Influence of Inoculation with Vesicular–Arbuscular Mycorrhizae on Posttransplant Growth of Prairie Forb Seedlings

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SUMMARY. The objectives of this study were to compare the growth of prairie forb seedlings inoculated with vesicular–arbuscular mycorrhizal (VAM) fungi to noninoculated seedlings transplanted to a highway right-of-way and to evaluate the effect of different VAM fungal species or combinations on posttransplant seedling growth. Four species of prairie forbs: pale-purple coneflower (*Echinacea pallida* Nutt.), prairie blazingstar (*Liatris pycnostachya* Michx.), prairie phlox (*Phlox pilosa* L.), and gray-headed coneflower [*Ratibida pinnata* (Venten.) Barnh.], were grown in greenhouse mix and inoculated with *Gigaspora margarita* Becker and Hall, or *Glomus interadicies* Schenk and Smith, or with a native Indiana prairie soil inoculum, or with a mix of all three. They were transplanted to a highway site in June, 1994. Only gray-headed coneflower exhibited a positive growth response to VAM inoculation. Inoculation of gray-headed coneflower with *G. margarita* produced the largest growth response by the end of the experiment.

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Vesicular–arbuscular mycorrhizal fungi are obligate parasites that form symbiotic relationships with plant roots, especially in low phosphorus soils (Bentivenga and Hetrick, 1992). VAM fungi have been associated with increased phosphorus uptake, increased growth, and increased drought resistance due to a fungal-hyphae-extended nutrient uptake zone around roots of many species (Hayman, 1982). Most grasses and forbs of the tall-grass prairie grow in association with VAM fungi and benefit from VAM inoculation (Anderson et al., 1994; Miller et al., 1986). For example, seedlings of blue wild indigo (*Baptisia australis* L.), rough blazingstar (*Liatris aspera* Michx.), and butterfly milkweed (*Asclepias tuberosa* L.) inoculated with four species of VAM fungi were taller and flowered more compared with noninoculated control plants after two growing seasons (Zajicek et al., 1987). VAM fungal inoculation of cut-leaf penstemon (*Penstemon baccharifolius* Mitch.) seedlings placed in a field setting resulted in taller plants with more branches than noninoculated plants (Crank, 1991).

Seedlings with mycorrhizae outperform nonmycorrhizal seedlings in situations where drought stress, low fertility, or pH extremes occur (Charest et al., 1997; Maroneck et al., 1981; Titus and del Moral, 1998). VAM fungi-inoculated seedlings have been planted on disturbed soils and eroded lands such as coal spoils to improve survival success compared with noninoculated seedlings. The practice also reintroduces VAM to disturbed areas where VAM soil populations are lacking (Harris and Jurgenson, 1977; Marx and Artman, 1979; St. John and Evans, 1994).

Highway right-of-way soils are often characterized by low fertility, soil compaction, and high pH (Harrington, 1994). Hence, prairie seedlings inoculated with VAM fungi may perform better there compared with noninoculated seedlings.

Different species of VAM have different growth promotional effects on particular plant species (Daniels and Menge, 1981). For example, McArthur and Knowles (1993) reported a greater growth response of potato (*Solanum tuberosum* L.) seedlings inoculated with *Glomus interadicies* compared with those inoculated with *Glomus mosseae* (Nicol. and Gerdemann) Gerdemann and Trappe. Inoculation with *Glomus etunicatum* Becker and Gerdman resulted in a greater shoot mass of sirato (*Macroptilium atropurpureum* Urb.) than seedlings inoculated with *G. interadicies* in a nonpasteurized field soil (Medina et al., 1990). Thus, when considering VAM inoculation, examining several different species for their effect on plant growth is important.

The objectives of this study were to determine if 1) VAM fungal inoculation during production of prairie forb seedlings would result in increased growth after transplanting compared with noninoculated seedlings, and 2) different species of VAM fungi would produce different growth responses. We sought to evaluate prairie forbs not previously studied, and to test the efficacy of VAM use when converting a highway right-of-way with well-established, conventional vegetation to prairie forbs. Prairie restorationists and transportation planning personnel can use these results to determine if VAM inoculation is warranted in prairie vegetation establishment.

Materials and methods

PRAIRIE SPECIES. Seed of four prairie forbs was obtained in Oct. 1992, from Prairie Ridge Nursery (Mt. Horeb, Wis.): pale-purple coneflower, prairie blazingstar, prairie phlox, and gray-headed coneflower. The four species were selected as a representative sample of prairie forbs with different rooting characteristics (Weaver, 1954) and transplant vigor (Schramm, 1978). Pale-purple coneflower develops a thick, fleshy taproot and is rated excellent for ease of establishment; prairie blazingstar forms a corm and is moderate in establishment vigor, prairie phlox is fibrously, shallowly rooted and moderate in vigor, and gray-headed coneflower is deeply, fibrously rooted and rated as aggressive in vigor. The seed was stored at 4 °C (40 °F) until the experiment began in Jan. 1994.

CULTURED VA MYCORRHIZAE. Two separate VAM fungal cultures (*Glomus interadicies* and *Gigaspora margarita*) were obtained from the International Culture Collection of Vesicular–Arbuscular Mycorrhizae (INVAM), West Virginia University, Morgantown, in July 1994. Both species were recommended by INVAM because each genus is well represented in prairie regions of the U.S. (S.P. Bentivenga, personal communication). Each species was maintained in 3 sand : 1 greenhouse mix (v / v) cultures using sudangrass [*Sorghum sudanense* (Piper) Stapf. 'Sudex'] as a nonspecific host. The greenhouse medium used in the sand cultures was a steam-pasteurized (80 °C) (176 °F) mix containing 2:2:1 (v / v / v) ratio of perlite, sphagnum peatmoss and soil amended with 890 g (1.96 lb) Ca $(H_2PO4)_2$, 593 g (1.30 lb) KNO_3, 593 g (1.30 lb) $MgSO_4$, 4.75 kg (10.47 lb) ground limestone and 74.2 g (0.16 lb) Peters fritted trace elements No. 555 (W.R. Grace & Co. , Fogelsville, Pa.), all per cubic meter (1.3 $yard^3$) of mix.

COLLECTED PRAIRIE SOIL VA MYCORRHIZAE. Soil was collected from the Ambia-Talbot, Indiana railroad prairie remnant in Oct. 1993, and maintained in a sand / greenhouse mix culture with sudangrass as described previously. The Ambia-Talbot soil was used as an inoculum because of its growth promotion of sudangrass compared to other soil inoculum obtained from other remnant sites (Kemery and Dana, 1995). Ambia-Talbot is an undisturbed prairie remnant located 45 km (28 miles) west of Lafayette, Ind. The soil at the site was classified as a Chalmers Silt Loam (fine silty, mixed, mesic Typic Haplaquoll) (Ulrich and Barnes, 1959). The soil pH was 6.8 with less than 6 $kg·ha^{-1}$ (5.3 lb / acre) N and available P was 78 $kg·ha^{-1}$ (69.6 lb / acre). The Ambia-Talbot soil was studied at INVAM and found to contain *Glomus mosseae*, *Glomus geosporum* (Nicol and Gerd) Gerdemann and Trappe., and another undescribed *Glomus* species (S.P. Bentivenga, personal communication).

PREPARATION OF VAM INOCULATED MEDIA. We examined sudangrass roots from each of the sand cultures described previously to confirm VAM infection. Root sections were randomly collected from each container, cleared, and stained using a containerized system of Claassen and Zasoski (1992) with the staining procedures of Koske and Gemma (1989). VAM inoculation was confirmed by the presence of many spores and hyphal segments on the root samples of all cultures used in this study.

The sudangrass was clipped to the soil line for each culture container. The root mass from each container was cut into 3-cm (1.2-inch) segments using sterilized garden shears and mixed thoroughly with the remaining sand / soil mix left in the container. This mixture was then combined with the pasteurized greenhouse growing medium described previously at the ratio (v / v) of 1 inoculum : 3 greenhouse mix. A 1 : 3 (v / v) mix was used because previous studies (Kemery and Dana, 1995) showed this ratio to result in rapid, thorough infection. Care was taken to avoid contamination of the mixes. Each mix of VAM and greenhouse soil was prepared separately, and shears were sterilized with sodium hypochlorite before each use.

PROPAGATION OF PRAIRIE FORBS. In Jan. 1994, we placed the forb seed on top of peat-lite mix in seedling trays and placed the trays under intermittent mist for 10 d until the seeds germinated. They were transferred to a greenhouse bench (24 °C / 18 °C [75 °F / 65 °F], day / night, ambient lighting) and watered daily. The plants were fertilized at each watering with 201 $mg·L^{-1}$ (ppm) N; this was supplied from KNO_3, Ca $(NO_3)_2$, and NH_4NO_3 at concentrations of 71, 65 and 65 $mg·L^{-1}$ (ppm), respectively, plus 200 $mg·L^{-1}$ (ppm) K from KNO_3 and 46 $mg·L^{-1}$ (ppm) P from technical grade H_3PO_4 via the irrigation system.

INOCULATING FORB SEEDLINGS WITH VAM. After 2 weeks in the greenhouse, 75 uniform seedlings of each species were transplanted to 3.7-cm (1.46-inch) diameter by 13-cm (5.1-inch) long plastic growing tubes (Super Stubby cell Ray Leach Cone-tainer, Stuewe and Sons, Corvallis, Ore.). Each tube contained one of the following inoculum treatments for a total of 15 seedlings (tubes) of each species per treatment.

Treatment 1: 1:3 (v / v) sand / pasteurized greenhouse mix (noninoculated).
Treatment 2: 1:3 (v / v) *Glomus interadicies* inoculum / greenhouse mix.
Treatment 3: 1:3 (v / v) *Gigaspora margarita* inoculum / greenhouse mix.
Treatment 4: 1:3 (v / v) Ambia-Talbot inoculum / greenhouse mix. Due to a shortage of inoculum, pale-purple coneflower seedlings were not inoculated with Ambia-Talbot inoculum.
Treatment 5: 1:3 (v / v) inoculum cocktail (equal volumes of *G. interadicies*, *G. margarita*, and Ambia-Talbot inoculum) / greenhouse mix.

All seedlings remained in the greenhouse (24 °C / 18 °C [75 °F / 65 °F], day / night, ambient lighting) for about 3 months, until May 1994. They then were moved to a cold frame and exposed to ambient conditions for 2 weeks before field transplanting. During that period, 10% of all experimental plants were evaluated for VAM colonization. Individuals were selected randomly across all treatment / species combinations, root samples were stained (Koske and Gemma, 1989) then scored as colonized (+) or not colonized (–). Colonization was observed in 100% of the inoculated seedlings and none of the noninoculated controls.

SITE CHARACTERISTICS. The transplant site was a 100 × 20 m (330 × 66 ft) plot located on a 2-ha (5-acre) infield of an Interstate 65 highway interchange located 6 km (3.7 miles) east of Lafayette, Ind. The soil at the site was classified as a Glenhall silt loam with a 0 / 2% slope (fine-loamy, mixed mesic, mollic Hapladuaf) before highway construction in 1960 (Ulrich and Barnes, 1959). The soil pH of the site at the time of the study was 7.9. The extant soil texture was clay loam (26% sand, 44% silt, 30% clay), eroded at many spots, with the surface of the site littered with small chunks of asphalt and concrete, suggesting that little of the site's original topsoil remained after highway construction. Tall fescue (*Festuca arundinacea* Schreb.) was the dominant species at the site growing in a patchy pattern. Soil tests (Ohio Agricultural Research and Development Center, personal communication) revealed that less than 6 $kg·ha^{-1}$ (5.3 lb / acre) N and 115 $kg·ha^{-1}$ (102.6 lb / acre) P were present. Subsequent soil culture tests conducted by Steven Bentivenga at INVAM showed *G. geosporum* was present in the soil.

TRANSPLANTING. The site was sprayed with a 4% solution of glyphosate 2 weeks before transplanting to kill the existing tall fescue. No soil tillage was practiced. We transplanted the prairie forb seedlings on 10 May 1994. The layout was a completely randomized design. Transplants were spaced 45 cm (18 inches) apart within rows, and rows were 60 cm (24 inches) apart . We planted each transplant using a large planting dibble (Stuewe and Sons, Corvallis, Ore.) that matched the size of the Super Stubby cells. The soil at the site was moist, resulting from 1.8 cm (0.7 inches) of rain 5 d before planting. Two days after planting, 4.5 cm (1.77 inches) of rain fell on the site.

The seedlings received no supplemental irrigation at or after installation. Total precipitation observed at a weather station in West Lafayette, Ind. (about 10 km [6.2 miles] from the site) over the entire experimental period nearly matched average levels. However, rainfall was above average during the 1994 summer period. Monthly rainfall values (expected : actual) for that period were June [10:15 cm (3.9:5.9 inch)], July [10:14 cm (3.9:5.5 inch)], August [10:12 cm (3.9:4.7 inch)] (J.R. Mcintyre, personal communication). No weed control measures were employed after the seedlings were transplanted to the site.

DATA COLLECTION 1994. In August 1994, we recorded survival, plant height and vegetative shoot number of gray-headed coneflower and pale-purple coneflower, because they were the only species that produced measurable top growth in 1994. The site was very weedy, being dominated by common ragweed (*Ambrosia artemisifolia* L.), giant foxtail (*Setaria faberi* Herrm.), and horseweed [*Conyza canadensis* (L.) Cronq.].

DATA COLLECTION 1995. Data were collected after each species reached anthesis. We recorded survival, plant height, shoot number, and shoot dry mass for prairie phlox in May, pale-purple coneflower in June, and gray-headed coneflower and prairie blazingstar in July. For dry weights, the aerial portion of each surviving transplant was removed at the soil line and dried for 48 h at 80 °C (176 °F), or for large specimens of gray-headed coneflower, 6 d at 80 °C (176 °F).

To assess VAM colonization at the conclusion of the experimental period, the roots of three randomly selected plants of each species / treatment combination were carefully dug, separated from weed roots, and washed. Thirty-gram (1.1-oz) samples randomly collected from each plant were combined in 25-mL (0.8-fl oz) containers. The combined root samples from each species / treatment combination were stained using the methods of Koske and Gemma (1989), and we determined the mean colonization percentage of the stained root samples using the grid-line intersect method (Giovannetti and Mosse, 1980).

DATA ANALYSIS. Analyses of variance (ANOVA) were conducted on shoot number, plant height, and dry weight data using SuperAnova (Abacus Concepts, Berkeley, Calif.). Means were compared using Fisher's protected test. The experimental design did not allow for statistical analysis of survival or colonization data.

Results

Year one, 1994

VEGETATIVE SHOOT NUMBER. Shoot growth could be measured on only two of the four prairie species at the end of the first growing season because most of the top growth of prairie phlox and prairie blazingstar died back to the ground during the hot summer months. The number of shoots per plant varied significantly among treatments for gray-headed coneflower, but not for pale-purple coneflower (Table 1). VAM-inoculated gray-headed coneflower seedlings developed more shoots per plant than noninoculated seedlings. However, no differences existed among the various VAM types.

PLANT HEIGHT. Plant height did not vary significantly among treatments for any species.

SURVIVAL. All gray-headed coneflower and 49 of 60 pale-purple coneflower seedlings survived until Aug. 1994.

Year two, 1995

SHOOT NUMBER, HEIGHT, AND DRY WEIGHT. Gray-headed coneflower plants inoculated with *G. margarita* developed more shoots per plant than noninoculated plants (Table 2) while other plant species and VAM treatments showed no significant responses. Dry weights and heights were not significantly different among treatments for any species (data not shown).

SURVIVAL. One-hundred percent of prairie phlox and gray-headed coneflower seedlings survived, while 27% of prairie blazingstar seedlings and 78% of pale-purple coneflower survived to the experiment's conclusion (Table 3).

MEAN PERCENT COLONIZATION. All seedlings that were evaluated for VAM colonization after the final harvest, including the noninoculated controls, exhibited some level of VAM colonization at the conclusion of the experiment (Table 3). The highest colonization level was observed in gray-headed coneflower seedlings at 68%, while the lowest was 20% for prairie blazingstar plants inoculated with the VAM cocktail. Most exhibited an infection level of 40% to 50%. Only sparse hyphae were present on most seedling roots and only an occasional, isolated arbuscle was noted.

Discussion

Gray-headed coneflower was the only species to show a significant positive growth response from VAM inoculation. The response was most pronounced in year one. In both years no differences existed among the various VAM inoculum types. This suggests a nonspecific association between gray-

Table 1. First year number of shoots per plant of vesicular–arbuscular mycorrhizae-inoculated or noninoculated gray-headed coneflower and pale-purple coneflower seedlings planted on a highway right-of-way.

Inoculation treatment	Shoots/plant (no.) Pale-purple coneflower	Gray-headed coneflower
Noninoculated	8.1[NS]	12.2 b[z]
Glomus interadicies	7.9	16.8 a
Gigaspora margarita	6.4	19.3 a
Ambia-Talbot[y]	NA[x]	16.5 a
VAM Cocktail[w]	5.4	19.5 a
Protected LSD$_{(P < 0.05)}$		3.9

[z]Mean separation in columns by Fisher's protected test. Items with the same letter are not significantly different from each other.
[y]Wild-collected inoculum from a native prairie soil located near Ambia, Ind.
[x]NA = treatment / species combination not applied.
[w]Mixture of *G. interadices*, *G. margarita*, and Ambia-Talbot inoculum.
[NS]Nonsignificant ANOVA main effect within this species.

Table 2. Second year number of shoots per plant and dry weight of vesicular–arbuscular mycorrhizae-inoculated or noninoculated prairie forb seedlings planted on a highway right-of-way. Data were collected in May (prairie phlox), June (pale-purple coneflower and prairie blazingstar), or July (gray-headed coneflower), 1995.

	Forb species							
	Pale-purple coneflower		Prairie blazingstar		Prairie phlox		Gray-headed coneflower	
Inoculation treatment	Shoots/ plant (no.)	Dry wt (g)	Shoots/ plant (no.)	Dry wt (g)	Shoots/ plant (no.)	Dry wt (g)	Shoots/ plant (no.)	Dry wt (g)
Noninoculated	2.7[NS]	18.7[NS]	2.2[NS]	9.6[NS]	11.6[NS]	7.2[NS]	37.4b[z]	272.8[NS]
Glomus interadicies	2.9	21.7	1.5	6.2	7.9	8.1	41.7 ab	309.6
Gigaspora margarita	3.1	22.4	1.0	NA	12.7	9.0	50.4 a	322.9
Ambia-Talbot[y]	NA[x]	NA	1.0	5.5	8.9	6.9	43.4 ab	260.8
VAM Cocktail[w]	2.1	20.7	1.0	4.8	10.4	9.4	45.2 ab	287.8
Protected LSD$_{(P < 0.05)}$							12.0	

[z]Mean separation in columns by Fisher's protected test. Items with the same letter are not significantly different from each other.
[y]Wild-collected inoculum from a native prairie soil located near Ambia, Ind.
[x]Treatment / species combination not applied.
[w]Mixture of *G. interadices*, *G. margarita*, and Ambia-Talbot inoculum.
[NS]Nonsignificant ANOVA main effect within this species.

headed coneflower and VAM fungi. Possible reasons for the treatment effect being limited to gray-headed coneflower include level of vegetative vigor, root morphology, and developmental phenology.

Gray-headed coneflower is regarded as a pioneer, aggressive, and in some cases nearly weedy species (Kirt, 1989; Schramm, 1978). It establishes more quickly than many other prairie species and is often one of the first species to spread to new areas (Betz, 1986). This vigor includes a rapidly expanding root system. The other species used in this study are less vigorous. Thus, because of this characteristic and especially at the early transplant stage, gray-headed coneflower may have offered a larger root system for VAM fungi to colonize.

The root morphology of gray-headed coneflower may have offered more root surface area for VAM colonization, too, compared with the other species in the study. Gray-headed coneflower develops a deep, fibrous root system. Conversely, pale-purple coneflower produces a thick taproot, prairie blazingstar forms a fleshy corm supported by a limited fibrous root system, and prairie phlox develops shallow fibrous roots (Kirt, 1989; Smith and Smith, 1980). In those species which failed to show a treatment effect, reduced root surface for VAM colonization may have been available compared to gray-headed coneflower.

Lastly, species phenology may help explain some of the uniqueness of the gray-headed coneflower response. Gray-headed coneflower grows vegetatively through May and June followed by flowering in July and early August. Prairie phlox is a May flowering species which has an active vegetative growth period in April. The experiment's planting out date (10 May) came at the early stage of the gray-headed coneflower development period, but was probably too late for the phlox to accrue much benefit from the pretransplant presence of VAM, and by year two, native VAM fungi in the soil had colonized the noninoculated prairie phlox, eliminating the opportunity for a treatment effect. A lesser but similar effect may have occurred in pale-purple coneflower which grows vegetatively only until flowering in June.

Mean colonization percentages of all species and treatments at the conclusion of the experiment were relatively low with none greater than 68%. The relatively abundant soil phosphorus [115 kg·ha^{-1} (102.6 lb / acre)] at the site may have reduced VAM infection (Anderson et al., 1994). The

Table 3. Number of plants surviving to anthesis in the second growing season, 1995, and vesicular–arbuscular mycorrhizae colonization percentage at harvest, of VAM-inoculated or noninoculated prairie forb seedlings planted on a highway right-of-way.

	Forb species							
	Pale-purple coneflower		Prairie blazingstar		Prairie phlox		Gray-headed coneflower	
Inoculation treatment	Survival (no.)	Colonization (%)	Survival (no.)	Colonization (%)	Survival (no.)	Colonization (%)	Survival (no.)	Colonization (%)
Noninoculated	14[z]	32	8	40	15	50	15	68
Glomus interadicies	15	44	2	46	15	45	15	54
Gigaspora margarita	11	48	1	60	15	60	15	66
Ambia-Talbot[y]	NA[x]	NA	7	52	15	42	15	50
VAM cocktail[w]	7	42	2	20	15	52	15	50

[z]Initially, 15 replications per species and treatment combination.
[y]Wild-collected inoculum from a native prairie soil located near Ambia, Ind.
[x]NA = treatment / species combination not applied.
[w]Mixture of *G. interadices*, *G. margarita*, and Ambia-Talbot inoculum.

noninoculated controls were colonized similarly to the inoculated treatments by the end of the experiment. This was most likely due to the fact that the site had been revegetated following road construction for over 30 years before the study. A greater effect of pretransplant VAM fungal inoculation might have been observed if the site had been in a recently disrupted and regraded condition.

We conclude from this study that VAM inoculation as a preplant practice intended to enhance seedling growth in the conversion of a currently vegetated landscape site to prairie forbs must be utilized conservatively and carefully. Previous work (Crank, 1991; Zajicek et al., 1987) has demonstrated increased growth in response to VAM inoculation, but despite that potential, our work points to critical limiting factors. They are 1) site mycorrhizal status, 2) site fertility status, and 3) transplant timing in relation to growth phenology of the plant species.

In this work, the experimental site had extant mycorrhizae that colonized our noninoculated seedlings. Also, the extant P level in the soil was high enough to reduce VAM influence as has been demonstrated by others (Claassen and Zasoski, 1993). Finally, timing of transplanting in relation to growth phenology of the transplant species is a key factor affecting success. Early posttransplant presence of VAM colonization is likely to be beneficial only when a plant is in an active growth phase. Such was the case for our grayheaded coneflower seedlings, but not for prairie phlox, in this study. Had the prairie phlox been transplanted in late March, the results might have been different.

VAM inoculation at the seedling production stage is a relatively low cost practice. It warrants further field study with attention to the factors described above and especially for those prairie forb species that are difficult to establish. Such additional investigation may lead to refined practices that will clarify VAM's horticultural potential in prairie plant establishment.

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