

## MYCORRHIZAE INFLUENCE PLANT COMMUNITY STRUCTURE AND DIVERSITY IN TALLGRASS PRAIRIE

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**Abstract.** In grassland ecosystems, symbiotic associations between plants and mycorrhizal fungi are widespread and have important influences on the life histories, demography, and species interactions of plants, and on belowground ecosystem processes. To assess the consequences of the symbiosis at the plant community level, we conducted a 5-yr field experiment in tallgrass prairie to investigate the influence of arbuscular mycorrhizal fungi on plant species composition, relative abundances, and diversity. Replicate plots in which mycorrhizal fungi were suppressed with benomyl application every two weeks during each growing season, were compared to nontreated mycorrhizal control plots on six watershed units at the Konza Prairie in northeastern Kansas. Benomyl successfully reduced mycorrhizal colonization to <25% of mycorrhizal control plots. Mycorrhizal colonization of roots in control plots was inversely related to annual precipitation. Suppression of mycorrhizae resulted in decreases in abundances of the dominant, obligately mycotrophic  $C_4$  tall grasses, compensatory increases in abundances of many subordinate facultatively mycotrophic  $C_3$  grasses and forbs, but no change in total aboveground biomass, as estimated from canopy density. Suppression of mycorrhizal symbiosis resulted in a large increase in plant species diversity. Two possible mechanisms for mycorrhizal mediation of plant species composition and diversity are: (1) alterations in resource distribution among neighbors via hyphal connections, and (2) differential host species responses to mycorrhizal fungal colonization in communities in which the competitive dominants are more strongly or more weakly mycotrophic than their neighbors. The results of this study demonstrate that mycorrhizal symbiosis can have large effects on plant community structure, and that differential host species response to fungal colonization is a key factor explaining the dominance of warm-season  $C_4$  grasses in tallgrass prairie and limiting plant species evenness and diversity. The results also underscore the importance of above- and belowground linkages in tallgrass prairie and indicate that alterations in belowground fungi and rhizosphere processes can have large effects on aboveground floristic composition and diversity in grasslands.

**Key words:** *arbuscular mycorrhizal fungi; community structure; diversity; fungicide; grasslands; species richness; tallgrass prairie.*

### INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are ubiquitous in terrestrial plant communities, forming symbiotic associations with the roots of the majority of plant species (Harley and Smith 1983, Trappe 1987). These plant–fungal relationships are generally considered mutualistic. The fungus gains a carbon source and the host plant gains several potential benefits from infection, including enhanced uptake and transport of poorly mobile soil nutrients, improved water relations, and reduced pathogenic infections (Cox et al. 1975, Abbot and Robson 1984, Allen and Allen 1986, Newman and Reddel 1987, Newsham et al. 1995). It has become increasingly recognized, however, that colonization by mycorrhizal fungi may result in no benefit or detrimental effects to host plants under certain conditions (Bethlenfalvay et al. 1982, Fitter 1986, Francis and Read 1995). This questions the widely accepted gen-

eralization that mycorrhizal associations are mutualistic and suggests that they may vary along a symbiotic continuum from strong mutualism to antagonism (Johnson et al. 1997). Furthermore, most work on the responses of individual plants to infection by AM fungi has involved plants growing individually in pots in the glasshouse or laboratory, or in monospecific stands, and field data relating plant performance to mycorrhizal symbiosis are inconsistent (Fitter 1985). Hence the role of mycorrhizas in natural plant populations and multispecies communities remains poorly understood. Several workers have hypothesized that mycorrhizas can regulate plant competitive relationships and the composition, species diversity, and successional dynamics of some plant communities (e.g., Fitter 1977, Allen and Allen 1984, Connell and Lowman 1989, Perry et al. 1989, Allen 1991, Hartnett et al. 1993), although the patterns and mechanisms remain the subject of much debate.

The objective of this study was to examine experimentally the role of mycorrhizas in structuring tallgrass

prairie plant communities. Several recent studies have demonstrated that AM fungi are ubiquitous and ecologically important in tallgrass prairie, and that co-occurring plant species vary considerably in their germination, growth, and flowering responses to mycorrhizal infection along a continuum from highly responsive, obligately mycotrophic species to facultatively mycotrophic, nonresponsive species (Hetrick et al. 1988, 1992, Hartnett et al. 1994, Wilson and Hartnett 1997, Wilson and Hartnett 1998). Mycorrhizas can significantly alter the competitive relationships among tallgrass prairie plant species, and there are significant interactions between mycorrhizal symbiosis and both fire and ungulate grazing, two important natural disturbances regulating tallgrass prairie community structure (Wallace 1987, Hetrick et al. 1990a, Bentivenga and Hetrick 1991).

Based on these interactions and strong differential plant species responses to AM fungi, we hypothesized that changes in the activity/abundance of AM fungi would result in significant shifts in plant species composition, relative abundances, and diversity in tallgrass prairie. More specifically, since the competitive dominants in tallgrass prairie are also the most strongly mycotrophic species, we predicted that active AM associations would decrease rather than increase floristic diversity in this system. Further, as a result of complex mycorrhizal effects on the biotic interactions of their host plants, patterns indicative of "apparent competition" (sensu Connell [1992]) and "apparent mutualism" may be common in tallgrass prairie. For example, it is likely that, in the field, the positive effects of AM fungi on the growth of some mycotrophic species may be offset by negative effects resulting from increased competitive effects of their more strongly mycotrophic neighbors. Thus, we hypothesized that growth and demographic responses of certain species to AM fungi in the field will differ in direction and magnitude from their responses to mycorrhizal colonization under glasshouse conditions. To test these hypotheses, changes in plant community structure were measured in a long-term field experiment in which AM fungi were suppressed in replicate tallgrass prairie plots over a 5-yr period. Because previous work in tallgrass prairie indicates that significant interactions occur among burning regimes, belowground biota and processes, and plant responses, the influence of mycorrhizae on plant community structure was also compared between frequently and infrequently burned sites.

#### METHODS

The experiment was conducted at the Konza Prairie Research Natural Area (KPRNA), a 3487-ha tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas (39°05' N, 96°35' W). The site is owned by The Nature Conservancy and is managed for ecological research by Kansas State University, Division of Biology (<http://climate.konza.ksu.edu>). The

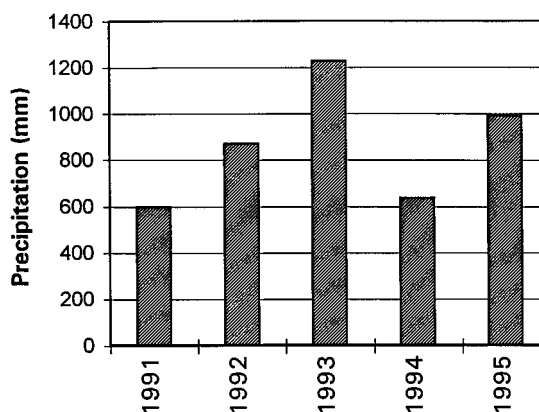


FIG. 1. Mean annual total precipitation for the years 1991–1995, recorded at Konza Prairie Research Natural Area, Manhattan, KS.

Flint Hills region encompasses  $>1.6 \times 10^6$  ha extending throughout much of eastern Kansas from near the Kansas–Nebraska border south into northeastern Oklahoma, and contains the largest remaining area of unplowed tallgrass prairie in North America.

The vegetation is native tallgrass prairie, dominated by the perennial, warm-season matrix grasses big bluestem (*Andropogon gerardii* Vit.), little bluestem (*Andropogon scoparius* Michx.), Indian grass (*Sorghastrum nutans* [L.] Nash), and switchgrass (*Panicum virgatum* L.) (Kuchler 1967, Freeman and Hulbert 1985). A highly diverse mixture of other less abundant species includes warm-season and cool-season grasses, composites, legumes, and other forbs. A few woody species such as leadplant (*Amorpha canescens* Pursh), buckbrush (*Symphoricarpos orbiculatus* Moench.), New Jersey tea (*Ceanothus herbaceus* Raf.), and smooth sumac (*Rhus glabra* L.) are locally common. The vascular flora of KPRNA includes  $>500$  species representing  $>90$  families (Freeman and Hulbert 1985). Average monthly temperature ranges from a January low of  $-2.7^\circ\text{C}$  to a July high of  $26.6^\circ\text{C}$ . Average annual total precipitation is 835 mm with 75% falling during the growing season (Bark 1987). During the study period (1991–1995) annual precipitation varied over two-fold, with a mean of 857 mm (Fig. 1). The residual soils are Chase silt loams and silty clay loams derived from Permian limestones, shales, and cherty limestones. Soil analyses of these study plots were typical of KPRNA soils, which are generally low in nutrients (3.5–6.0  $\mu\text{g/g}$  available P [Bray test 1], pH of 6.0, 2.3–5.0% organic matter, 265–285  $\mu\text{g/g}$  potassium, and 2.0–6.0  $\mu\text{g/g}$   $\text{NO}_3\text{-N}$ ). Spores of 13 species of mycorrhizal fungi were identified in soil samples taken from the study sites. In terms of spore densities, *Glomus aggregatum*, *G. constrictum*, and *G. macrocarpum* are the dominant species (Eom 1998).

Replicate long-term burning and grazing treatments on KPRNA are applied at the watershed level. KPRNA

is divided into 60 watershed units (average size = 0.55 km<sup>2</sup>), each subjected to a specific combination of prescribed burning regime (burned at 1, 2, 4, 10, and 20-yr intervals, and burned in February, April, July, or November) and grazing treatment (grazed by bison [*Bison bison*], cattle [*Bos taurus*], and ungrazed). Six ungrazed sites were used for this study, including an upland (shallow Florence cherty silt loam) prairie site in each of two annually burned watersheds (1B and 1D), an upland site in each of two infrequently burned watersheds (10B and 20D) and two lowland (Tully silt clay loam) sites, one annually burned and one infrequently burned (HQB). Prescribed fires in each of these watersheds occur in the spring (late April) of their assigned years.

At each site 20 replicate permanent 2 × 2 m plots were established in early 1991 along a randomly located transect, with a 2-m space between each plot. Ten of the plots were randomly assigned as long-term mycorrhizal suppression plots. In each of these plots, AM fungi were suppressed by the application of the fungicide benomyl as a soil drench (7.5 L per plot) at the rate of 1.25 g/m<sup>2</sup> (active ingredient). The mycorrhizal suppression plots were treated every two weeks throughout each growing season (April through October) beginning in 1991. The control plots each received no fungicide, but an equivalent volume of water (7.5 L) was applied every two weeks. To evaluate the effectiveness of the fungicide, three soil cores (2.5 cm diameter × 14 cm deep) were removed from both fungicide-treated and control plots each October throughout the study. Roots were extracted from the soil, washed free of soil, stained in trypan blue (Phillips and Hayman 1970), and examined microscopically to assess percentage root colonization by mycorrhizal fungi using a Petri dish scored in 1-cm squares (Daniels et al. 1981).

Although its potential effects on other soil microflora components are poorly known, benomyl application has the fewest drawbacks of all potential methods of AM fungal suppression and has been used successfully in a wide array of greenhouse and field studies (e.g., Fitter 1986, Fitter and Nichols 1988, Hetrick et al. 1989, 1994, Carey et al. 1992, Hartnett et al. 1993, 1994). Benomyl is effective in reducing AM fungal colonization (Fitter and Nichols 1988, Sukarno et al. 1993, Wilson and Hartnett 1997) and has no direct effects on a wide range of plants in the absence of fungi (Paul et al. 1989). The following lines of evidence also indicate that the primary effect of benomyl is suppression of mutualistic mycorrhizal associations. (1) Previous experiments have shown that effects of benomyl on host plant growth can be reversed by increasing phosphorus availability (e.g., Hetrick et al. 1986). (2) Prairie plants grown in native soil treated with benomyl show identical growth responses to those grown in pasteurized soil amended with a sieved (30-μm) suspension of nonsterile soil to add back other

soil microflora components (Hetrick et al. 1986). (3) Application of benomyl results in significant decreases in the growth of obligately mycotrophic prairie plants, rather than increases that would be predicted if the greatest effect of the fungicide were on pathogenic fungi or other antagonistic species. Furthermore, relative to forests and other more mesic habitats, there is no evidence that pathogenic fungi play a significant role in the life histories and population biology of prairie plants, compared to the large role of mycorrhizal fungi. Benomyl may suppress pathogenic fungi as well as AM fungi, in which case any measured growth enhancement of plants not treated with fungicide over treated plants will underestimate rather than overestimate mycorrhizal benefit (Carey et al. 1992). It is unknown, however, to what extent benomyl may also influence other mutualistic endophytic fungi such as mycophyllas or saprophytes, or their interactions with AM fungi. Assessment of soil microbial biomass of our KPRNA long-term plots showed no significant change in total fungal or bacterial biomass, fungal : bacterial ratios, or microbial carbon and nitrogen after 8 yr of benomyl treatment, although potentially mineralizable carbon and nitrogen and soil respiration were higher in benomyl-treated plots (Smith 1998). Responses by the nematode community also suggest the effects of benomyl were selective (Smith 1998).

The vegetation within all plots was sampled in May and September of 1991, 1993, and 1995. Sampling twice each season was necessary because the plant species vary in their growth and flowering phenology, and a single sampling would introduce significant bias in abundance estimates against those species not growing actively during the sampling period. In each plot, the cover and frequency of each plant species was estimated using a modified point-frame method (Cook and Stubbendieck 1986). A frame containing 10 1 m long vertical pins arranged in parallel at 10 cm apart was placed systematically at four locations (each 25 cm apart) within the central 1 m<sup>2</sup> of the plot (four frames = 40 pins per plot). Every contact of the aboveground structures of each plant species with each pin was recorded. From the pin-contact data, the relative cover was calculated for each plant species (total number of pin-contacts made by individuals of species  $x$  ÷ total number of pin-contacts of all species) for each of the two sample dates each year, and for each species the maximum value attained between the two sample dates was retained for analysis. The frequency (percentage of the 10-pin frames in which species  $x$  was encountered) also was estimated for each plant species. The total number of pin contacts of all species was used as an index of total canopy density in each plot. Previous use of this pin-contact method on these tallgrass prairie sites showed that the total number of pin contacts of all species is also strongly correlated with total aboveground plant biomass (Hickman 1996). Plant species richness (mean number of species per plot), species

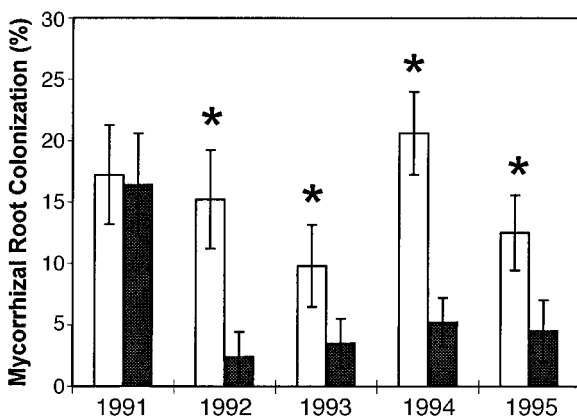


FIG. 2. Average mycorrhizal root colonization (%) in roots isolated from prairie soil in control (nonfungicide) and Benomyl (fungicide) plots for the years 1991–1995. Error bars show  $\pm 1$  SE. Solid bars represent fungicide-treated plots, and open bars represent controls. An asterisk above a bar indicates that the control is significantly ( $P \leq 0.05$ ) different from fungicide plots as determined by least significant difference (LSD).

diversity (Shannon's  $H'$ ), and evenness were calculated using both types of abundance data (frequency and cover). Effects of benomyl and fire frequency on each response variable (species abundances, richness, diversity, evenness, canopy density) were analyzed for each sampling date via two-way ANOVA, using the SAS statistical package (SAS Institute 1989). An analysis using transects as replications revealed no significant fire frequency  $\times$  mycorrhizal interaction. Thus, data from the annually burned watersheds were combined and subsequent ANOVA of mycorrhizal effects (benomyl treatment vs. mycorrhizal control) was conducted using plots as replicates.

### RESULTS

The benomyl treatments every two weeks were successful in greatly reducing mycorrhizal colonization of roots. There were no significant initial differences in root colonization between treatment and control plots in 1991 (the time when benomyl applications were initiated), but benomyl successfully reduced percent mycorrhizal root colonization to  $<5\%$  each season from 1992 through 1995 (Fig. 2). Because root samples were consistently collected under canopies dominated by the matrix grasses *Andropogon gerardii* and *Sorghastrum nutans*, these data reflect a decrease in the mycorrhizal colonization of the same plant species rather than a decrease in the proportion of mycorrhizal plants. On average, root colonization levels in benomyl-treated plots were maintained at 3.9%,  $\sim 25\%$  of untreated control plots. There was significant interannual variation in root colonization levels in the control plots. Mycorrhizal root colonization was significantly negatively correlated to annual precipitation ( $P = 0.01$ ) during this 5-yr period (Fig. 3).

Significant shifts in the relative abundances of tall-grass prairie plant species occurred over the 5-yr period in the fungicide-treated plots. Benomyl applications resulted in a significant decrease in the percent cover of the dominant warm-season grasses *Andropogon gerardii*, *Sorghastrum nutans*, and *A. scoparius* (Fig. 4a). The only exception to this pattern among the warm-season tallgrasses was switchgrass (*Panicum virgatum*), which showed no significant difference between control and fungicide-treated plots in any year. Conversely, several subdominant warm-season and cool-season grasses increased significantly in percent cover over the same period with AM fungal suppression. Of this group, the cool-season  $C_3$  graminoids Scribner's panicum (*Dichanthelium oligosanthes*), Kentucky bluegrass (*Poa pratensis*), and sedges (*Carex* spp.) showed the largest responses, increasing in cover to  $>150\%$  that of control (no fungicide) plots by 1993 (Fig. 4a). Two subdominant warm-season  $C_4$  grasses, side oats grama (*Bouteloua curtipendula*) and prairie dropseed (*Sporobolus* spp.) increased significantly with mycorrhizal suppression to  $\sim 50\%$  greater than controls by 1993 (Fig. 4a). Other subdominant grasses varied in cover among years and showed no significant differences between mycorrhizal-suppression and control plots.

The fungicide treatments also resulted in significant increases in the relative abundances of several tallgrass prairie forbs. Heath aster (*Aster ericoides*), aromatic aster (*A. oblongifolius*), Pitcher's sage (*Salvia azurea*), false boneset (*Kuhnia eupatorioides*), and prairie goldenrod (*Solidago missouriensis*) all increased significantly in relative abundances with fungal suppression (Fig. 4b). *S. missouriensis* showed the greatest response, increasing in abundance to  $>400\%$  that of control plots by 1995. The low abundances and large tem-

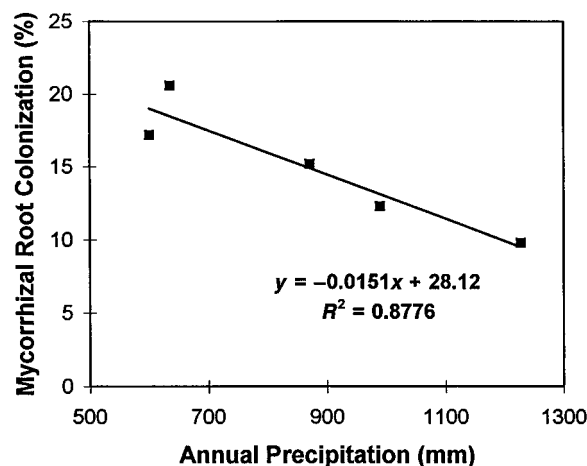


FIG. 3. Linear regression model describing the relationship between annual precipitation (mm) and mycorrhizal root colonization (%) from 1991 through 1995. Data points designate mean root colonization of control plots vs. mean annual precipitation for a given year.



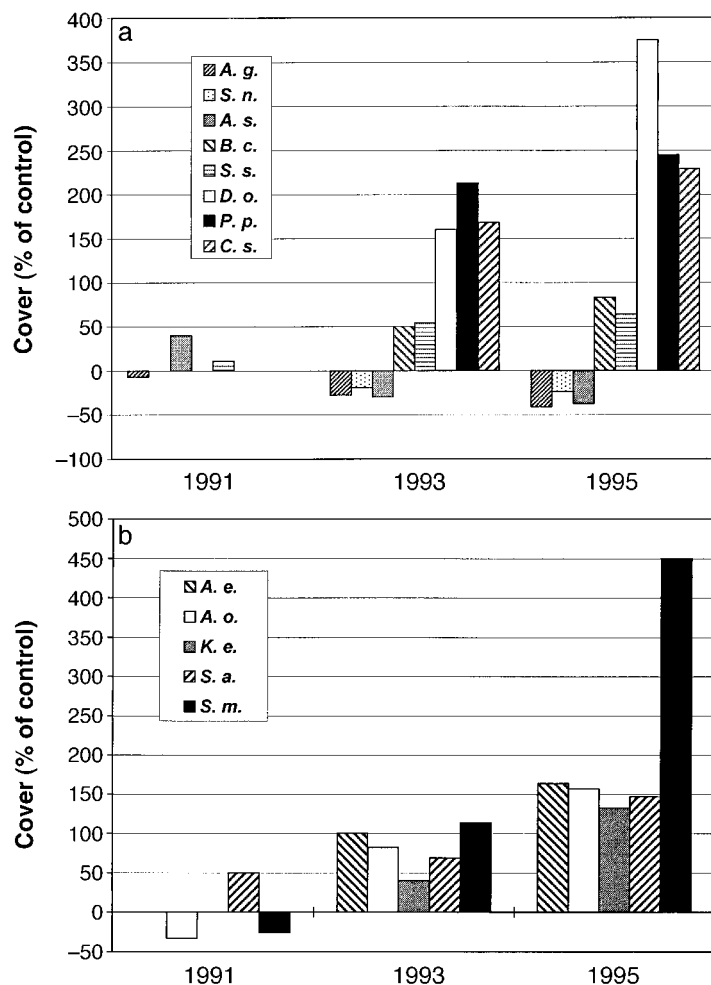


FIG. 4. (a) Differential responses of tallgrass prairie grasses to fungicide application as indicated by change in percent cover of each species. Cover for each species at each sampling date was calculated as:  $[(\text{cover of control plot} - \text{cover in fungicide plot}) / \text{cover of control plot}] \times 100\%$ . Only those species whose cover was significantly different from the control are shown. A. g. = *Andropogon gerardii*; S. n. = *Sorghastrum nutans*; A. s. = *Andropogon scoparius*; B. c. = *Bouteloua curtipendula*; S. s. = *Sporobolus* ssp.; D. o. = *Dichanthelium oligosanthes*; P. p. = *Poa pratensis*; C. s. = *Carex* ssp. (b) Differential responses of tallgrass prairie forbs to fungicide application as indicated by change in percent cover of each species. Cover for each species at each sampling date was calculated as:  $[(\text{cover of control plot} - \text{cover in fungicide plot}) / \text{cover of control plot}] \times 100\%$ . Only those species whose cover was significantly different from the control are shown. A. e. = *Aster ericoides*; A. o. = *Aster oblongifolius*; K. e. = *Kuhnia eupatorioides*; S. a. = *Salvia azurea*; S. m. = *Solidago missouriensis*.

poral variation in cover among other forbs resulted in the inability to detect significant effects of the mycorrhizal-suppression treatment. However, there was a consistent trend among these rarer forb species in that, for all species in both 1993 and 1995, their mean cover was greater in fungicide-treated plots relative to controls.

The net result of these different species responses was a significant increase in components of plant species diversity with suppression of AM fungi over the 5-yr period. Plant species richness showed no initial differences between fungicide-treated and control plots in 1991, but was significantly greater in fungicide-treated compared to control plots in both spring and fall of 1993 and 1995 (Fig. 5a). In both 1993 and 1995, mean plant species richness was 6.0 species/m<sup>2</sup> in control plots and 7.1 species/m<sup>2</sup> in the benomyl-treated plots, an 18% increase in alpha species richness due to mycorrhizal suppression. The evenness of species relative abundances showed similar patterns, with no initial differences in 1991 and significantly greater evenness in mycorrhizal-suppressed plots compared to controls

(Fig. 5b). Plant species diversity (Shannon's  $H'$ ) was significantly increased by suppression of AM fungi (Fig. 5c). There was no initial difference in species diversity (mean  $H'$ ) between fungicide-treated and control plots in 1991. Thereafter, however, plant species diversity in the mycorrhizal plots remained relatively constant, whereas diversity in the fungicide-treated plots was significantly increased (Fig. 5c). For both the spring and fall vegetation sampling, the enhancement in plant species diversity with fungicide treatment was greater in 1995 than in 1993. In 1993 the mean diversity of benomyl-treated plots was 14% greater than mycorrhizal control plots. In 1995 the effect of benomyl treatment was enhanced even further and diversity of benomyl-treated plots was 42% higher than controls.

Despite these marked shifts in plant community composition and species diversity in response to AM fungal suppression, the fungicide treatment resulted in no change in total aboveground canopy density or biomass, as estimated by the total number of plant contacts with the 40 vertical pins within each plot (Fig. 5d). Total canopy density varied considerably between

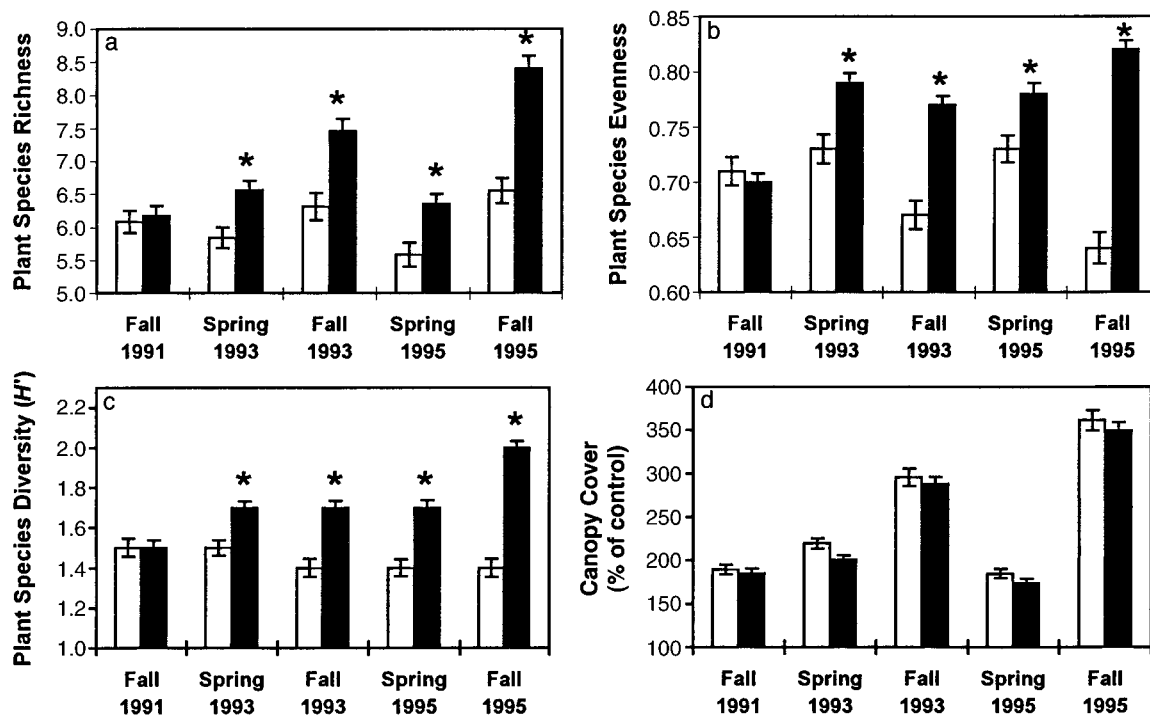


FIG. 5. Plant species richness, evenness, diversity, and canopy cover of control (nonfungicide) and Benomyl (fungicide) plots. Solid bars represent fungicide-treated plots, and open bars represent controls. Bars represent means of six transects (10 plots/transect) for each sampling date (error bars show  $\pm 1$  SE). An asterisk above a bar indicates that control plots are significantly different ( $P \leq 0.05$ ) from fungicide plots as determined by least significant difference (LSD).

spring and fall sampling and among years, but was almost identical in control and fungicide-treated plants at all sample dates from 1991 through 1995 (Fig. 5d).

#### DISCUSSION

Suppression of mycorrhizal fungi over several growing seasons in tallgrass prairie resulted in marked changes in species composition of the aboveground plant community. The dominant warm-season matrix grasses all declined in abundance with mycorrhizal suppression, whereas most of the subordinate  $C_3$  grasses and forbs increased concomitantly. Those species that decreased in benomyl-treated plots (*Andropogon gerardii*, *Sorghastrum nutans*, and *A. scoparius*) are all obligately mycotrophic  $C_4$  grasses with a mycorrhizal dependency/responsiveness of  $>99\%$  (Hetrick et al. 1990b). Mycorrhizal dependency is calculated as the difference in mean biomass between mycorrhizal and nonmycorrhizal plants as a proportion of the mean biomass of mycorrhizal plants (Hetrick et al. 1990b). In contrast, the subordinate grass and forb species that increased in the fungicide-treated plots are mostly facultatively mycotrophic species with lower mycorrhizal dependencies and growth responses. For example, the mycorrhizal dependencies of three forb species that showed significant increases in fungicide-treated plots, *Aster ericoides*, *Salvia azurea*, and *Kuhnia eupatroides*, are 63, 87, and 22%, respectively. *Dichanthelium oli-*

*gosanthes*, a cool-season grass that showed a large increase in abundance in benomyl-treated plots, has a mycorrhizal dependency of 50%.

Despite these large changes in species abundances, there was no effect of the benomyl treatment on total aboveground canopy density or biomass, as estimated by the total number of pin-contacts per plot. This lack of effect, and the above patterns, suggest that the primary effects of suppression of fungi on the aboveground plant community were a strong suppression of the competitively dominant matrix grasses, and a concomitant increase in the subordinate species. This compensatory response of subordinate competitors resulted in no change in total aboveground canopy density. These results are consistent with our earlier greenhouse studies of tallgrass prairie microcosms (Wilson and Hartnett 1997), and indicate that subordinate facultative mycotrophs competing with highly mycorrhizal-dependent species experience competitive release when mycorrhizae are suppressed.

The significantly greater plant species diversity in the benomyl-treated plots supports our hypothesis that active AM associations decrease floristic diversity in tallgrass prairie. To our knowledge, this is the first multiyear field study to demonstrate a significant role of soil fungi on plant species composition and diversity in a natural grassland. In a greenhouse experiment, Grime et al. (1987) showed that mycorrhizal associa-

tions increased plant species diversity in  $C_3$ -dominated turfgrass microcosms, and Gange et al. (1993) showed that fungicide application decreased plant species richness in an early successional plant community, both the opposite response of our tallgrass prairie field experiment.

Several workers have hypothesized different mechanisms whereby mycorrhizal associations may increase plant species diversity. Allen (1991) suggested that mycorrhizal fungi may increase plant species diversity due to spatial heterogeneity of fungal infectivity in field soils, allowing nonmycotrophic and mycotrophic species to coexist in patches of low and high inoculum, respectively. Other workers, (e.g., Grime et al. 1987, Perry et al. 1989, Read 1997, Simard et al. 1997a, b) have suggested that interplant transfer of resources via hyphal links may result in more even distribution of resources within the plant community, reducing the ability of certain species to monopolize resources, thus creating more equitable competitive effects and promoting coexistence and greater host plant species diversity. This facilitation hypothesis assumes that all or most plants in the community are interconnected to a similar extent and benefit equally, or that subordinate species gain greater advantage from access to resources available within the hyphal network. Earlier  $^{32}P$  labeling studies in tallgrass prairie showed that neighboring plant species differed significantly in the amount of phosphorus transferred between them, and that less mycorrhizal-dependent subordinate grasses and forbs received more phosphorus from the dominant obligately mycotrophic grass species than did other neighboring dominant grasses (Fischer-Walter et al. 1996). In ectomycorrhizal forest communities, Simard et al. (1997b) showed a net transfer of carbon from birch to fir but no such transfer between these species and cedar. Until experiments can demonstrate that mycorrhizal fungi result in more equitable distribution of resources among interspecific host plant neighbors, or greater net resource transfer to subordinate competitors, this hypothesized mechanism remains open to question.

We suggest that a second and perhaps more parsimonious explanation for mycorrhizal effects on plant species diversity, is simply that differential host plant species responses to colonization by mycorrhizal fungi result in changes in species diversity if the dominant competitors are significantly more strongly or more weakly mycotrophic than their neighbors. In the microcosm experiment conducted by Grime et al. (1987), the dominant  $C_3$  grass competitors were more weakly mycotrophic than their neighbors. Thus, active mycorrhizal associations conferred greater benefit to the subordinate competitors and increased coexistence and species diversity. By contrast, in our tallgrass prairie field experiment, the dominant  $C_4$  grass competitors were more strongly mycotrophic than their interspecific neighbors. Thus, AM fungal colonization further enhanced their dominance, resulting in a reduction in spe-

cies diversity. The compensatory increase in abundances of the facultative mycotrophs in response to benomyl treatment further supports this hypothesis. Connell and Lowman (1989) argued that mycorrhizae may similarly enhance competitive dominance and reduce species diversity in some tropical forest communities.

Given the large variation in response to mycorrhizal colonization among tallgrass prairie plant species, and the effects of different abiotic and biotic factors such as grazing, fire, and water availability on mycorrhizal activity (e.g., Hetrick et al. 1990a, Bentivenga and Hetrick 1991), it is likely that plant community responses to these factors may be at least partially due to changes in mycorrhizal activity. For example, the inverse relationship between annual precipitation and mycorrhizal colonization demonstrated in this study suggests that interannual variability in plant species composition and relative abundances associated with annual precipitation (Knapp et al. 1998) may be partly due to host species responses to changes in mycorrhizal activity.

Previous studies have shown that mycorrhizal symbiosis has significant effects on a number of life history and demographic traits in tallgrass prairie plants (Hartnett et al. 1994, Wilson and Hartnett 1997). The present field study shows that these effects have large consequences at the community level, and that mycorrhizal symbiosis and differential host species responses to fungal colonization are key factors explaining the dominance of  $C_4$  perennial grasses in tallgrass prairie and limiting plant species evenness and diversity. Regardless of whether the long-term benomyl treatments in this study had effects on other types of fungi, the results underscore the importance of above- and belowground linkages in tallgrass prairie and clearly indicate that alterations in belowground fungi and rhizosphere processes have large effects on aboveground floristic composition and diversity in these grasslands.

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