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Grazing Effects on Mycorrhizal Colonization and Floristic Composition of the Vegetation on a Semiarid Range in Northern Nevada

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Abstract

The effect of grazing on the colonization of range plants by vesicular-arbuscular mycorrhizal (VAM) fungi was investigated within an enclosure and on degraded Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) rangelands at Medell Flat, near Reno, Nev. Implications of the interaction between mycorrhizae and grazing, relevant to the ecology and management of rangelands, are discussed. Density of forage grasses and their colonization by VAM fungi was significantly reduced as a result of grazing, in some cases by more than 50%. No differences in colonization were found in forage or nonforage broadleaf plants. A significant shift in the floristic composition and density of range plants occurred as a result of the presence or absence of grazing pressure. The decrease in VAM-fungal colonization of grasses under grazing is ascribed to a decrease in leaf areas and an increase in root to shoot ratios—conditions which result in decreased source capacity and increased sink demand.

The interactions between vesicular-arbuscular mycorrhizal (VAM) fungi, their host plants, and the soil are complex (Mosse 1973) and little known in semiarid rangelands (Trappe 1981). Plants benefit from their VAM-fungal endophyte when available P in the soil is limiting (Mosse 1973) and within a certain concentra-

tion range (Bethlenfalvay et al. 1983). Under these conditions the endophyte enhances P uptake to the host (mycotrophy). At higher or lower P concentrations, VAM fungi may act as parasites and may contribute to the growth depression observed in range plants under certain levels of P availability (Hays et al. 1982, Lorenz 1970). As these fungi are obligate biotrophs, they are entirely dependent on their host plants as a source of energy (Snellgrove et al. 1982). Any factor affecting photosynthesis will therefore affect the VAM fungal symbiont (Allen et al. 1981, Daft and El-Giahmi 1978, Trappe 1981). However, the effects of grazing on VAM fungi are little known (Davidson and Christensen 1977, Wallace 1981), and the influence of these symbionts on the tolerance of plants to grazing stress is unknown (Reece and Bonham 1978). This gap in our knowledge of the mechanisms of relationship between mycorrhizal colonization and grazing has added significance, since VAM fungi appear to play a role in soil aggregation and stabilization (Jehne and Thompson 1981, Sutton and Sheppard 1976). These are important problems in the management of lands under cultural stress in arid climates (Cannell and Weeks 1979).

The purpose of this study was to determine grazing effects on VAM fungal colonization of range plants in a heavily grazed Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) community.

Materials and Methods

Study Area

The survey was conducted at Medell Flat, 35 km north of Reno, Nev., in a 20-30 cm precipitation zone at 1,600 m elevation. Rainfall in the spring preceding the survey was approximately 7 cm. The study area was burned by wildfire 25 years ago and it is now

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dominated by cheatgrass (*Bromus tectorum*) and other herbaceous species. Some native perennial grasses occur with Sandberg bluegrass (*Poa sandbergii*), Indian ricegrass (*Oryzopsis hymenoides*), squirreltail (*Sitanion hystrix*), and species of *Stipa* being the most common. Shortly after the burn, standard crested wheatgrass (*Agropyron desertorum*) was seeded in the general area. Only a marginal stand was established. In some areas in the enclosure various wheatgrasses (*Agropyron* spp.) had been planted. There were also scattered stands of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) green rabbitbrush (*Chrysothamnus viscidiflorus*) and horsebrush (*Tetradymia glabrata*). The soils of the study area are derived from quartz diorite and are classified as Mollic Haplargids (Evans et al. 1967) and were characterized by Young and Evans (1974).

From about 1890 until 1920 Medell Flat was used in the spring and fall by range sheep operations, turning the area virtually into a dust bed at the turn of the century (Kennedy and Doten 1901). From 1920 until 1978 the area was subject to very severe, year-long grazing and in 1978 was put in a three pasture, rest-rotation grazing system. When grazed, (April 1 to December 31, second year and July 15 to December 31, third year) the stocking rate was 3.85 ha (9.5 acre)/animal unit (cows) month.

Measurements

Vegetation and the associated VAM mycoflora was sampled during the second year (June 1982) of the three-year grazing cycle in a grazing enclosure (approximately 2 ha, constructed in 1963) and in the surrounding grazed land. All plants except redstem filaree (*Erodium cicutarium*) and Sandberg bluegrass were sampled for density in 10 quadrats (10 m²) on both sites. One plant of each species was collected from each of the 10 quadrats inside and outside the enclosure for the determination of VAM-fungal colonization and plant dry weights. Roots of needle-and-thread grass (*Stipa comata*) and squirreltail (*Sitanion hystrix*) were excavated to a depth of 30 cm, and roots of the forb tapertip hawkbeard

(*Crepis acuminata*) to 60 cm. Roots and shoots of these plants were oven-dried at 70°C for 2 days. Dry weights were used to determine root dry-weight ratios (grazed/ungrazed) and root/shoot ratios for grazed or ungrazed plants.

The intensity of VAM-fungal colonization (percentage of root length infected) was determined by staining and evaluated according to Bethlenfalvai and Yoder (1981). To establish intra-species variation in the intensity of colonization, all 10 samples of 2 grasses (cheatgrass and needle-and-thread grass) and of 2 forbs [tapertip hawkbeard and desert phlox (*Phlox austromontana*)] were assayed individually for VAM fungi. The roots of the remaining plant species were not evaluated individually. Root systems of all 10 specimens of a species were pooled, cut in 1-cm sections, and dispersed in water. Root segments were selected at random for the evaluation procedure, and it was assumed that variability within grasses or forbs would be similar to that for the species assayed in detail. Statistical differences between VAM-fungal colonization of plants from grazed or ungrazed areas were determined by student's *t*-test.

Taxonomic identification of VAM fungi was preceded by culturing the fungi in a medium of perlite and nutrient solution with sorghum (*Sorghum bicolor*) as the host plant. The fungal inoculum was made up of pooled soil and root samples from all plants, and was mixed with the perlite (1/1, v/v). Inocula from inside and outside the enclosure were cultured separately. Roots and growth medium were assayed for VAM fungi after 4 months of growth in a greenhouse equipped with supplementary lights providing a photosynthetic photon flux density of 400 μmol·m⁻²·s⁻¹ and extending daylength to 16 h. Fungal spores isolated from soil and roots were identified according to Trappe (1982).

Soil was tested for available (NaHCO₃-extractable) P content according to Watanabe and Olsen (1965) at depths of 5 to 13 and 27–35 cm. Four samples, pooled from 24 field replications, were analyzed. Samples at each depth were taken from inside and outside the enclosure.

Table 1. Floristic composition and species density of range plants near Reno, Nevada. Vegetation was surveyed in an ungrazed (19 yr) enclosure and in the heavily grazed surrounding area.

Family	Species	Density (plant/10 m ²) ¹		VAM colonization
		ungrazed ² $\bar{x} \pm S.D.$	grazed ³ $\bar{x} \pm S.D.$	
Compositae	<i>Erigeron linearis</i>	—	3 ± 13	+
	<i>Chrysothamnus viscidiflorus</i>	2 ± 2	10 ± 9	+
	<i>Tetradymia glabrata</i>	1 ± 1	1 ± 4	+
	<i>Crepis acuminata</i>	69 ± 26	13 ± 20*	+
	<i>Lygodesmia spinosa</i>	—	30 ± 38	+
	<i>Artemisia tridentata</i>	1 ± 1	3 ± 4	+
Cruciferae	<i>Descurainia pinnata</i>	17 ± 14	19 ± 9	+ ⁴
	<i>Sisymbrium altissimum</i>	14 ± 10	16 ± 5	—
Gramineae	<i>Agropyron intermedium</i>	29 ± 50	—	+
	<i>Bromus tectorum</i>	1581 ± 546	526 ± 227*	+
	<i>Oryzopsis hymenoides</i>	8 ± 2	4 ± 4	+
	<i>Stipa comata</i>	9 ± 4	3 ± 2*	+
	<i>Sitanion hystrix</i>	15 ± 9	3 ± 3*	+
	<i>Agropyron desertorum</i> ⁵	11 ± 2	2 ± 2*	+
	<i>Stipa thurberiana</i>	12 ± 7	2 ± 3*	+
Leguminosae	<i>Agropyron trichophorum</i>	27 ± 55	—	+
	<i>Astragalus</i> sp.	3 ± 4	15 ± 7*	+
Polemoniaceae	<i>Lupinus</i> sp.	—	6 ± 7*	+
	<i>Phlox austromontana</i>	26 ± 40	29 ± 22	+
	<i>Leptodactylon pungens</i>	—	6 ± 5	+

¹Means and standard deviations based on ten quadrats, each 10 m².

²Species shown as missing were not found in the grazing enclosure.

³Species shown as missing were introduced in the enclosure by seeding and were not present outside.

⁴Trace infection of the root tips only in tansy mustard. Colonization was not quantified in the legumes.

⁵Seeded inside and outside the enclosure.

*Indicates significant differences between plant densities on grazed or ungrazed sites by student's *t*-test (*P* < 0.05).

Results

Effect of Grazing on Plants

Elimination of grazing from a portion of the rangelands at Medell Flat resulted in a shift in vegetation within the grazing enclosure (Table 1). Certain plant species either did not occur in the enclosure [fleabane (*Erigeron linearis*), lupine (*Lupinus* sp.), prickly phlox (*Leptodactylon pungens*), and thorny skeleton plant (*Lygodesmia spinosa*)] or had considerably lesser density [Wyoming big sagebrush, green rabbit brush, horsebrush, and locoweed (*Astragalus* sp.)]. The density of other species [tapertip hawksbeard, standard crested wheatgrass (*A. desertorum*), cheatgrass, Indian ricegrass (*Oryzopsis hymenoides*), squirrel tail, needle-and-thread grass, and Thurber's needlegrass (*Stipa thurberiana*)] was significantly higher in the enclosure than in the surrounding grazed land. A few species [desert phlox, tansy mustard (*Descurainia pinnata*)] and tumble mustard (*Sysimbrium altissimum*) did not show a response to grazing. Amur intermediate wheatgrass (*Agropyron intermedium*) and Tobar pubescent wheatgrass (*Agropyron trichophorum*) were seeded only inside the enclosure and did not serve for grazing comparison.

Grazing had a dramatic effect on the grasses in the area sampled. Within the enclosure bunchgrasses had full tufts with hundreds of well-developed leaf blades while under grazing leaf blades were small, sparse, and restricted to the perimeter of the bunch (Fig. 1). The root systems of bunchgrasses declined in weight under grazing but did not suffer a decrease comparable to the shoots (Table 2). Grazing had little effect on the palatable forb (tapertip hawksbeard). These plants were of the same size in- and outside the enclosure (Table 2), but were much reduced in number on the outside (Table 1).

Table 2. Root dry weight and root/shoot ratio comparisons as a result of grazing. Root dry weight ratios (grazed/ungazed) express the decline in root development in the grazed area relative to that in the enclosure.

Parameter	Species		
	Needle-and-thread grass	Squirrel tail	Hawksbeard
Root dry weight ratio ¹	0.48	0.53	0.95
Root/shoot ratio ¹			
ungrazed	1.2	1.1	0.6
grazed	15.3	14.6	0.6

¹Numbers are calculated from means of ten replications.

Effect of Grazing on Mycorrhiza and Soil P

Grazing significantly decreased VAM colonization of all grasses, in some cases by more than 50% (Table 3). With broadleaf species, grazing had no significant effect on the extent of colonization. Only one VAM-fungal species, *Glomus fasciculatum* (Thaxt. *sensu* Gerd. & Trappe (Gerdemann and Trappe 1974) (Fig. 2), was found in the grazed area. Within the enclosure a second species, *Glomus clarum* Nicol. & Schenck (Nicolson and Schenck 1979) was also present. Concentrations of available (NaHCO₃-extractable) P were similar at a depth of 5 to 13 cm inside and outside the enclosure (10.2 and 10.4 μg P/g soil, respectively). At a depth of 27 to 35 cm, however, P concentrations were significantly ($p < 0.05$) higher on grazed land (6.0 μg P/g soil) than inside the enclosure (3.7 μg P/g soil).

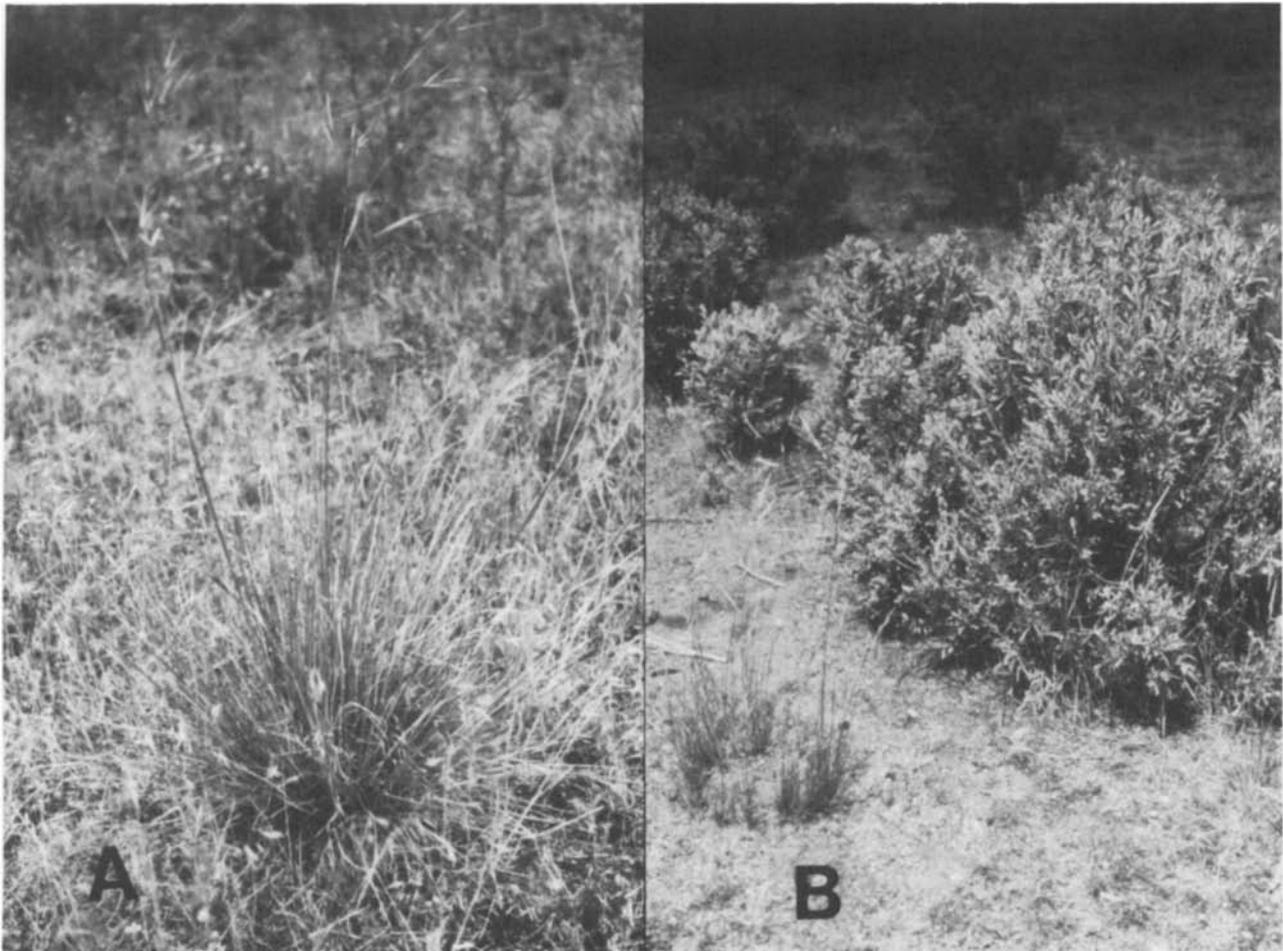


Fig. 1. A. Needle-and-thread grass in a grazing enclosure. Plants in the enclosure were not subject to grazing for 19 yr. B. Needle-and-thread grass subject to heavy grazing.

Table 3. Colonization of range plants by vesicular-arbuscular mycorrhizal (VAM) fungi near Reno, Nevada during June 1982.

Family	Species	VAM colonization (%) ¹	
		ungrazed ²	grazed
Compositae	<i>Erigeron linearis</i>	—	47
	<i>Chrysothamnus viscidiflorus</i>	46	45
	<i>Tetradymia glabrata</i>	25	26
	<i>Crepis linearis</i>	47 ± 14	40 ± 11
	<i>Lygodesmia spinosa</i>	—	67
Gramineae	<i>Artemisia tridentata</i>	27	25
	<i>Agropyron intermedium</i>	85	—
	<i>Bromus tectorum</i>	76 ± 10	33* ± 9
	<i>Oryzopsis hymenoides</i>	86	40*
	<i>Stipa comata</i>	82 ± 9	33* ± 9
	<i>Sitanion hystrix</i>	83	53*
	<i>Agropyron desertorum</i>	88	63*
	<i>Stipa thurberiana</i>	88	40*
	<i>Agropyron trichophorum</i>	96	—
Polemoniaceae	<i>Phlox austromontana</i>	63 ± 14	54 ± 10
	<i>Leptodactylon pungens</i>	—	57

¹Percent colonization expressed as proportion of root length infected.

²Ungrazed plants were located in a 19 year enclosure.

*Significance at the 5% level.

Discussion

The VAM-fungal symbiont is dependent on photosynthate availability (Bethlenfalvay and Pacovsky 1983, Daft and El-Giahmi 1978), and clipping or grazing of the host plant has an adverse effect on its development (Wallace 1981). The inhibition of VAM-fungal colonization of grasses in this study can thus be ascribed to the reduction of the foliage under grazing, and to the concomitant shift in root/shoot ratios. The high root/shoot ratios produced by grazing indicate that source capacity in grazed plants may be insufficient to satisfy sink demand for photosynthates by the relatively large root system and the fungal endophyte. Although roots were not completely excavated, it is estimated that 85% of the total root mass of the grasses was retrieved (Weaver 1950) providing adequate comparison for grazing effects.

While positive effects of VAM fungi on individual physiological

processes of the host, such as water relations and photosynthesis, have been reported (Allen et al. 1981), the mechanism of the relationship between VAM fungi and grazing and its impact on the arid-range ecosystem is still hypothetical (Wallace 1981). Correlations between grazing intensity and mycorrhizal infection have rarely been made (Davidson and Christensen 1977, Wallace 1981) and are difficult to interpret, as such evaluations are almost exclusively based on VAM-fungal colonization of the root cortex. This, however, is a less reliable measure of symbiotic effectiveness than the development of an extensive extraradical VAM-fungal mycelium (Bethlenfalvay et al. 1982, Graham et al. 1982), and its affinity for P absorption (Cress et al. 1979). The relevance of VAM fungi to soil structure formation and stability (Sutton and Sheppard 1975, Trappe 1981) and to the revegetation of disturbed lands (Reeves et al. 1979) is beginning to be appreciated. Other functions such as an effect on seedling establishment, soil permeability to water and soil deterioration due to compaction are likely and should be investigated.

The effect of the decrease in VAM-fungal colonization on the P nutrition of the grazed plants was not determined in this study. However, as plant-available soil P levels were low (between 4 to 10 $\mu\text{g P/g soil}$) and within the range (4 to 12 $\mu\text{g P/g soil}$) where growth enhancement due to VAM fungi was previously shown to occur (Bethlenfalvay et al. 1983), one may conclude that plants under grazing with low levels of VAM-fungal colonization were also deficient in P and suffered growth depression relative to nongrazed plants.

The absence of *G. clarum* from the pooled inoculum collected from all plants outside the enclosure indicates a severe reduction (or elimination) of this species of VAM fungus under conditions produced by grazing pressure. It may be inferred that *G. clarum* is more sensitive to photosynthate stress than *G. fasciculatum*, which may outcompete and displace the former when carbohydrates are limiting. Thus, grazing appears to cause not only a shift in the composition of the vegetation but also in the accompanying mycoflora.

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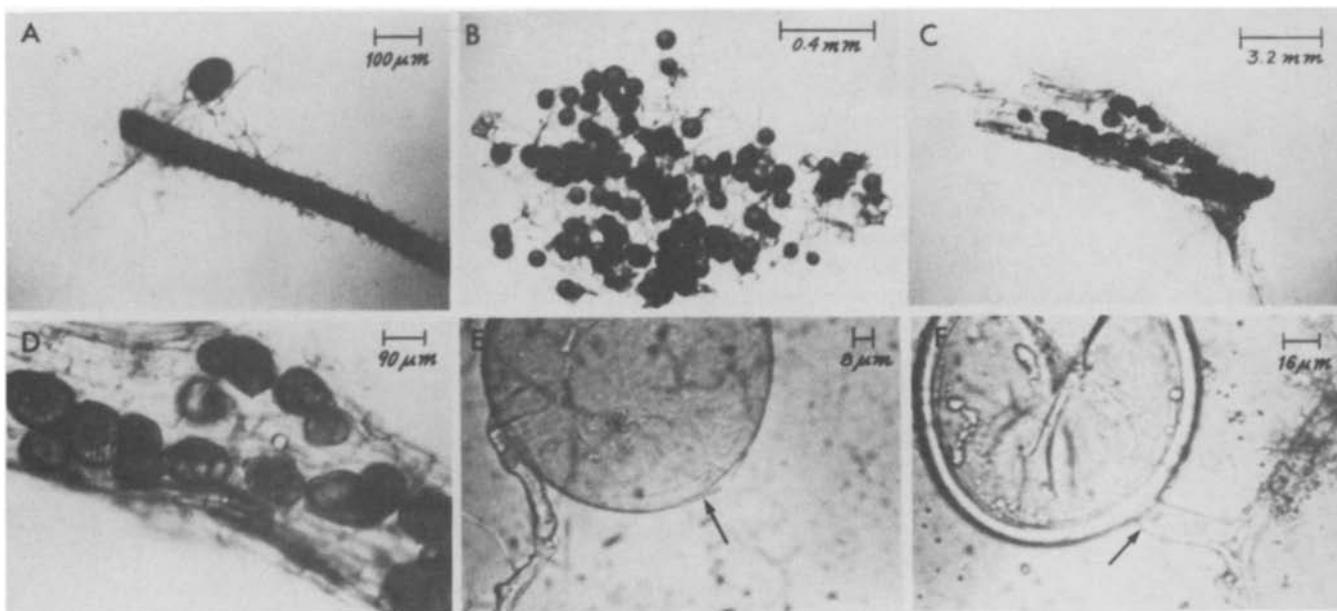


Fig. 2. *Glomus fasciculatum*, the dominant species of vesicular-arbuscular mycorrhizal fungus found at Medell Flat near Reno, Nevada. A-root segment with extraradical hyphae and spore, B-loose sporocarp showing extraradical hyphae and spores, C and D-root segment with intraradical hyphae and vesicles, E and F-some species characteristics of *G. fasciculatum*: double wall (E) and constriction of hyphal attachment (F).

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