

Growth and nutrition of combinations of native and introduced plants and mycorrhizal fungi in a semiarid range*

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ABSTRACT

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The symbiotic responses of native and introduced plant–fungus combinations were determined. Indian ricegrass (*Oryzopsis hymenoides* (R.&S.) Ricker) and crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) were pre-inoculated with an introduced fungus, three native fungi, or a mixed native inoculum (VAM plants), and transplanted to fumigated field plots on a semiarid range in western Nevada. Non-fumigated and fumigated plots with non-VAM plants were used as controls. No treatment produced significant plant growth responses relative to controls. Crested wheatgrass generally had the lowest levels of VAM fungal colonization, yet the highest levels of nutrient uptake when compared with Indian ricegrass. Differences in nutrient concentrations, but not contents, were significant among fungal inoculum treatments. *Glomus pallidum* increased N shoot concentrations above the fumigated control levels for both Indian ricegrass and crested wheatgrass, and the native *Glomus mosseae* increased N concentration for Indian ricegrass only. For Indian ricegrass, *G. pallidum* increased P shoot concentrations above controls. *G. mosseae* and *G. pallidum* enhanced the uptake of P when compared with the introduced isolate. The introduced *G. mosseae* and the native *Glomus etunicatum* enhanced Mn uptake for Indian ricegrass only. The uptake of N and P were reduced in plants colonized by a mixture of three native isolates when compared with uptake by single native isolates for Indian ricegrass. The lack of a shoot growth effect for Indian ricegrass and crested wheatgrass in the presence of introduced or native VAM fungi suggests that these plants are facultative mycotrophs. Mycorrhizae appear to facilitate luxury consumption of nutrients by these grasses, which may be an important adaptation in nutrient-poor desert environments. Further knowledge of effects by native and introduced VAM fungi, and of host effects on the symbiotic association will contribute to more effective establishment of plants in new areas.

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INTRODUCTION

Root systems are typically colonized by more than one vesicular-arbuscular mycorrhizal (VAM) fungal species (Daft, 1983). Although mutual exclusion by fungi has not been observed, success in occupancy varies and is not always related to host response (Lopes-Aguillon and Mosse, 1987; McGonigle and Fitter, 1990). Host response differs with fungal species (Graw et al., 1979; Menge, 1982; Wilson, 1988) and even with edaphotypes (geographic isolates) within a species (Bethlenfalvay et al., 1989). Differences in host response may be the result of seasonal factors in different endophytes (Daft et al., 1981), varying uptake or exclusion capabilities of VAM fungi for nutrients (Menge, 1982), or to the degree of VAM dependence and root architecture of the host plants (Hetrick et al., 1991). Thus, multiple colonization by mixed inocula containing VAM fungi with different symbiotic strategies might reduce variation and give more consistent benefits to the host plant (Daft, 1983). Knowledge of such specific relationships between symbiotic plant-fungus associations is therefore of fundamental importance for the effective utilization of VAM fungi in agriculture (Graw, et al. 1979).

In the semi-arid Intermontane Basin of the Western United States, crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) has been introduced as a range improvement species (see Cluff et al., 1983). VAM fungi colonizing crested wheatgrass are affected by the level of grazing pressure imposed on the host plant (Bethlenfalvay et al., 1985), but little is known of the differences in nutritional and growth effects of the individual fungal components that together makes up the mycorrhizae of these plants, and how these effects compare with those observed in native plants.

The objectives of this study were to: (1) compare responses of a native and introduced grass species pre-inoculated with individual or mixed native VAM species; (2) compare plant responses elicited by native and introduced edaphotypes of one VAM-fungal species.

MATERIALS AND METHODS

Study area and plot preparation

The study was conducted at Bedell Flat, 35 km north of Reno, NV, in a semi-arid basin big sagebrush (*Artemisia tridentata* spp. tridentata) community characterized previously (Young and Evans, 1974). Average annual precipitation of this site for the years 1985–1988 was 217 mm. Sixty-two percent of the precipitation may occur in the winter months (November–February). Soils of the study area were derived from granodiorite and are classified as Mollic Haplargids (Evans et al., 1967). At the experimental site, the soil had pH 6.3, bound water (1.5 MPa) content of 74 mg kg⁻¹, KCl extract-

able NH_4^+ and NO_3^- of 1.8 and 5.4 mg kg^{-1} , bicarbonate extractable P of 8 mg kg^{-1} and 0.51 % soil organic carbon. The study site was cleared of vegetation during the autumn preceding the transplanting of pre-inoculated seedlings. Individual plots were delimited by boards sunk into the soil to a depth of 1 m. These wooden borders provided protection against chance intrusion of roots and hyphae from non-fumigated soil outside the plots. Vegetation was also removed from the area surrounding the plots. The soil within plots was loosened by spading to a depth of 0.5 m prior to fumigation with methyl bromide (170 g m^{-2}). The fumigant was incubated under a tarp for 48 h, and aerated for 48 h. The soil was then spaded to a depth of 0.5 m. Two plots, used as native-mycoflora controls, were prepared similarly, but they were not fumigated. Ten samples of soil were taken randomly from each plot after fumigation. The samples were mixed and placed into 1.5 l plastic pots. Sorghum (*Sorghum bicolor* L.) was grown for 35 days in two pots with soil from each plot to test for the survival of VAM propagules after fumigation.

Inoculation and transplanting

Soil samples containing root fragments were collected from the root zones of eight specimens of six different species of native grasses in the study area. Spores of VAM fungi were isolated (Daniels and Skipper, 1982) from the pooled samples and identified as *Glomus etunicatum* Becker and Gerd., *Glomus mosseae* (Nicol.&Gerd.) Gerd and Trappe, and *Glomus pallidum* Hall. These species were grown for two generations (4 months each) on sorghum and tested for purity. An inoculum of *G. mosseae* originating from a mesic area of soil pH 6.0 (Agronomy Farm, Gainesville, FL) was also cultured. It was obtained from the International Culture Collection of VA Mycorrhizal Fungi (INVAM) (Plant Pathology Department, University of Florida, Gainesville, FL, isolate INVAM-156). In addition to the single isolate treatments, a treatment utilizing a mixture of the native fungi (with propagule numbers proportionately adjusted to equal those of the other treatments) was also grown.

Propagule densities (spores and root fragments) of the inocula were quantified by the infection unit method (Franson and Bethlenfalvay, 1989). Amounts of inocula of all isolates, determined previously to produce equal numbers of infection units (300 units g^{-1} root fresh mass) on sorghum, were mixed with Bedell Flat soil, placed into growth tubes (200 ml) and planted with pre-germinated seeds of a native bunchgrass, Indian ricegrass (*Oryzopsis hymenoides* (R. and S.) Ricker) and introduced bunchgrass, crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.). Seedlings were grown without fertilization for 42 days under greenhouse conditions. Seedlings with undisturbed, root-permeated soil plugs, which had formed in growth tubes, were transplanted to the field plots. Plants in the greenhouse were prepared for

seven soil manipulations which consisted of five mycorrhizal fungal inoculum treatments and two controls. The treatments were: (1) native *G. mosseae* inoculum (GmNat); (2) native *G. etunicatum* inoculum; (3) native *G. pallidum* inoculum (GpNat); (4) introduced *G. mosseae* inoculum (GmInt); (5) an inoculum consisting of the three native isolates (Mixnat); (6) uninoculated controls in fumigated soils (Fum); (7) uninoculated controls in non-fumigated soils (NonFum). Root colonization of both host species exceeded 40% on extra plants just prior to transplanting.

Experimental design

Fourteen plant–fungus combinations (seven fungal exposures as main-plots; two plant species as sub-plots) were transplanted to the field on 4 April, 1988 in a split-plot factorial design with two experimental blocks. The fungal main-plots were 1.8m × 1.5 m in size and arranged at random. Sub-plots contained ten plants of each of the two plant species. Seedlings were harvested on 9 July, 1988 and plant tops were cut at soil level. Two plants of each treatment were pooled, providing ten subsamples per block of each plant–fungus combination for nutrient and dry-mass evaluations. Macro- and micronutrient concentrations were determined by standard procedures. Nutrient contents were also determined by multiplying plant weight by nutrient concentration. Root cores were taken from four plants of each species in each treatment-block combination to determine VAM colonization. Thus, colonization (gridline intersect method, after staining with trypan blue) was estimated for each subsample.

Statistics

In the overall analysis of variance (ANOVA), soil manipulations (referred to as fungal effects) were tested by the fungal × block interaction term (d.f. = 6) and plant species sub-plot effects were tested by the fungal × plant species × block interaction term (d.f. = 7). When ANOVA were conducted for individual plant species, fungal effects were tested using the fungal × block interaction term (d.f. = 6). Mean separations were conducted on the fungal effects for each plant species using least significant differences (LSD; $P < 0.05$). LSD were conducted only when $P < 0.05$ according to the ANOVA.

RESULTS

Test plants grown indoors in soils collected from the field plots showed no VAM colonization in ten of the 12 fumigated plots and trace colonization (<0.1%) in the remaining two plots. Test plants from the two non-fumigated control plots produced 20% colonization. Figure 1 gives levels of colonization

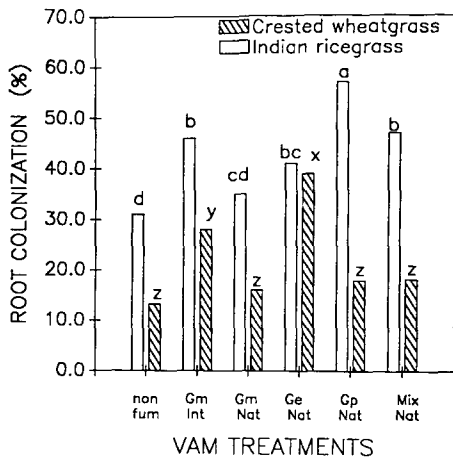


Fig. 1. Colonization of Indian ricegrass and crested wheatgrass by VAM fungi. Three native (GeNat, GmNat, and GpNat) fungi, a mixture of the three (MixNat), and an introduced fungus (GmInt) were used in fumigated field plots. A non-fumigated plot contained the natural soil microflora as inoculum (NonFum). Analysis of variance showed a significant fungal, plant species, and fungal \times plant species interaction ($P < 0.05$). Differences in colonization by VAM treatments within a host plant are indicated when data points are not followed by the same letter (LSD $P = 0.05$).

for all treatments. When averaged over fungal treatments, levels of colonization were significantly greater in Indian ricegrass than in crested wheatgrass. Colonization was 37.5 % and 19.4 % for Indian ricegrass and crested wheatgrass, respectively. In addition, there were both significant fungal effects ($P < 0.001$) and significant fungal treatment \times plant species interactions ($P < 0.001$) for VAM colonization. The fungal treatment \times plant species interaction can be explained by the unusually high level of colonization by GeNat for crested wheatgrass (Fig. 1). This level of colonization was non-significantly different among the two plant species ($P = 0.63$). The GpNat and GeNat treatments were the most aggressive colonizers of Indian ricegrass and crested wheatgrass, respectively (Fig. 1). The introduced *G. mosseae* was a more aggressive colonizer than the native *G. mosseae* for both Indian ricegrass and crested wheatgrass.

When averaged over all fungal treatments, crested wheatgrass had higher nutrient concentrations and total nutrient contents than Indian ricegrass, except for B and Zn (Table 1). The potentially toxic elements Al and Na were three times higher in crested wheatgrass than in Indian ricegrass. Significantly lower P concentration, but equal biomass and P content, in Indian ricegrass vs. crested wheatgrass indicated relative dilution of this element in Indian ricegrass (see Jarrell and Beverly, 1980). Crested wheatgrass had signifi-

TABLE 1

Shoot dry mass, nutrient concentration and nutrient content of Indian ricegrass and crested wheatgrass colonized by VAM fungi in field plots

Response variable	Concentration (mg g ⁻¹)			Content (mg)		
	Rice	Wheat	<i>P</i> -value	Rice	Wheat	<i>P</i> -value
Dry mass (g)	7.5	7.1	0.44			
<i>Nutrient</i>						
N	27.1	34.3	<0.001	203	239	0.056
P	3.5	4.3	<0.001	26	29	0.23
K	21.5	35.0	<0.001	163	247	0.001
Ca	4.8	5.2	0.016	35	35	0.91
Mg	1.3	1.9	<0.001	10	13	0.005
B	0.01	0.01	0.56	0.09	0.08	0.34
Cu	0.09	0.11	0.05	0.63	0.73	0.38
Fe	0.23	0.86	<0.001	1.69	5.61	<0.001
Mn	0.05	0.07	<0.001	2.90	9.85	0.028
Zn	0.05	0.06	0.15	0.37	0.38	0.57
Al	0.41	1.49	<0.001	2.90	9.85	<0.001
Na	0.04	0.15	<0.001	0.27	0.99	<0.001

Data were averaged over the seven fungal treatments ($N=14$).

cantly greater contents of N, K, Mg, Fe, Mn, Al, and Na than Indian ricegrass (Table 1).

The fungal effects on nutrient contents of shoots were nonsignificant according to ANOVA. However, there were significant fungal effects on concentrations of N, P and Mn ($P<0.05$). There were no fungal effects on shoot concentrations of K, Ca, Mg, B, Cu, Fe, Zn and Al. The remainder of the paper focuses on the fungal effects on N, P and Mn concentrations.

For crested wheatgrass, only the GpNat treatment elevated N to levels that were higher than the fumigated control and GmInt (Fig. 2). However, GmInt was not significantly different from the GmNat treatment. For Indian ricegrass, both GmNat and GpNat significantly elevated N levels when compared with the fumigated control. However, all single native isolates were similar to each other as well as to the introduced isolate. All single native isolates significantly enhanced N uptake when compared with the mixed native inoculum, yet the mixed native inoculum was similar to the controls and the introduced isolate.

With respect to P uptake, significant fungal treatment effects prevailed for Indian ricegrass only (Fig. 2). Only GpNat elevated P to levels that were statistically higher than the fumigated control. Both, GpNat and GmNat were superior to the introduced isolate (GmInt). All single native isolates were superior to the mixed native inoculum. The mixed native inoculum was sim-

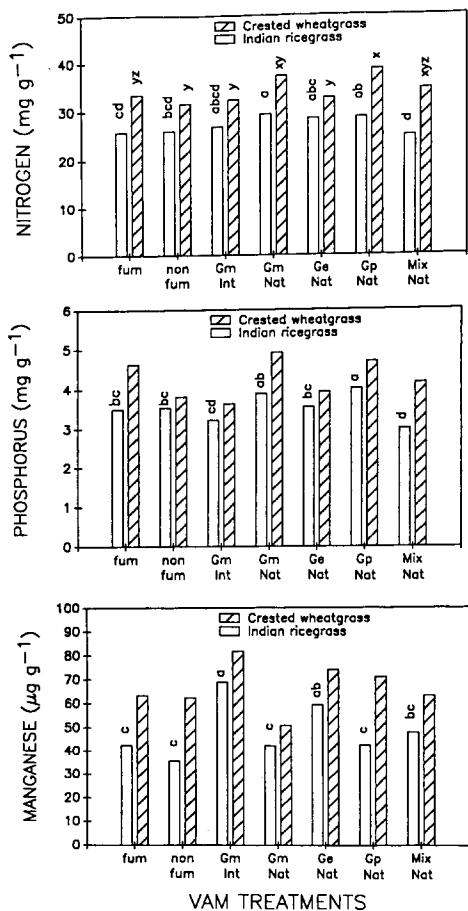


Fig. 2. Shoot concentrations of N, P and Mn. Data points for crested wheatgrass that are not designated by letters were not significantly different according to analysis of variance. Differences in shoot nutrient concentration within a host plant are indicated when data points are not followed by the same letter. (LSD $P=0.05$; Treatments are described in Fig. 1).

ilar to the introduced isolate, however it was inferior to both the fumigated and non-fumigated controls.

As with P, significant fungal effects for Mn were found only for Indian ricegrass (Fig. 2). Both GeNat and GmInt elevated Mn to levels significantly greater than the fumigated control. The GmNat, GpNat and the MixNat treatments were not significantly different from the fumigated control.

The non-fumigated treatment was not significantly different from the fumigated control for Indian ricegrass with respect to N, P and Mn (Fig. 2).

The non-fumigated treatment was also most similar to the mixed inoculum treatment for both N and Mn yet significantly greater than the mixed inoculum treatment for P.

DISCUSSION

A goal of mycorrhizal research is the utilization of VAM fungi to alleviate agricultural problems. In order to translate successful introduction and establishment of fungal isolates into desired responses in plant productivity or soil conservation, the potential for managing VAM fungi in the face of competition with other VAM mycoflora must be known.

This management potential depends on an understanding of the factors limiting plant growth and on the extent of mycorrhiza formation in the prospective host plant and the host soil. Management potential is also influenced by the effects of agricultural practices upon the formation of, and benefits from, the symbiosis (Abbott and Robson, 1991). However, the contributions which native VAM fungi make to the nutrition of introduced crop plants are little known (Abbott and Robson, 1982) and are likely to change with host plants, agricultural practices, and with the identity and composition of the VAM fungal flora. In addition to endophyte effects, host effects are also expressed through selective preference of plants for some of the members of the VAM-fungal community (Johnson et al., 1991). Thus, when plants are introduced as dominant species, a radical restructuring of the VAM mycoflora may occur (Read, 1991).

Neither plant species was responsive in terms of shoot growth, but VAM-fungal effects on nutrient uptake were still apparent, especially for Indian ricegrass. Reduced P uptake by Indian ricegrass colonized by the introduced fungus may be ascribed to the lack of soil adaptation (Lambert et al., 1980) of the latter. The native VAM fungus, GmNat enhanced the uptake of P when compared with GmInt. For P, these data confirm findings that native VAM fungi can be more effective than introduced ones (Hetrick et al., 1986; Sainz and Arines, 1988). Conversely, introduced fungal species can be superior to native fungal species (Hall, 1984; Hung et al., 1990). The Mn data support this contention. The introduced fungus (GmInt) was more effective than GmNat in Mn uptake. In addition, GmInt was functionally similar to GeNat but taxonomically similar to GmNat. Hence, functional attributes cannot be based on taxonomic characteristics alone. A comparison of all single native isolates with the introduced GmInt indicates that the natives were more effective in enhancing P uptake, which suggests that the native fungal isolates resembled one another more in this respect than the introduced isolate.

The merits of mixed inocula containing fungi of differing strategies and providing for more consistent benefits to the host plant have been proposed (Daft, 1983) and seconded (Koomen et al., 1987). In this study, the mixed

inoculum effectively colonized Indian ricegrass roots, but was less effective in nutrient uptake than either introduced or native single isolate inoculum.

The positive uptake of N, P, and Mn by single isolates suggests that VAM fungi may facilitate luxury consumption of nutrients beyond the needs of the plant for shoot growth. Luxury consumption is an important adaptation for stress tolerant plants growing in nutrient poor desert environments (Grime, 1979). Nutrients can be sequestered and placed in reserve for later growth. In contrast, the mixed inoculum treatment reduced the effect of luxury consumption in Indian ricegrass, resulting in nutrient levels no different or slightly lower than the fumigated and non-fumigated controls. If the mixed inoculum treatment more closely resembled the natural field condition, then it might be concluded that mycorrhizae are less important with respect to luxury consumption in Indian ricegrass.

The lack of a P and N uptake effect by mycorrhizae in the non-fumigated control and the mixed inoculum treatment as well as the lack of growth response by either grass indicates that grasses adapted to arid sites are facultatively mycotrophic, as suggested by Allen and Allen (1990). It is suggested that such mycorrhizal grasses have a broadened niche breadth and are better adapted to a greater range of environmental conditions than non-mycorrhizal species (Allen, 1991; Allen et al., 1984). With respect to rehabilitation and restoration of rangelands, facultative mycotrophy may be a positive attribute in plants. Facultatively mycotrophic species may be desirable in revegetation efforts, since mycorrhizal inoculum potential can vary in the soil depending on soil disturbance (Reeves et al., 1979; Doerr et al., 1984). It has already been shown that crested wheatgrass becomes mycorrhizal, yet accumulates nutrients effectively in both the mycorrhizal and non-mycorrhizal state. Perhaps this is why crested wheatgrass is such a successful revegetation species in the Great Basin region of the western United States.

CONCLUSIONS

Non-native crested wheatgrass was a superior nutrient accumulator than native Indian ricegrass. Shoot biomass was not different between the two plant species and was not affected by mycorrhizal inoculation. Only the single native isolate, *G. pallidum* enhanced N shoot concentration above control levels for crested wheatgrass. Neither P nor Mn nutrient uptake were influenced by mycorrhizal colonization of crested wheatgrass. For Indian ricegrass, the native *G. mosseae* enhanced N concentrations above control levels and the native single isolates were superior to the non-native with respect to P uptake. *G. pallidum* was the only fungal treatment that elevated P levels above the controls for Indian ryegrass. The non-native isolate was superior to most natives in the uptake of Mn. The mixed inoculum was less effective in N and P nutrition than single native isolates. Single native isolates induced luxury

consumption of N and P, and mixed natives inhibited luxury consumption. Both grass species were facultatively mycotrophic which makes them well adapted to a wide range of mycorrhizal inoculum potentials.

In addition to the response between the host plant and its VAM fungal endophyte, the equally important relationships between the soil and the mycorrhizal soil mycelium must be elucidated before introduction of either organism to a new area can produce positive results. Such positive attributes of mycorrhizae cannot be restricted only to plant response, but should be expanded to understand their effects on soil, especially with respect to soil aggregation and nutrient cycling.

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