

Fungal Root Endophytes in Fourwing Saltbush, *Atriplex canescens*, on Arid Rangelands of Southwestern USA

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This research was conducted to determine the nature and incidence of fungal root endophytes on fourwing saltbush, Atriplex canescens (Pursh) Nutt. Root cortex cells of fourwing saltbush in arid rangelands of the southwestern United States were analyzed and found to be regularly colonized with three types of endophytic fungi: septate, vesicular-arbuscular mycorrhizae (VAM), and Chytridiomycetes. Septate fungi were 2.7 times more prevalent than VAM and formed intimate non-pathogenic associations characterized by inter- and intracellular hyphae, coils, microsclerotia, and occasional labyrinthine or "Hartig net" structures similar to those affiliated with ectendomycorrhizae. External hyphae formed intimate associations with soil and sand particles. Typically, VAM were characterized by hyphae, vesicles, and (at times) coils. VAM were 2.2 times more prevalent than chytrids. Chytrids were rather common and were expressed as resting and active sporangia found within root cortex cells. The widespread occurrence of these non-destructive fungal associations with plants implies that they have an important role in plant survival in arid environments.

Keywords arid ecology, chytrids, land restoration, mutualism, mycorrhizae, rangeland, saprophytic fungi, symbiosis, VAM

Symbiotic associations between forage plants and fungi have been studied extensively. Endophytic fungi benefit both crop and native plants in all ecosystems. For pasture lands, an example of a mutualistic relationship is found between *Acremonium* fungi and forage grasses (Clay, 1990; Siegel et al., 1984). *Acremonium* hyphae grow between plant cells without injury and colonize developing ovules. These fungi are dispersed by seed to ensure establishment in subsequent generations (Hinton & Bacon, 1985). Other documented benefits of fungal colonization to the grass host are varied and include reduced herbivory (Strahan et al., 1987), increased insect resistance (Funk et al., 1983), improvements in plant growth (Latch et al., 1985), resistance to disease (White & Cole, 1985), and

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resistance to drought (Arachevaleta et al., 1989). These fungi also modify morphological expressions in the host (Siegel et al., 1987).

More frequently investigated are mycorrhizal fungi that modify plant roots and enhance water and nutrient uptake for production and survival (George et al., 1991). Vesicular-arbuscular mycorrhizae (VAM) are particularly important in phosphorus nutrition of both crop and native plants growing in regions where nutrients and water are generally seasonally limited. Ectomycorrhizal fungi associated with forest shrubs and trees preferentially occupy soil regions that are high in organic matter, and many species degrade protein and make nitrogen and other nutrients available to the host (Abuzinadah & Read, 1989; Read et al., 1989).

Plants in arid environments are specifically challenged in both (a) accessing nutrients and water from limited and immobile resources, and (b) making these resources available when conditions are favorable for performing vital functions such as growth or flowering. Read (1992) described mycelial attributes of three mycorrhizal classes, the VAM, ecto-, and ericoid mycorrhizae. Each class has distinctive features of distribution, structure, and function, enabling each to play a central role in the nutrition, growth, and survival of their host plants. These fungi influence the structure of the ecosystem in which they predominate. In arid ecosystems, we should ask: Are there specialized fungal associations that assist in supplying essential resources to plants?

In initial unpublished studies, we found that dominant grasses and shrubs on arid rangelands were regularly colonized with three types of non-pathogenic fungi. Therefore, the objective of this study was to characterize the nature and extent of fungal root endophytes associated with fourwing saltbush, *Atriplex canescens* (Pursh.) Nutt., an important native shrub on arid southwestern-USA rangelands. Understanding the plant-microbe-soil complex is essential for managing and maintaining native plants in arid ecosystems.

Materials and Methods

Roots of *Atriplex canescens* (Pursh.) Nutt. were sampled from eight native sites in New Mexico and southern Colorado (Table 1). The sites were sampled twice: first in June 1995, at the beginning of seasonal growth, and again in October 1995. Ten different randomly selected plants were sampled each time. The sites varied in precipitation, ambient air temperature, elevation, soil types, and moisture content. Classification of soil at each site is listed in Table 2.

Soil was taken from the surface 20 cm at the base of each plant. This zone was reported by Schwab and Reeves (1981) to have the highest incidence of mycorrhizal fungi. Soil was sieved through a 6-mm screen, and small feeder roots were collected and sealed in plastic bags, returned to the laboratory, and dried at 25°C. Within 7 days, roots were cleared by the method of Brundrett et al. (1984) and stained with chlorazol black E, specific for fungal tissue; 20-cm sections of roots from each plant were mounted on a microscope slide. Colonization for VAM, septate, and chytridiomycete fungi was assessed microscopically to determine the decimal fraction of the root length colonized.

Data were analyzed as a randomized complete block design with plants, sites, and dates as blocks. The dependent variable was colonization, expressed as a decimal fraction of the total root length examined. Mean differences were tested using LSD ($p \leq 0.05$).

In our initial study, we observed that both grass and shrub roots were regularly

Table 1
Collection sites for roots and soil moisture from fourwing saltbush and associated grasses in New Mexico and Colorado

Site	% Soil moisture		Elevation (m)	Dominant plants ^a	Location ^c
	June	October			
Ft. Stanton	3.1	8.8	1950	PJ, Bg	1.5 km, SE Capitan Lincoln, NM
Corona	2.1	7.8	1920	PJ, BG	21 km, SW Corona, Lincoln, NM
Willard	5.8	10.6	1830	4W, AS	11 km, S Willard, Torance, NM
Cimarron	11.0	11.0	1950	PJ, BG	1.6 km, S Cimarron, Colfax, NM
Rio Grande	2.3	2.2	2320	BS, BG	27 km, E Antonito, Conejos, CO
Bisti	2.5	2.2	2010	BS, BG	21 km, S Farmington, San Juan, NM
Saltlake	1.6	4.8	1950	4W	31 km, NE Quemado, Cibola, NM
Jornada Experimental Range	0.7	1.3	1310	4W	43 km, NE Las Cruces, Dona Ana, NM

^aDetermined by visual observation at time of sampling. PJ, pinyon (*Pinus edulis* Engelm.) and juniper (*Juniperus* sp.); BG, blue grama [*Bouteloua gracilis* (HBK.)Lag.]; 4W, fourwing saltbush [*Atriplex canescens* (Pursh)Nutt.]; AS, alkali Sacaton (*Sporobolus airoides* Torr.); BS, broom snakeweed (*Gutierrezia* spp.).

^cPlace names are City, county, state. NM, New Mexico; CO, Colorado.

colonized by all three fungal classes. In this study, roots from a single grass plant of the dominant grass species were collected at each of the eight sites. Roots were stained, and 20-cm sections were mounted and analyzed microscopically (but not statistically) to compare relative fungal colonization. The dominant grass was *Bouteloua gracilis* (H.B.K.) Lag. for seven sites, and *Sporobolus flexuosus* (Thurb.) Rydb. at our Jornada Experimental Range (JER) site. About 300 g of soil were also collected from the shrub root zone at each site, weighed in the laboratory, heated at 100°C for 72 h, and re-weighed to determine the percent moisture.

Results

Septate fungi grew extensively in the inter- and intracellular spaces of *A. canescens*, forming vegetative hyphal masses, coils, and microsclerotia (Figure 1). “Hartig net”-like structures were occasionally observed as loosely matted fungal sheaths or mantles on the root surfaces. Most frequently, however, the external hyphae grew directly from the root surface into the soil. In sandy soils, the external hyphae aggregated sand grains at the root

Table 2
Soil classification of fourwing saltbush, *Atriplex canescens* collection sites

Site	Soil series	Soil family
Ft. Stanton	Reventon loam	Fine-loamy, mixed, mesic, typic Argiustolls ^a
Corona	Rock taubarlc	Loamy, gypsic, mesic, shallow ustic Torriorthents ^b
Willard	Willard loam	Fine-silty, mixed, mesic ustollic Calciorthids ^c
Cimarron	Swastika	Fine, mixed, mesic aridic Argiustolls ^d
Rio Grande	Luhon	Fine, loamy, mixed Borollic River Calciorthids ^e
Bisti	Shepphard	Mixed, mesic typic Torripsamments ^f
Saltlake	Hubbel	Ashy, mesic aridic Argiborolls ^g
Jornada		
Experimental		
Range	Dona Ana	Fine-loamy, mixed, thermic typic Haplargids ^h

^{a,b}Sprinkle, D. G. 1983. Soil Survey of Lincoln County Area, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^cBourlier, B. G., R. E. Neher, D. B. Crezee, K. J. Bowman, and D. W. Meister. 1970. Soil Survey of Torrence Area, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^dAnderson, G. W., et al. 1982. Soil Survey of Colfax County, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^eHacker, L. W., and J. O. Carleton. 1982. Soil survey of Taos County and parts of Rio Arriba and Mora County, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^fKeetch, W. C. 1980. Soil Survey of San Juan County, NM, Eastern Part. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^gJohnson, W. R. 1985. Soil Survey of Catron County, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

^hBullock, H. E., and R. E. Neher. 1980. Soil Survey of Dona Ana County Area, NM. USDA-SCS. U.S. Gov. Print. Office, Washington, D.C.

surface. When roots were sieved at sampling, external hyphae were observed attached to sand and soil aggregates, suggesting extensive soil colonization.

VAM colonization was characterized primarily by internal hyphae and vesicles. Internal hyphal coils were less frequent but were seen regularly. Arbuscules were not observed in *A. canescens* or in the associated grasses (*B. gracilis* and *S. flexuosus*) of this study.

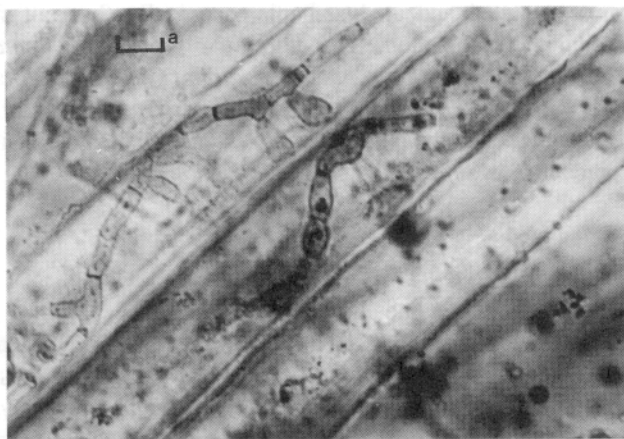


Figure 1. Septate fungi within root cortex cells of blue grama, *Bouteloua gracilis*. Scale (a) = 10 μ m.

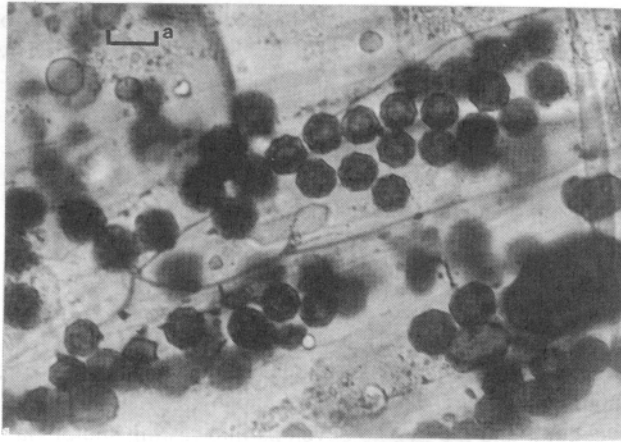


Figure 2. Resting sporangia of chytrids in root cortex cells of fourwing saltbush, *Atriplex canescens*. Scale (a) = 15 μ m.

Resting and active sporangia of Chytridiomycetes (chytrids, mostly aquatic fungi) were the only structures observed within root cortex cells (Figure 2). Other structures may not have been visible with the staining methods used, and the sporangia may have developed as feeder roots became dormant or inactive in drying soils.

In most plants, feeder root tissues were colonized with at least two, and often with all three, fungal types. Septate fungi were 2.7 times more prevalent than VAM, and VAM were 2.2 times more prevalent than chytrids (Table 3). Correlations and interactions among fungal classes were not significant, suggesting that colonization by each type was independent. A general trend was observed, however, that fungal incidence for all classes was greater following precipitation events at a location. For example, the incidence for each class was low at Corona, Bisti, and the JER sites where winter and spring soil moisture was low preceding the June collection. In contrast, the incidence of fungal class

Table 3

Mean incidence of vesicular-arbuscular mycorrhizae (VAM), septate fungi, and chytridiomycetes colonization in fourwing saltbush, *Atriplex canescens*, at eight locations in New Mexico and southern Colorado in June and October of 1995

Site	VAM		Septate		Chytrids	
	June	October	June	October	June	October
Ft. Stanton	0.414	0.233	0.837	0.938	0.161	0.235
Corona	0.059	0.264	0.596	0.943	0.054	0.087
Willard	0.513	0.131	0.879	0.922	0.191	0.096
Cimarron	0.661	0.142	0.906	0.870	0.317	0.225
Rio Grande	0.586	0.692	0.735	0.871	0.093	0.091
Bisti	0.035	0.085	0.639	0.979	0.002	0.01
Saltlake	0.186	0.047	0.829	0.978	0.098	0.104
Jornada Experimental Range	0.094	0.370	0.649	0.930	0.049	0.192
Mean	0.319	0.279	0.789	0.929	0.121	0.155
Fungal mean	0.309B		0.844A ^a		0.138C	

^aFungal means are different ($\alpha = 0.05$ and LSD = 0.047).

was higher at Cimarron, where soil moisture was high before collection (Table 3). A similar pattern was noted in October, except that VAM colonization was high at Rio Grande and Bisti and low at Cimarron sites. Fungal activity is likely related to soil moisture, nutrient availability, and the physiological activity of the host and fungi before sampling. Soil was dry at most locations and collections, except Cimarron, which was wet (11% actual water content by weight). Soil moisture was generally higher in October at most sites following a typical July–September monsoonal season (Table 1).

Discussion

Chytrids are commonly parasitic on algae, fungi, and protozoa, and saprophytic on dead plants and chitinous substances. Their hyphae range from simple to a well-organized, multinucleate mycelium, and the zygote develops into resting sporangia (Alexopoulos & Mims, 1979). We did not observe active hyphae, but sporangia were common in *A. canescens* roots and may have developed as feeder roots became dormant or inactive in dry soils. The regular, non-destructive colonization by chytrids of roots in this study suggests that they have a significant but unknown function. Our preliminary studies suggest that they survive surface sterilization and regulate fungal colonization and nutrient uptake (unpublished data).

Mycorrhizal research in arid ecosystems has focused on VAM, primarily because of its well-known role in phosphorus (P) uptake in other ecosystems. In these studies, VAM colonization of *A. canescens*, *B. gracilis*, and *S. flexuosus* was common. However, we concur with others (Miller, 1979; Saif et al., 1977; Trappe, 1981; Williams & Aldon, 1976) that VAM expression in many desert plants differs from that found in more mesic environments. Hyphae and vesicles are extensive, while arbuscules are rare.

Since arbuscules are the principal exchange site for P and carbon between the host and VAM fungi (Gianinazzi & Gianinazzi-Pearson, 1979; Cox & Tinker, 1976), some have suggested that Chenopodiaceae species such as *Atriplex* spp. may not be mycorrhizal (Hirrel et al., 1978). Arid environments could have significant influence on VAM expression and function. In drying soils, P uptake decreased (Jupp & Newman, 1987) while P translocation to the plant generally occurred during snow melt in arid regions (Chapin, 1980). Allen (1983) also observed a brief period of arbuscule formation in *A. gardneri*, previously considered to be non-mycorrhizal, during spring snow melt. Conditions favoring P uptake and arbuscule formation in arid environments would be erratic and brief. We might expect in arid environments that alternative methods of nutrient exchange with the host, such as those used by other mycorrhizal fungi or better-adapted fungal associations, may be found. This was suggested by Williams et al. (1974), when they found that *A. canescens* had enhanced production and survival in mine spoil plantings when colonized with VAM hyphae and vesicles, without arbuscules.

Other benefits of mycorrhizal colonization were suggested by Allen et al. (1981), when they found that mycorrhizal colonization increased transpiration and photosynthetic rates while leaf resistances to water diffusion were decreased in *B. gracilis* under arid conditions. Chlorophyll and phosphate concentrations were increased by 28% and 70%, respectively. This ability to alter important physiological processes would substantially enhance plant survival in arid environments.

Nutrients and water are absorbed from the soil by mycorrhizal hyphae, which retain dormancy and viability in very dry soils (Jasper et al., 1989). Many soil fungi can grow rapidly in dry soils at -6.0 to -8.0 MPa (Griffin, 1979). This would enable them to

function during drought and to respond quickly to short-duration pulses of soil moisture resulting from brief precipitation events. Miller and Jastrow (1992) reviewed the role of mycorrhizal and other soil fungi in forming stable soil aggregates that improve soil structure and nutrient conservation.

Septate fungi similar to those we observed have been described as being weakly pathogenic, neutral, endophytic, or pseudomycorrhizal (Odell et al., 1993). Odell et al. (1993) isolated a septate fungus, *Phialocephala fortinii* Wang and Wilcox, which colonized the roots of *Lupinus latifolius* Agardh. and *Pinus contorta* Dougl. Hyphae grew between and within cortex cells and formed sclerotia in both hosts. In pine roots the hyphae sporadically formed labyrinthine structures similar to the "Hartig net" of ectomycorrhizas. Although their function is unknown, they were considered to be ecologically significant.

We observed a widespread colonization of desert plants by septate fungi. This suggests a significant carbon expenditure for their maintenance and a corresponding benefit to the host. From our studies, these fungi are similar in several respects to mycorrhizal fungi in that they form intimate and non-destructive interfaces with the host root. They aggregate sand and soil particles near the root surface that would enhance soil stabilization and nutrient and water retention. We propose that these fungi form a hyphal network in the soil to access and absorb nutrients and water from organic and inorganic resources, and to transport them to host plants when conditions are favorable. Conservation and release of resources during stress could enhance survival and stability of the plant, microbe, and soil components of the ecosystem. Future research will focus on identifying responsible fungal organisms and their interface with the roots and adjacent soil.

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