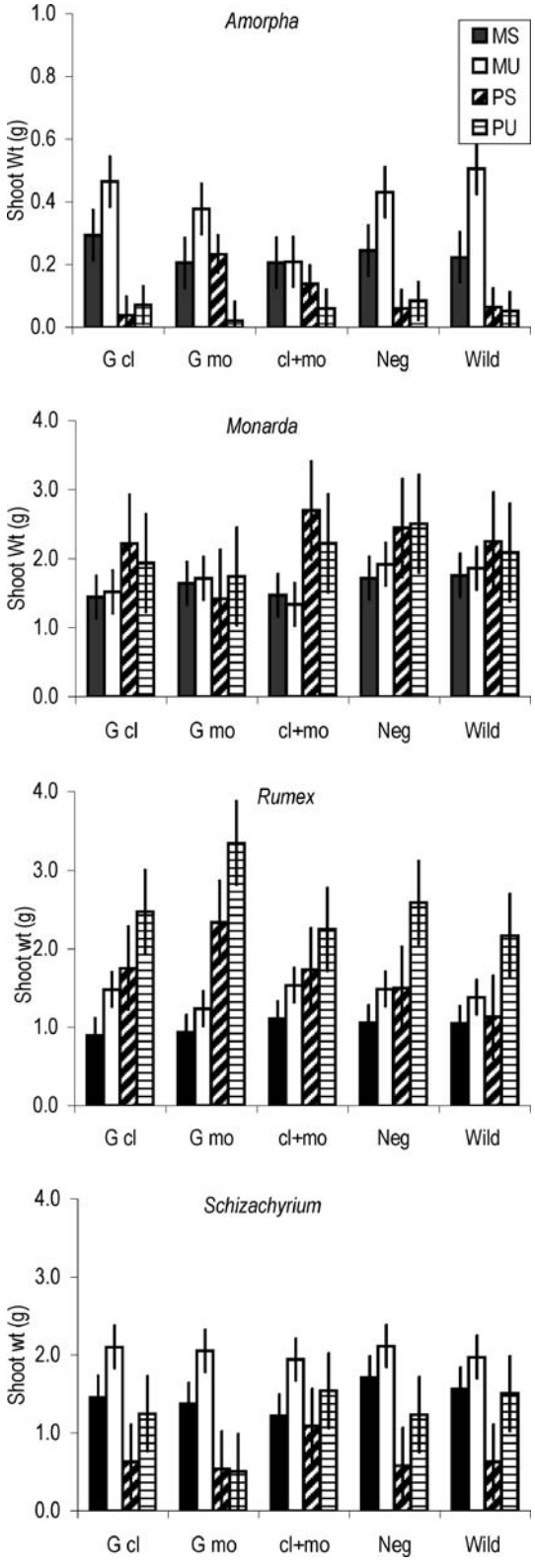

Fig. 2 Shoot biomass. Mean dry biomass per shoot (±SE from Light×AMF interaction) in grams is shown. The letter codes follow Tables 1 and 2. (*MS*, monoculture, shaded, etc.)

Table 2 Shoot weight ANOVA and Tukey's test results

	Amorpha	*Monarda*	*Rumex*	*Schizachyrium*
All treatments				
Competition	****M>P	****P>M	****P>M	****M>P
Light	n.s.	n.s.	****U>S	****U>S
AMF	n.s.	n.s.	*G mo>wild	n.s.
Competition×Light	*	n.s.	*	n.s.
Competition×AMF	n.s.	n.s.	***	n.s.
Light×AMF	n.s.	n.s.	n.s.	n.s.
Competition×Light×AMF	n.s.	n.s.	n.s.	n.s.
Intraspecific monocultures (solid colors)				
Light	****U>S	n.s.	****U>S	****U>S
AMF	*	n.s.	n.s.	n.s.
Light×AMF	n.s.	n.s.	n.s.	n.s.
Interspecific polycultures (striped)				
Light	n.s.	n.s.	****U>S	*U>S
AMF	n.s.	n.s.	*G mo>wild	n.s.
Light×AMF	*	n.s.	n.s.	n.s.

Coding follows Table 1, with the addition of *M* (monoculture) and *P* (polyculture) within the competition treatments. As with Table 1, the asterisks or n.s. indicate ANOVA results, whereas the letters indicate treatment combinations that are significantly different ($p<0.05$) under Tukey's HSD test
G mo G. mosseae, *wild* wild control
*$p<0.05$, ***$p<0.005$, ****$p<0.001$

smaller than the controls, especially the negative control (Figs. 2 and 3). Both pot dry biomass (Table 1) and shoot weights (Table 2) under *G. claroideum* treatment were significantly almost twice those under double inoculation, according to Tukey's tests. Although the Light×AMF treatment interaction was significant for shoot weights in the polyculture pots (Table 2), no combination of treatments differed significantly. Within the monocultures, plants infected with *G. mosseae* and with both AMF species were roughly 25% less variable in weight than those in the other treatments (Fig. 3, Table 3). In polycultures, unshaded plants were 6% more variable than shaded plants (Fig. 3, Table 3), an effect due to the differences between shaded and unshaded plants treated with *G. mosseae*. This also created a marginally significant Light×AMF interaction term in the polyculture treatment (Fig. 3, Table 3).

For the mint *Monarda*, competition and light had more effect than did AMF treatments. Polyculture shoot weights were 130% heavier than monoculture weights (Fig. 2, Table 2), but polyculture shoot weights were over 160% more variable than those from monocultures (Fig. 3, Table 3). Shade-grown plants were 1.2 times (monoculture) or 1.5 times (polyculture) more variable than those grown in the sun, and the Competition×Light interaction term was significant as well (Fig. 3, Table 3). Mycorrhizal treatments had no effect on mean shoot weights. However, monoculture shoot weights under *G. claroideum* treatment were 30% less variable than the negative control, leading to a significant AMF treatment term (Fig. 3, Table 3). No other interaction terms were significant.

The nonmycorrhizal *Rumex* showed significant responses to competition, light, and AMF treatments, especially when grown in polyculture. In monocultures, unshaded plants were 142% heavier than shade-grown plants (Fig. 2, Table 2), but no other treatment effects were observed within the monoculture pots. Shoot weights in the polyculture pots averaged 175% heavier than in monoculture, and unshaded polyculture plants were 150% larger than their shaded counterparts, leading to a significant Competition×Light interaction (Fig. 2, Table 2). Although the Light×AMF interaction was marginally significant for the polyculture shoot weights and differences, no combination of treatments differed significantly at the 95% level.

Surprisingly, *Rumex* responded positively to AMF treatments, but only in the polycultures. Plants inoculated with *G. mosseae* (the heaviest treatment mean) were 170% heavier than and twice as variable as wild controls (the lightest mean), leading to significant AMF effects for each (Figs. 2 and 3, Tables 2 and 3). Polyculture plants under all AMF treatments were 135–260% larger, and 170% more variable, than their monocultural counterparts, leading to a significant Competition×AMF interaction effects (Figs. 2 and 3, Tables 2 and 3).

In the C_4 grass *Schizachyrium*, monoculture shoot weights were significantly 185% heavier than polyculture weights (Table 2, Fig. 2), but polyculture weights were 130% more variable than monoculture weights (Table 3 and Fig. 3). Unshaded shoot weights were 140% larger (monoculture) or 175% larger (polyculture) than plants grown in the shade (Fig. 2, Table 2). Otherwise, neither AMF treatments nor other interaction terms differed significantly.

Discussion

Essentially, this experiment showed strong, significant effects of light and weaker, but still significant, effects of AMF treatments on competition among the four savanna species. Differing treatment effects were seen on interspecific and intraspecific competition, on biomass, and on variation of biomass among plants within pots. Interactions between light and AMF treatments were seen only in *Amorpha*. The other three species showed no such

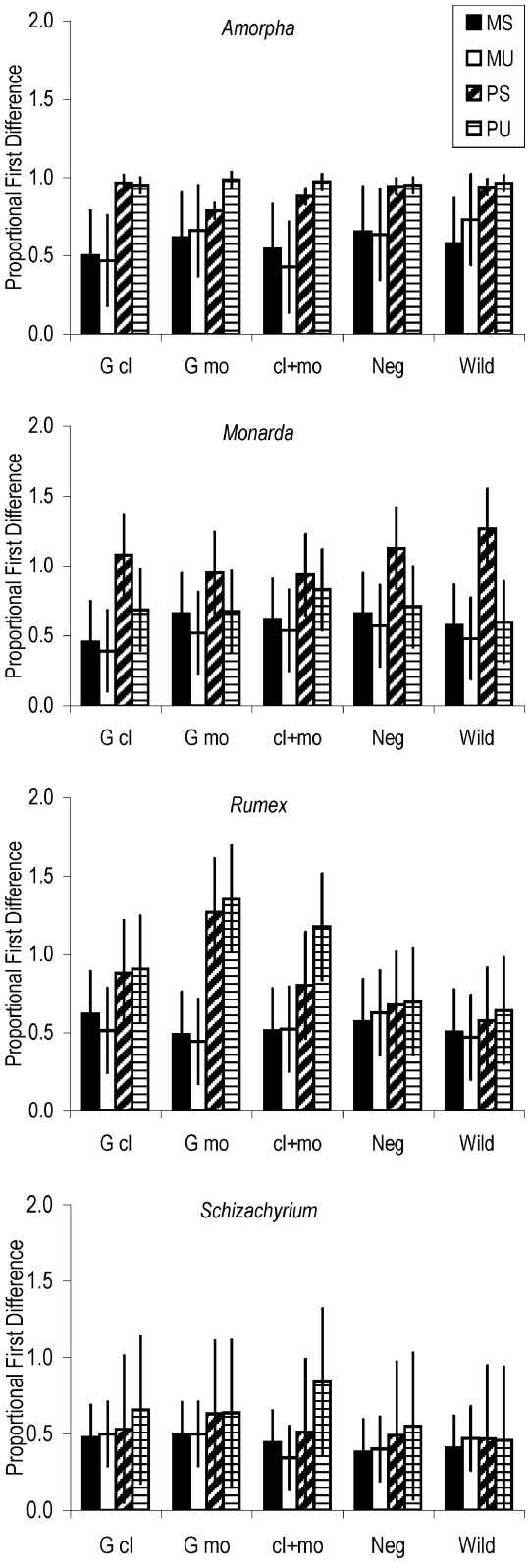

Fig. 3 Proportional first differences in shoot weights. The letter codes follow those in Tables 1 and 2

interaction effects, suggesting that light and AMF effects were additive for them.

However, the effects were the opposite of what we had predicted. Infected individuals of putatively mycorrhizal species such as *Amorpha* and *Schizachyrium* were the same size or smaller than the negative controls. Furthermore, although nonmycorrhizal *Rumex* showed no significant response to AMF treatment in monocultures as expected (e.g., Fransson et al. 2003), in polycultures it had by far the greatest response to *G. mosseae* inoculation, potentially even suppressing other plants. Finally, variation in shoot weights tended to increase under treatment, contrary to the decrease expected if AMF promoted plant coexistence by decreasing competition for the smaller plants, as suggested by earlier research (Grime et al. 1987). It appears that this experimental design induced a parasitic AMF response.

We believe that this response resulted from three factors: long duration, small pot size, and very sandy, well-watered soil. Due to the long duration of the experiment and the small pot size dictated by the replication needs and limited greenhouse space, most of the pots were totally rootbound by the end of the experiment. Roots were tightly interwoven, and most plants could not be separated. Visual inspection suggested that there were few spaces in any pot that were more than 1 mm away from a root. Arbuscular mycorrhizal fungi are better than plants at gathering immobile soil nutrients because their hyphae are able to grow beyond the depletion zone around each root and because their narrow hyphae can enter smaller pores within soil than can root hairs. In our pots, the entire rootbound pot was a potential depletion zone, and regular watering would have disrupted any depletion zone formed by slow nutrient diffusion. Moreover, the sandy soil was so coarsely textured that there was little pore space that AMF could reach that could not also be exploited by the plants. While AMF could extract carbohydrates from plant roots, they provided no nutritional benefit to the plants, thus acting as parasites on susceptible plant species.

The evidence supports this scenario: Nonmycorrhizal *Rumex* showed increased biomass when competing with infected AMF host plants, but not when competing with conspecifics under the same AMF treatment. The other species showed corresponding, albeit nonsignificant, dips in biomass in interspecific competition, particularly under *G. mosseae* infection, but no gain in biomass when grown in monoculture with AMF. Admittedly, we did not examine the roots for AMF—both biomass measurement and AMF colonization are destructive measures that cannot be performed on the same root. However, the AMF spores used in this study were grown in part on *Schizachyrium* host plants, grown in 15-cm pots in almost identical sandy soil, so we knew a priori that both AMF species could grow under these experimental conditions and would infect one of the experimental hosts. Root colonization would have been helpful, but as with the companion study (Landis

Table 3 Proportional first differences ANOVA and Tukey's test results

	Amorpha	*Monarda*	*Rumex*	*Schizachyrium*
All treatments				
Competition	****P>M	****P>M	****P>M	****P>M
Light	n.s.	****U>S	n.s.	n.s.
AMF	n.s.	n.s.	****G mo>neg	n.s.
Competition×Light	n.s.	****	n.s.	n.s.
Competition×AMF	n.s.	n.s.	****	n.s.
Light×AMF	n.s.	n.s.	n.s.	n.s.
Competition×Light×AMF	n.s.	n.s.	n.s.	n.s.
Intraspecific monocultures (solid colors)				
Light	n.s.	*U>S	n.s.	n.s.
AMF	*	*G cl>neg	n.s.	n.s.
Light×AMF	n.s.	n.s.	n.s.	n.s.
Interspecific polycultures (striped)				
Light	*U>S	**U>S	n.s.	n.s.
AMF	n.s.	n.s.	*G mo>wild	n.s.
Light×AMF	*	n.s.	n.s.	n.s.

Coding follows Tables 1 and 2
neg Negative control
*p<0.05, **p<0.01, ***p<0.005, ****p<0.001

et al. 2005) simple logistic problems precluded the additional work necessary.

More importantly, these results are consistent with a companion experiment run at the same time (Landis et al. 2005), with a gradient analysis of plant and AMF communities that included Upper Tarr Creek (Landis et al. 2004), and with a yearlong fungicide suppression study run at that savanna (unpublished data). Field research found few AMF species present at Upper Tarr Creek, and a year of monthly benomyl treatments on plots there showed no effect of the fungicide on plant community composition. Finally, the companion study showed little or no AMF effect on plant community composition in microcosms. Significantly, that study used pots that were seven times the size of the pots used here, and although the root systems of most plants were extensive, they could be disentangled with some effort.

These results do conform to previous knowledge of AMF. First, as others have found, the plants responded idiosyncratically to different AMF species (e.g., van der Heijden et al. 1998a,b; van der Heijden and Kuyper 2001; Klironomos 2003). *Rumex* responded to the presence of *G. mosseae* (presumably on other plants), *Amorpha* to infection by both species. Second, where in other experiments, AMF mutualistically decreased interspecific competition by increasing the size of host plants (e.g., Grime et al. 1987; van der Heijden et al. 1998a,b), here they apparently increased competition by parasitizing susceptible hosts, favoring the nonmycorrhizal species. In either role, AMF can influence plant competition and hence plant community composition. Dominant nonmycorrhizal plant species are often found in nature—for instance, the dominant understory species at Upper Tarr Creek is the nonmycorrhizal *Carex pensylvanica*. Results such as these show how nonmycorrhizal species can persist in AM plant communities, or can even invade or dominate them. As many other researchers have stressed (e.g., Smith and Read 1997), the nature and dynamics of arbuscular mycorrhizal symbioses depend strongly on environment and experimental setups.

Acknowledgements This work was funded in part by a grant from the National Science Foundation (DEB-0104928), by the estates of Elspeth Burgwin and Dr. DeWitt Landis, and by the Davis, Raper, and Allen funds. The authors wish to thank the US Department of Defense for providing access to Upper Tarr Creek. Many people contributed valuable time and expertise including Lyn Hummel, Steve Bentivenga, Kim Mello, and Mark Leach. Carrie J. Andrew, Luisa Arnedo, and Anne Barko deserve thanks for their work on this experiment. Finally, the authors wish to thank Paul Zedler, Robert Goodman, James Bockheim, Elisabeth Landis, and Terra Theim and two anonymous reviewers for their excellent comments on drafts of this work.

References

Anderson RC, Hetrick BAD, Wilson GWT (1994) Mycorrhizal dependence of *Andropogon gerardii* and *Schizachyrium scoparium* in two prairie soils. Am Midl Nat 132:366–376

Eissenstat DM, Newman EI (1990) Seedling establishment near large plants—effects of vesicular–arbuscular mycorrhizas on the intensity of plant competition. Funct Ecol 4:95–99

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. Baker. New Phytol 141:535–547

Fitter AH (1977) Influence of mycorrhizal infection on competition for phosphorous and potassium by two grasses. New Phytol 79:119–125

Fransson A-M, Aarle IM, Olsson PA, Tyler G (2003) *Plantago lanceolata* L. and *Rumex acetosella* L. differ in their utilisation of soil phosphorus fractions. Plant Soil 248:285–295

Goodwin J (1992) The role of mycorrhizal fungi in competitive interactions among native bunchgrasses and alien weeds—a review and synthesis. Northwest Sci 66:251–260

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

Hamel C, Furlan V, Smith DL (1992) Mycorrhizal effects on interspecific plant competition and nitrogen transfer in legume grass mixtures. Crop Sci 32:991–996

Hartnett DC, Hetrick BAD, Wilson GWT, Gibson DJ (1993) Mycorrhizal influence on intraspecific and interspecific neighbor interactions among cooccurring prairie grasses. J Ecol 81: 787–795

Hetrick BAD, Hartnett DC, Wilson GWT, Gibson DJ (1994) Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. Can J Bot 72:168–176

Klimes L, Klimesova J (1999) Root sprouting in *Rumex acetosella* under different nutrient levels. Plant Ecol 141:33–39

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

Kytoviita MM, Vestberg M, Tuom J (2003) A test of mutual aid in common mycorrhizal networks: established vegetation negates benefit in seedlings. Ecology 84:898–906

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 1. Plant community composition. Mycorrhiza DOI 10.1007/s00572-005-0365-2

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

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

Moora M, Zobel M (1996) Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia 108:79–84

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

van der Heijden EW, Kuyper TW (2001) Laboratory experiments imply the conditionality of mycorrhizal benefits for *Salix repens*: role of pH and nitrogen to phosphorus ratios. Plant Soil 228:275–290

van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998a) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082–2091

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

van der Heijden MGA, Wiemken A, Sanders IR (2003) Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. New Phytol 157:569–578