Mycorrhizae and rehabilitation of disturbed arid soils: Processes and practices

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Abstract *Vesicular-arbuscular mycorrhizae (VAM) are critical components of arid ecosystems that regulate plant growth by improving plant nutrient and water uptake capacities. All arid plant species are capable of forming mycorrhizal associations except a limited suite of annual weeds. Almost any perturbation associated with human development serves to reduce VAM inoculum. Thus the restoration of disturbed lands depends, in part, on the restoration of viable VAM symbioses.*

Two means are available for restoring the symbiosis: artificial inoculation and application of succession theory. Although artificial inoculation is possible, due to the current inability to grow the endophyte, it has limited applicability. There are a wide variety of vectors of VAM fungi including animals and wind. Proper use of existing information can enhance the natural restoration of VAM symbioses. These include patch planting, planting of facultative VAM plants, and allowing animals to migrate freely across the site. These activities resulted in the rapid restoration of VAM in a test site and should be tested over a broad range of arid soils in need of restoration. If these procedures are found adequate, VAM could significantly enhance the reconstruction efforts in arid lands.

Keywords: vesicular-arbuscular mycorrhizae, restoration, reconstruction, arid ecosystem, patch dynamics.

Introduction

Desertification is a process that is widely recognized and discussed in general terms but remains difficult to define precisely. This definition problem is symptomatic of the lack of systematic approach to resolving problems associated with desertification. The literature is composed of case studies describing practices in an area with little attempt to search for generalizing principles that might be applicable to a wide range of sites. These principles are essential to provide directions for specific studies on management techniques necessary to prevent further desertification and enhance reclamation of lands previously lost. For my purposes here I use the definition of Biswas and Biswas (1980): "desertification is the diminution or destruction of the biological potential of land and can lead ultimately to desert-like conditions . . ." and generally " . . . arises from sudden and severe disturbance . . ." (Tolba 1977). This definition allows the use of succession theory as a set of hypotheses with which to construct a model of interacting components necessary to describe the process of desertification. We might view deserti-

fication as a disturbance event that, depending on subsequent events, leads to a renewed, productive ecosystem (progressive succession) or a loss of productive capacity (retrogressive succession) resulting in desertification of a site (Fig. 1).

Walker *et al.* (1981) suggested that if nutrients are retained, progressive succession should occur resulting in a long-term productive system. However, if nutrients are lost or leached below the rooting zone, retrogressive succession will occur with attendant low productivity. Odum (1969) listed a number of characteristics distinguishing an early versus a mature ecosystem trending from an abiotically regulated, leaky system to a biotically regulated, nutrient conservative system. Included in this list are a trend with succession toward spatial integration among abiotic and biotic components and an increasing degree of symbiosis. Mycorrhizae, mutualistic associations between below ground parts of plants and fungi may be one of the components essential to restoring biotic regulation to a disturbed ecosystem.

Descriptions of Mycorrhizae

Mycorrhizae are common in almost all terrestrial habitats. The vast majority of land plants, including most species used for grazing of agriculture, are mycorrhizal (Trappe 1981). They have been found in the earliest land plants and thus have coevolved with
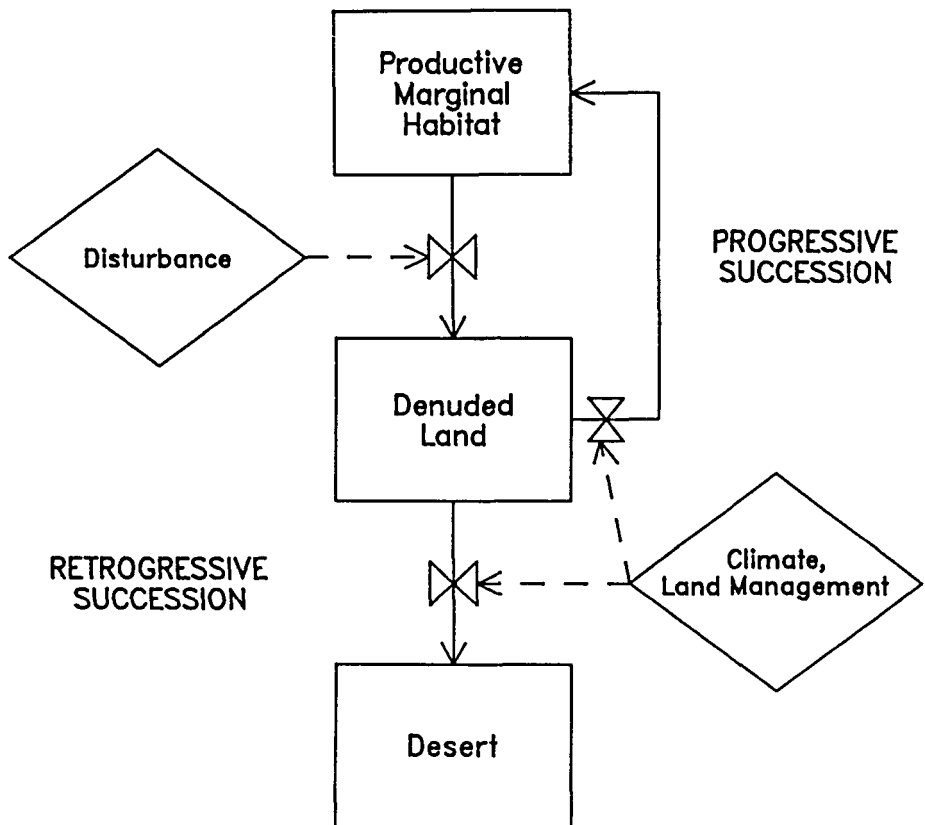

Figure 1. The process of desertification from a successional perspective.

plants for millions of years (Pirozynski 1981). Any consideration of manipulating or restoring cultivated or grazing lands must include analyses of these associations for the results to be understood.

Although mycorrhizae are functionally defined (Frank 1885), the associations are generally recognized and quantified on a morphological basis. There are several types ranging from ectomycorrhizae in which the fungus remains external to the cell wall to endomycorrhizae wherein the fungus penetrates the wall (e.g., Schenck 1982). Endomycorrhizae incorporate several distinctive morphological types, but the most common is known as the vesicular-arbuscular mycorrhiza (VAM). In this article, I concentrate on the VAM type for two reasons. First, this type is most common in arid plant species excepting only a few species (Trapp 1981) and the list of nonmycotrophic species is decreasing as more arid systems are surveyed (e.g., Newman and Reddell 1987). Second, the majority of arid land research on VAM has concentrated their growth benefits to plants. For these reasons they represent a system that might improve land rehabilitation practices.

Responses to Desertification

By definition, a mycorrhiza is composed of both plant and fungus where the fungus is generally considered to be the obligate symbiont. Thus any perturbation affecting the plant presupposes a fungal reaction. The process of desertification presumes major reductions in plant production and often results in plant species shifts in response to a variety of interacting changes in soils, climate, and grazing patterns. In addition, these resultants may alter decomposers, consumers, and carnivores with relatively unknown consequences to community processes (e.g., Whitford 1988). The major perturbations associated with desertification include nudation, drought, nutrient deficiencies, energy budget changes, salinization, increased heavy metal concentrations, overgrazing, and weed invasion. These effects are associated with three major activities, tillage agriculture, pastoralism, and mining disturbances, which all affect mycorrhizal persistence and establishment.

Tillage agriculture trends to reduce inoculum densities or alter fungal species compositions, which ultimately might result in lowered resilience of an agroecosystem. The tillage itself can alter the aeration of a field. VAM spores located near the surface and presumably more aerated appear to decompose more rapidly than buried soils in both mesic and arid habitats (Christensen and Allen 1980, M. F. Allen 1988). Often in arid regions, land is fallowed with no green cover crop to increase soil water recharge. It has been suggested that these alternate years with no plant symbiont have reduced the small-spored, drought-tolerant *Glomus fasciculatum* from wheat lands in western Nebraska whereupon it was replaced by the large spored *G. mosseae* (Allen and Boosalis 1983). Intensive use of inorganic fertilizers (especially P) and fungicides is known to inhibit VAM persistence (Hayman 1982, Menge 1982). Overirrigation, especially flood irrigation, often results in loss of VAM fungi possibly due to lowered oxygen tension (Saif 1981, Allen and St. John 1982). Irrigation can also lead to salinization of a field. Even moderate salinity can inhibit germination of some VAM fungi and reduce infection in crop plants (Hirrel and Gerdemann 1980, Hirrel 1981). Often a combination of agricultural practices changes VAM intensity and results in lowered productivity of arid sites (e.g., Trappe 1981, Allen and Boosalis 1983).

Intensive pastoralism can also seriously reduce VAM persistence, although the effect

is usually indirect. If we assume that the majority of the carbon for growth of the fungus comes directly from the plant, we might hypothesize that any factor reducing the amount of C fixed by the plant will reduce fungal growth (e.g., Ferguson and Menge 1982). Literature published to date suggests that severe overgrazing can reduce VAM infection frequency (Wallace 1981, Bethlenfalvay and Dakessian 1984), number of vesicles (Reece and Bonham 1977), and spore density and species composition (Bethlenfalvay *et al.* 1985). Also, under intense grazing pressure, carbon might become the limiting factor to production due to the loss of leaf area. If carbon becomes a major limiting factor, the fungus potentially might act temporarily more as a pathogen then as a mutualist (Bethlenfalvay *et al.* 1982). High grazing intensity can reduce VAM inoculum via erosion (e.g., Powell 1980) and by soil compaction (Wallace 1987).

Disturbances by mining and the VAM response have been studied by a number of workers (e.g., Williams and Allen 1984). In the mining process, not only are plants physically removed, but upon soil replacement changes in texture, deposits of salts and heavy metals, and dilution or elimination of VAM inoculum can result. Allen and Allen (1980) noted that heavy clay soils were replaced in reclaimed sites where the surrounding native topsoils were predominantly sandy loams. They suggested that the observed low sporulation might be a response to the small pore sizes. Sites of high salt content or heavy metals are often found following mining disturbances. Although ecotypes might survive that can tolerate these conditions (Gildon and Tinker 1981, Allen and Cunningham 1983), some VAM fungi can be extremely sensitive to high concentrations (e.g., Hepper 1979, Call 1981, Gildon and Tinker 1981, Hirrel 1981).

A secondary consequence that can result from all above disturbances and affect reestablishment of desirable plants and VAM fungi is invasion by weeds (E. Allen 1988). *Salsola kali*, for example, can invade disturbed sites rapidly and compete with desired grasses of forbs for water and nutrients (Allen and Allen 1984), changing the grass establishment and successional trajectory (E. Allen 1988). Allen and Allen (1980) have reported sites up to 10 years old without VAM inoculum still dominated by *Salsola kali* and *Halogeton glomeratus*.

Physiological Importance of VAM

Proposed Mechanisms

Arid regions are generally characterized by one predominate limit to productivity: low precipitation. However, a major feature of arid zones is not only harsh mean values of temperature, precipitation, and soils, but also the variability in climatic regimes (MacMahon 1980) and extreme patchiness of soils (e.g., Allen and MacMahon 1985, M. F. Allen 1988). VAM phenology is tightly coupled to seasonality and many sites can show extreme variability in environmental conditions even within a single growing season (M. F. Allen 1983, 1988). Based on the potential range for biological interactions among symbiotic mutualisms, I suggest that the functioning of VAM in arid communities is based on several interacting physiological mechanisms.

The foremost and best-described response of VAM action is the increased P uptake in P-deficient soils (e.g., Safir 1987). The major mechanism is generally considered to be hyphal transport of available P from soil to plant (e.g., Safir 1987). Other proposed actions include use of organic phosphates (Allen *et al.* 1981a), increased affinity by fungal hyphae for P (Cress *et al.* 1979), a greater phosphate sink generated by increased

photosynthetic rates of VAM plants (Allen *et al.* 1981a, b), and mineralization and uptake of clay-bound P (Jurinak *et al.* 1986).

Although far less work has been done on the role of the VAM in N assimilation, the limits to productivity in arid systems caused by N deficiencies (e.g., Whitford 1988) suggest that more work is needed in this area. Ho and Trappe (1975) noted that *Glomus mosseae* and *G. macrocarpum* had the capacity for reducing nitrate. Ames *et al.* (1983) reported hyphal transport of N from soil to a host plant. The interactions between mycorrhizae and symbiotic N_2-fixers should not be overlooked as these systems may contribute significant amounts of N to a system (e.g., Redente and Reeves 1981).

Generally, in arid systems the major limit to both nutrient uptake and productivity is drought. VAM infection has been shown to increase water uptake and increase drought tolerance of several plant species (e.g., Safir 1987, M. F. Allen 1988). Several mechanisms for enhanced water uptake are hypothesized. Others (see Fitter 1988) suggested that the effect was P mediated; plants took up more P, which resulted in an increased plant conductivity. Others have suggested that the potential role of hyphal transport of water not be overlooked as some direct transport of water might account for increase drought tolerance of clover (Hardie 1985) and some grasses (Allen 1982). Allen and Cunningham (1983) noted that despite increased P concentrations with VAM in *Distichlis spicata*, there was no measurable increase in water transport. They suggested that the lack of response might be explained by the low number of external hyphal penetrations. Levy and Krikun (1980) and Allen *et al.* (1981b) suggested that VAM infection also affected leaf physiology, specifically by altering stomatal control. Allen *et al.* (1980, 1982) noted major leaf and root hormonal changes, which might account for the observed improvement of stomatal control of *Bouteloua gracilis* with VAM formation (Allen *et al.* 1981b). Allen and Boosalis (1983) reported that two species of VAM fungi had differing effects on the water relations of wheat during drought stress. Both species increased stomatal conductivity, but *Glomus fasciculatum* infection resulted in reduced osmotic potentials, whereas *G. mosseae* did not; plants infected with *G. fasciculatum* could maintain open stomates and positive turgor under greater drought than either *G. mosseae*-infected or nonmycorrhizal plants. Allen *et al.* (1984) also noted that two co-occurring grasses, *Bouteloua gracilis* and *Agropyron smithii*, had different degrees of responses to drought and survival with the same VAM fungus (*Glomus fasciculatum*) and intensity of infection. Most importantly, in the field addition of VAM increased water flux in grasses but did not improve leaf P status (Allen and Allen 1986). Thus the intensity and type of response of plants to mycorrhizal formation may be dependent on host plant, fungal species, and extant environmental conditions.

A common resultant of desertification in many regions is salinization of a site following improper irrigation or disturbance. Germination of agricultural VAM fungi was inhibited by moderate salt concentrations (Hirrel 1981), but VAM infection did overcome some of the detrimental effects of low salt additions (Hirrel and Gerdeman 1980). Buwalda *et al.* (1983) reported that VAM wheat and barley took up higher concentrations of Br and Cl than nonmycorrhizal plants. They indicated that this response could be detrimental but concluded that these responses may be necessary to balance carbon loss to the fungus, thereby retaining a proper cation-anion balance. In a detailed study on VAM responses to NaCl stress by the halophytic grass *Distichlis spicata*, Allen and Cunningham (1983) reported that, although mycorrhizal plants took up more NaCl that nonmycorrhizal plants, VAM plants also took up more K maintaining a constant Na/K ratio and increased P uptake. They reported that VAM infection did not increase phytomass during a short-term experiment and suggested that a longer term survival study is

needed. It also should be noted that the fungus used, an ecotype of *Glomus fasciculatum* from highly saline soils, was capable of establishing on root systems under much higher salt concentrations than the agricultural *G. fasciculatum* used by Hirrel and Gerdemann (1980). Thus the possibility for using salt-tolerant fungal strains for revegetating saline areas needs much more attention.

Field Observations

Few field correlative or direct experimental studies on the effects of VAM on plant growth and survival in arid regions have been reported. However, those completed suggest a variable role for using VAM in restoring disturbed lands. Aldon (1975) noted that VAM-inoculated *Atriplex canescens* had higher rates of survival and greater productivity than nonmycorrhizal outplants after eight years in a disturbed mine spoil. Call (1981) reported that mycorrhizal shrubs did better on oil shale spoils than nonmycorrhizal shrubs. Allen and Boosalis (1983) reported that lowered productivity in wheat coincided with reduced VAM infection and a fungal species shift in western Nebraska fields from one promoting drought tolerance (*Glomus fasciculatum*) to one not promoting tolerance (*Glomus mosseae*) in greenhouse experiments. We contrasted phenology and water relations of VAM inoculated and nonmycorrhizal *Agropyron* spp. in overburden spoil material containing no inoculum in western Wyoming (Allen and Allen 1986). Mycorrhizal grasses had significantly lower stomatal resistances and lowered xylem stress than adjacent nonmycorrhizal plants in equal water-status soils. Mycorrhizal plants also had an extended growing season in response to increasing drought. Thus the potential increased carbon gain with VAM due to the increased CO_2 conduction and longer growing season could significantly enhance the survival of these grasses. However, in one site the VAM inhibited the annual weed cover that was required for snow trapping and soil moisture important to the reestablishment of grasses. At this site, the VAM subsequently reduced the establishment of the grasses (Allen and Allen 1988).

The possibility that VAM infection can simultaneously affect plant response to several types of stresses can be hypothesized from observations of environmental variability at our research site. Precipitation is highly seasonal and VAM infection in shrubs appears to be tightly coupled to periods of adequate soil moisture (Allen 1983). Patches of soils with differing combinations of N deficiencies, high P, and high salinities are found throughout the site. However, there appears greater year-to-year variability in infection and spore counts than among locations on the plants (Allen *et al.* 1987). There is a large gradient in decomposer activity, nutrient status, and mycorrhizal activity from under the base of the shrub to interspace areas; VAM fungal hyphae were concentrated near the edge of the canopy where maximum decomposer activity was occurring (Allen and MacMahon 1985). Thus VAM are a necessary component for increasing water uptake and salinity tolerance while maximizing nutrient uptake in optimum locations and during optimum periods of nutrient availability.

Methods for Restoration of VAM

There are several tested and experimental methods proposed for reestablishing VAM to promote recovery of desired communities. In this section I concentrate on work from arid communities whenever possible while recognizing that work in some sites is still beginning.

Artificial Inoculation

Artificial inoculation of plants with mycorrhizae has long been a common practice in ectomycorrhizal trees wherein techniques for growing masses of axenic fungal mycelia have been described and improved (e.g., Molina and Trappe 1982). However, techniques do not yet exist for growing VAM fungi without a host (e.g., Allen and St. John 1982, Hepper 1983). Several attempts at field inoculation have suggested that various procedures might be effective at least on a small scale in mesic habitats. Hattingh and Gerdemann (1975) successfully applied sieved inoculum as a seed coat to citrus and enhanced VAM reformation in fumigated fields. In an alternative inoculum procedure, Kormanik *et al.* (1980) added a small amount of inoculum to a fumigated plot, built the inoculum up with an annual cover crop that stimulated high fungal sporulation, and then introduced the desired plants.

Aldon (1975) inoculated individual *Atriplex canescens* shrubs and planted them successfully onto disturbed arid lands. Call (1981) also inoculated various shrub species and successfully planted them onto oil shale spoil material. Wood (1984) has discussed the potential for inoculating shrubs in a nursery and planting them onto disturbed sites. The limiting factor to all inoculation techniques to aid in preventing or reversing desertification is simply mass of inoculum for the large-scale efforts needed. Until a technique is designed for growing VAM fungal inoculum in mass for large-scale efforts, artificial inoculation will remain as a potentially effective tool for small-scale efforts alone.

Proper Land Management

In cases where land is to be disturbed and desertification has not yet occurred, proper land management is probably the most effective means to preserve VAM and protect plant growth. I would identify two qualities that must be retained and a common practice that must be curtailed to preserve inoculum. Organic matter management is critical to retain nutrients and reduce erosion (M. F. Allen 1988). In addition, moderate to high levels of organic matter seem to promote VAM establishment and persistence (e.g., Christensen and Allen 1980, Warmer and Mosse 1980, St. John and Coleman 1983). A relatively continuous cover crop may be essential to maintaining an adequate carbon source for fungal survival (e.g., Allen and Boosalis 1983). Agriculturalists using alternate "no green" fallow years for soil water recharge should begin experimenting with low-water use alternate crops or covers. For example, alternate cropping of wheat (a water-demanding species) with pearl millet (a small, C4 grass) might still allow spring water recharge and use minimal water during alternate years while retaining a carbon for the VAM fungi. Intensive use of inorganic fertilizers, especially super phosphate, can drastically inhibit VAM formation (e.g., Hayman 1982, 1987). Careful fertilizer management is essential to retaining VAM fungi.

In areas disturbed for mining, retention and reuse of topsoil have been shown to reestablish VAM and desirable species effectively. Allen and Allen (1980) reported that infection frequency and spore counts recovered to within 50% of undisturbed sites in three years when topsoil was directly reapplied to disturbed sites. In another study, Waaland and Allen (1987) found little or no recovery in abandoned subsoils after 30 years, but when topsoil was saved and respread, VAM activity was relatively similar to adjacent native communities. These results contrasted sharply with another site in which topsoil was not retained; no VAM fungi were observed and *Salsola kali* and *Halogeton glomeratus* still predominated 10 years after reclamation efforts began. Notably, even

the addition of 2 to 4 cm of fresh topsoil to a site can result in 60% of the roots of grasses being infected in the first growing season. No infection was observed in adjacent "sterile" soil (Allen and Allen 1986). We have recently observed that even topsoil stored for 5 years retains viable VAM propagules capable of reinfecting desirable plants (Allen and MacMahon 1985). The longevity of inoculum needs further study, but some data suggest that in a Wyoming cold desert, spores persisted for 5 years but declined sharply between 5 and 8 years (Christensen and Allen 1980).

Succession Theory Approach

An alternate approach to reconstruction of disturbed arid ecosystems is to use succession theory as a guide to managing lands. Rather than attempting to override normal successional processes and environmental variables, we are attempting to prime natural processes to enhance the rate of succession and thereby reestablish a desirable community more rapidly.

Among those attributed Odum (1969) ascribes to a mature ecosystem are spatial integrity and a high degree of symbiosis. Arid zones may be an extreme test of this hypothesis. Phillips and MacMahon (1978, 1981) have suggested that shrubs initially establish in clumps. Several researchers (e.g., M. F. Allen 1988) have noted "islands of fertility" associated with these clumps. We have shown that these islands are also sites of highest VAM activity and that disturbance results in a loss of that spatial integrity (Allen and MacMahon 1985). Reconstruction of a disturbed arid ecosystem to a persisting community may depend on the ability to reconstruct the spatial nature of the site.

MacMahon (1981) has argued that the general successional model proposed by Clements (1916) represents "a succinct categorization of successional processes" that can be used to understand dynamics of community establishment. These may also represent processes subject to management activities that can be used to enhance succession rates. Our approach is to test this mode using one basic primer: planting shrubs in patterns and densities designed to optimize natural processes. By initially planting shrubs in clumps, viable VAM propagules were retained in the topsoil and low levels of infection were initially established during the first year (Allen et al. 1987). Recent discussions have centered on the role of vectors of VAM transport (Warner et al. 1987). MacMahon and Warner (1984) proposed a model of VAM fungal migration. Subsequently, we have identified both abiotic and biotic vectors for dispersal of VAM spores (Table 1.). By planting shrubs in clumps, changes in turbulence patterns are apparent, resulting in increased deposition of wind- and snow-borne spores (M. F. Allen 1988). Shrubs also ameliorate the harsh environmental conditions of the site (Parmenter and MacMahon 1983) enhancing animal deposition of spores and mycelial fragments (M. F. Allen 1988). Our results indicate that more spores are deposited near larger shrubs than in adjacent interspace sites (Table 2). Thus we project that immediate patch planting techniques alone, i.e., manipulation of plant invasion can enhance natural mycorrhiza reestablishment by (1) altering residual survival through reducing the nudation intensity, and (2) concentrating VAM fungal migration into "safe sites." These shrub units can then serve as islands for reinoculating a given area. This process might be adaptable for both restoring natural vegetation by careful planting of patches and for enhancing cultivation areas by carefully understanding dynamics of biotic wind breaks.

Table 1

Identified spore vectors
for dispersing VAM fungi
from a site near Kemmerer, Wyoming.[a]

Abiotic	Wind
	Snow
Biotic	*Pogonomyrmex occidentalis*
	Microtus montanus
	Peromyscus maniculatus
	Eutamias minimus
	Onychomys leucogaster
	Lepus californicus
	Marmota flaviventris
	Antilocarpa americana
	Odocoileus hemionus
	Cervus elaphies
	Alces alces

[a]From Warner *et al.* 1987.

Conclusions

It is apparent that VAM are an essential component of both agricultural and native vegetation communities. Obviously, the best alternative is to carefully manage a site preventing loss of VAM and plant cover. Rehabilitation of disturbed sites in arid lands should include techniques designed to stimulate reformation of VAM symbioses. If vectors preventing nutrient loss and enhancing plant production such as VAM can be spatially integrated, progressive succession to the point of agricultural potential or to native community reconstruction should be achievable even in arid lands. The alternative is desertification; derelict lands incapable of sustaining biotic resources necessary for fostering human communities.

Table 2

Microscale patterns of VAM fungal reinvasion
onto a planted istrubed site.[a]

Location	Mean spore mass $(g\ kg^{-1}$ dry soil)
Upwind of shrubs	402
Under shrubs	622
Downwind of shrubs	510
Under *Artemisia tridentata*	630
Under *Atriplex gardneri*	586
Under *Chrysothamnus viscidiflorus*	493
Interspace	366

[a]Allen, unpublished data. 1987.

Acknowledgments

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