

The Role of Mycorrhizal Fungi in Competitive Interactions Among Native Bunchgrasses and Alien Weeds: A Review and Synthesis¹

Abstract

The role of vesicular-arbuscular mycorrhizal (VAM) fungi in competitive interactions among native bunchgrasses and alien weeds is reviewed. Brief reviews of the mycorrhizal symbiosis and rangeland ecology provide a background for discussion of the role of VAM fungi in inter- and intraspecific competition in sagebrush-grass systems.

Plants can be significantly better competitors for soil resources when mycorrhizal than when not mycorrhizal, and VAM fungi can alter the outcome of competitive interactions among plants. Additionally, soil resources can be transferred from one plant to another through a network of hyphae produced by VAM fungi; such transport can improve growth in the receiver plant. The response of a plant to the formation of mycorrhizae depends upon the taxa of the plant and fungal symbionts, their phenologies, and on the severity of environmental stress.

Native bunchgrasses of the Intermountain West are mycorrhizal. Alien weeds introduced to the sagebrush steppe include both mycorrhizal and nonmycorrhizal species. When a rangeland site is colonized by nonmycorrhizal species, VAM fungi populations decline. In the absence of VAM fungi, mycorrhizal bunchgrasses are at a competitive disadvantage compared to nonmycorrhizal species in capturing limited soil resources. However, the opposite is also true: mycorrhizal species out-compete nonmycorrhizal species when VAM fungi are abundant.

One naturalized alien, cheatgrass (*Bromus tectorum*), is a facultative host of mycorrhizal fungi. Cheatgrass is an effective competitor in the rangeland environment, and its relative competitive ability, compared to native bunchgrasses, is unlikely to be altered by VAM fungi. Though mycorrhizal fungi would enhance the competitive ability of native bunchgrasses, cheatgrass would reap comparable or greater benefit since it also hosts VAM fungi and, due to a rapid rate of growth, acts as a strong sink for soil resources. This is probably one of the factors behind continued, long-term occupancy and/or dominance of rangeland sites by cheatgrass.

However, it is not unreasonable to expect greater efficiency among coevolved mutualists compared to a profiteering alien. If assimilates are more efficiently transferred from a native bunchgrass to its progeny, then VAM fungi have an important role to play in the restoration of Intermountain rangelands. Research into the role of mycorrhizal fungi in competitive interspecific interactions, rhizosphere community dynamics, the mycorrhizal dependence of rangeland grasses, and patterns of translocation is needed before definitive answers can be presented.

Introduction

This review examines the role of vesicular-arbuscular mycorrhizal (VAM) fungi in the dynamics of sagebrush-grass communities, with particular attention to the possible role of VAM fungi in mitigating interspecific interference. I begin with a brief review of the mycorrhizal symbiosis and an introduction to rangeland ecology. These sections lay the groundwork for examining the role of VAM fungi in ameliorating the competitive superiority of alien species that have invaded western rangelands. Though much research remains to be conducted in this area of community ecology, evidence compiled over the last 15 years suggests an important, possibly essential, role for VAM fungi in the population dynamics of native bunchgrasses.

The Mycorrhizal Symbiosis

Vesicular-arbuscular mycorrhizal fungi are common in terrestrial ecosystems, forming obligatory

symbioses with most higher plants (Read *et al.* 1976, Mosse *et al.* 1981). The correlation between taxa and the symbiotic habit is strong. For example, members of the family Graminae typically host VAM fungi (are mycotrophic), whereas the families Cruciferae and Chenopodiaceae generally do not (are nonmycotrophic) (Trappe 1981, Pendleton and Smith 1983, Newman and Reddell 1987). However, mycorrhizal dependency varies within all plant families. Some chenopod taxa, for example, may be briefly mycorrhizal during their life cycle (Trappe 1978, Allen and Allen 1990). Additionally, pioneer or ruderal species are more frequently nonmycorrhizal than are perennial species (Trappe 1987).

Mycorrhizal fungi often play a vital role in the mineral nutrition of a host plant (Trappe 1981), increasing the amount of both macro- and micro-nutrients acquired (Read *et al.* 1985, Killham 1985, Smith *et al.* 1986). Commonly, VAM fungi improve the host's phosphorus nutrition, particularly when soil phosphorus is limiting (Smith *et al.* 1986, Schubert and Hayman 1986). Drought

¹Research funded in part by a Student Research Grant from Northwest Scientific Association.

tolerance in herbaceous species has also been improved with colonization by VAM fungi (Allen and Allen 1984, 1986). The host plant benefits since mycorrhizal fungi function as an extension of the host's root system, increasing the efficiency with which a soil volume is exploited (Koucheiki and Read 1976, Schubert and Hayman 1986). In exchange, the fungal symbiont(s) obtains carbon from the host plant (Snellgrove *et al.* 1982, Paul *et al.* 1985).

The outcome of competitive interactions between plants can be markedly influenced by VAM fungi (Allen and Allen 1986, Grime *et al.* 1987). For example, Fitter (1987) found inoculation with mycorrhizal fungi to alter the outcome of competition for soil phosphorus and potassium between velvetgrass (*Holcus lanatus*) and perennial ryegrass (*Lolium perenne*). In the absence of VAM fungi, the two species were roughly equivalent competitors. However, given mycorrhizae, velvetgrass clearly emerged as the more successful contestant, sequestering roughly twice as much of each nutrient as did ryegrass.

In natural communities, hosts are colonized by VAM fungi shortly after germinating, often while still in the cotyledon stage and frequently by more than one species of VAM fungi (Read *et al.* 1976, Chiariello *et al.* 1982, Dodd and Jefferies 1986). Host plants may be colonized by germinating VAM fungal spores or contact with the hyphae of VAM fungi or another colonized root. Extensive networks of hyphae, with distributions similar to that of plant roots, are found in undisturbed soils (Mosse *et al.* 1981, Schwab and Reeves 1981).

Mycorrhizal hyphae have been shown to connect host plants of the same and different species (Heap and Newman 1980a, Chiariello *et al.* 1982), and intra- and interspecific transfer of nutrients, both from host to fungi and between different hosts of a fungal symbiont via mycorrhizal hyphae, has been documented (Ho and Trappe 1973, Heap and Newman 1980b, Francis and Read 1984, Grime *et al.* 1987). Neighboring mature individuals may subsidize the early growth of seedlings, particularly shaded seedlings, through a hyphal network, thereby increasing the probability of successful establishment and survival (Francis *et al.* 1986).

Whittingham and Read (1982) investigated nutrient transfer via mycorrhizal hyphae using sheep fescue (*Festuca ovina* L.). Roots of a source plant

were split among two halves of a divided pot, and source plants were either colonized by VAM fungi or lacking mycorrhizae. Sink plants were added to one side of the pots, and either distilled water or a nutrient solution containing ^{32}P was added to the other side. When source plants were mycorrhizal, significantly more phosphorus was transferred to sink plants. The relative growth rates of seedlings (sinks) in the nutrients+mycorrhizae, water+mycorrhizae, and nutrient only treatments were 0.1138, 0.0692, and 0.0319, respectively. At 18 weeks, seedlings from the nutrient+mycorrhizae treatment had dry weights three times that of any other treatment. Similar results were obtained by Grime *et al.* (1987) using labeled carbon. Mycorrhizal plants obtained ^{14}C from source plants, while nonmycorrhizal plants in the same pot did not take up the label. Francis *et al.* (1986) concluded that nutrient transfer to seedling sinks via VAM hyphae was sufficient to "sustain significant enhancement of both growth and nutrient composition."

Recruitment of seedlings and species diversity decline in the absence of VAM fungi, particularly during secondary succession (Grime *et al.* 1987, Gangc *et al.* 1990). The early establishment phase may be the period in a host's life cycle when it is most dependent upon the fungal symbiont (Mosse *et al.* 1981).

Benefits to hosts of VAM fungi are potentially great in nutrient poor soils and extreme environments, where the symbiosis acts to ameliorate plant stress (Molina *et al.* 1978, Miller 1979, Bethlenfalvay *et al.* 1984, Allen and Allen 1986) and where plants exhibit a stress-tolerant (*sensu* Grime 1977) strategy. In stressful environments, mycorrhizal species are likely to enjoy a competitive advantage over nonmycorrhizal species (Doerr *et al.* 1984, Fitter 1985).

Rangeland Ecology

The Intermountain West features large expanses of semi-arid rangeland supporting sagebrush-grass plant communities (e.g., Franklin and Dyrness 1973, Daubenmire 1970). These communities often include an overstory of western juniper (*Juniperus occidentalis*) and sagebrush (*Artemisia tridentata*), with numerous grasses and forbs in the understory. Annual alien weeds, such as cheatgrass (*Bromus tectorum*), are also common. Apparently, the native species are mycorrhizal (Williams and Aldon 1976, Molina *et al.* 1978, Trappe 1981,

Pendelton and Smith 1983, Doerr *et al.* 1984, Schwab and Loomis 1987, Benjamin and Allen 1987).

Settlement greatly altered the vegetation of sagebrush-grass systems. Since the native bunchgrasses of western rangelands evolved without selective pressure from large herbivores, the effect of livestock on these bunchgrasses was particularly detrimental (Mack and Thompson 1982) since grazing occurred every year and often year round (Strong 1940, Galbraith and Anderson 1971). Native perennial bunchgrasses generally declined in abundance and cover as grazing by introduced livestock increased (Pechanec *et al.* 1937, Mack and Thompson 1982). Fire suppression also altered vegetation dynamics and nutrient cycling in rangeland communities (Burkhardt and Tisdale 1976, Wright *et al.* 1979).

Subsequent to the introduction of livestock, the introduction of cheatgrass and other competitive aliens resulted in an invasion of western rangelands at a rate and to an extent so great that it has become a classic in the literature of biological invasions (e.g., Mack 1981). Rangeland plant community dynamics were fundamentally altered by these alien introductions (Piemeisel 1951, Harris 1967, Young *et al.* 1972).

Prior to these introductions, sagebrush-grass systems were dominated by competitive, stress-tolerant (*sensu* Grime 1977) perennial bunchgrasses, such as bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*), and sagebrush (Driscoll 1964, Daubenmire 1970). Following the introductions, rangeland communities have come to be dominated by woody species, such as western juniper, and the understory may be dominated by competitive alien annuals as well (Piemeisel 1951, Young *et al.* 1972, Allen and Knight 1984). Many of the introduced annuals are nonmycorrhizal (Trappe 1981, Allen and Allen 1980, Pendelton and Smith 1983).

Typically, early seral alien annuals, such as Russian thistle (*Salsola kali*), enable the establishment of cheatgrass (Piemeisel 1951), a winter annual which does poorly on bare soil (Evans and Young 1984). Cheatgrass is a facultative host of VAM fungi. When cheatgrass grows in communities of nonmycorrhizal plants, it is nonmycorrhizal; in the presence of mycorrhizal plants, cheatgrass is mycorrhizal (Trappe 1981, Pendelton and Smith 1983). Since the native perennial bunchgrasses are

mycorrhizal, and since alien annuals are predominantly nonmycorrhizal, belowground dynamics have changed along with plant community dynamics.

Competition, Succession and Mycorrhizae

Succession in sagebrush-grass communities now includes an early seral stage where community composition is dominated by nonmycorrhizal species, and this stage may last from two to more than six years (Piemeisel 1951, Allen and Knight 1984, Biondini *et al.* 1985). The early seral alien species are displaced by cheatgrass, which may or may not be mycorrhizal, and cheatgrass dominance of the understory can last for 20 or more years. When composition of the plant community is predominantly nonmycorrhizal, VAM fungi decline in abundance (Reeves *et al.* 1979), and VAM fungi populations remain depressed until host plants become re-established (Miller 1987, Biondini *et al.* 1985). Moorman and Reeves (1979) found soil from an alien-dominated community to be 40 times less effective as a mycorrhizal inoculant than soil from a nearby sagebrush-grass community; the soil of the alien-dominated community had been severely disturbed three years earlier.

An example of the decline of mycorrhizal fungi populations with invasion by nonmycorrhizal aliens is provided by Russian thistle. Seedlings of Russian thistle responded to colonization of their roots by VAM fungi by sacrificing the colonized cells (Allen *et al.* 1989a). In some cases, the entire vascular tissue of the affected root segment collapsed; less frequently, entire root systems died. Stomatal resistance increased in colonized seedlings, indicating increased water stress probably due to root mortality. When soils were inoculated with VAM fungi, the abundance of Russian thistle declined; Russian thistle density was reduced by a factor of three and cover by a factor of two given inoculation.

Mature Russian thistle is better able to resist invasion by VAM fungi (Schmidt and Reeves 1984, Allen *et al.* 1989a). Even so, some mycorrhizal fungi are able to survive and sporulate beneath Russian thistle, possibly in a parasitic interaction, though spore densities are extremely low (Schmidt and Reeves 1984, Allen and Allen 1990). Thus, in communities dominated by nonmycorrhizal alien annuals, VAM fungi lack both a host and, during the majority of the year, a source of carbon, and

VAM fungi populations decline as a result. The implications for plants dependent upon mycorrhizal fungi are clear; re-establishment of these plant species may not occur until both plant propagules and the spores of VAM fungi occupy the same site at the same time (Doerr *et al.* 1984, Trappe 1988).

The Importance of Shrubs

In rangeland systems, woody shrubs reduce wind velocity at ground level and trap organic debris, soil and snow, and provide shade. Additionally, the phenomenon of hydraulic lift seen in mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) can improve the water relations of neighboring bunchgrasses during summer (Richards and Caldwell 1987, Caldwell and Richards 1989). The result is the creation of "islands" favorable for plant growth (Doescher *et al.* 1984, Allen and MacMahon 1985). Miller (1987) found the presence of shrubs to greatly aid the re-establishment of native perennial grasses in communities dominated by alien annuals.

The spores of VAM fungi are transported with wind blown soil particles in rangelands (Warner *et al.* 1987, Allen *et al.* 1989b) and are, consequently, trapped by shrubs. Biondini *et al.* (1985) found a strong correlation between the re-establishment of rangeland shrubs and the recovery of VAM fungi populations in disturbed soils. The spores of mycorrhizal fungi are thus placed in an environment where the probability of germination and establishment of a host is relatively high. A grass seed germinating beneath a shrub potentially enjoys a greater availability of water and nutrients, moderated microclimate, and the benefits of mycorrhizal symbiosis. Light attenuation by the shrub canopy could potentially reduce growth of the grass, but light is probably not limiting in rangelands, even beneath shrub canopies (Smith and Nowak 1990; Winward 1991).

VAM Fungi and the Competitiveness of Bunchgrasses

The colonization of plants by VAM fungi may have two effects: greater uptake of nutrients and soil moisture by the host, which translates to better growth (Koucheiki and Read 1976, Fitter 1977, Killham 1985, Allen and Allen 1986, Schwab and Loomis 1987), and the re-establishment of networks of mycorrhizal hyphae in the soil (Read *et al.* 1976, Whittingham and Read 1982). Once

these have happened, mycorrhizal species enjoy a competitive advantage over nonmycorrhizal species in the rangeland environment (Reeves 1985, Ocampo 1986, Miller 1987).

An example of the influence of VAM fungi on the outcome of competitive interactions is provided by Allen and Allen (1984), who grew western wheatgrass (*Agropyron smithii*) and blue grama (*Bouteloua gracilis*) in both monocultures and mixed cultures with Russian thistle. When competing with the alien, both grasses had greater shoot mass and higher stomatal conductance when mycorrhizal than when nonmycorrhizal. Colonization by VAM fungi increased shoot biomass by roughly 25 percent. Mycorrhizal western wheatgrass attained the same shoot biomass when grown in competition with Russian thistle as when grown in pure culture, but when nonmycorrhizal, shoot biomass was about 30 percent less than that of the pure culture plants. While shoot biomass of Russian thistle remained greater than that of either grass regardless of culture type or mycorrhizal status, colonization by VAM fungi consistently reduced shoot biomass of the alien. Stomatal conductance was significantly increased in the grasses with the formation of mycorrhizae, by as much as 300 percent, in both pure and mixed cultures. In contrast, conductance in Russian thistle was significantly reduced with colonization by VAM fungi. The formation of mycorrhizae was clearly beneficial to the grasses, improving water relations and growth, and clearly detrimental to Russian thistle, which had reduced growth and water uptake. In the presence of VAM fungi, the competitive ability of mycorrhizal plants is enhanced whereas that of nonmycorrhizal plants is reduced so long as the plants are competing for the same limited soil resources (Reeves 1985).

VAM Fungi, Alien Weeds, and Rangeland Community Dynamics

Early seral nonmycorrhizal species, such as Russian thistle, are replaced by mycorrhizal species with the restoration of the inoculum potential of the soil (Biondini *et al.* 1985, Miller 1987). It is at this point in community development that cheatgrass, a facultative host, often becomes the dominant herbaceous species, and further successional change is inhibited.

The safe sites that allow native perennials to germinate and establish also provide cheatgrass

seed with favorable microsites (Evans and Young 1984), and cheatgrass seedlings usually out-compete the seedlings of native bunchgrasses (Piemeisel 1951, Harris and Goebel 1976, Thill *et al.* 1984). By virtue of its root phenology and rate of root growth, cheatgrass is able to exploit soil moisture much more effectively than native bunchgrasses (Harris 1967, 1977), thereby inhibiting the establishment of native perennial bunchgrasses and impeding successional change.

The relative competitive abilities of cheatgrass and native perennial grasses are probably not changed by mycorrhizal fungi, so long as both are colonized (e.g., Benjamin and Allen 1987). As networks of mycorrhizal hyphae are re-established, cheatgrass and any native perennials present are likely to be incorporated into these networks. Any benefit derived from the symbiosis would probably be enjoyed by both cheatgrass and the native grasses. The inhibition of successional change by cheatgrass suggests it retains its competitive advantage. In fact, cheatgrass may derive more benefit from the symbiosis than do the native grasses. In cereal crops, mycorrhizal colonization has given greater growth increases in winter-sown as compared to spring-sown grains (Buwalda *et al.* 1985). Dodd and Jefferies (1986, 1989) reported a high degree of root colonization by VAM fungi in autumn-sown crops by November or December, though environmental factors affected the persistence of the symbiosis. Later planting resulted in slower root growth during winter, and colonization generally declined with reduced rates of root extension. Since cheatgrass sustains root growth in lower, warmer soil horizons during winter, when native grasses are dormant, cheatgrass may benefit from mycorrhizal colonization from shortly after germination until senescence. The rapid rate of growth of cheatgrass would provide a strong sink for water and nutrients taken up by VAM fungi as well.

Additionally, the rate at which a plant's roots are colonized by VAM fungi can be influenced by the plant itself. Graham *et al.* (1991) compared the rates of mycorrhizal colonization of roots of woody species having low, intermediate, and high mycorrhizal dependencies. Species having a low mycorrhizal dependency were colonized less rapidly than were the other species, though the ultimate extent of colonization was the same. The authors noted that if a plant derived little benefit from mycorrhizal colonization and could also in-

hibit formation of the symbiosis, carbon that would otherwise flow to symbionts would be available for "needs that give a more immediate return on the investment [such as] production of new leaf area."

Cheatgrass is a facultative host, and its mycorrhizal dependence is lower than that of native perennials (Schwab and Loomis 1987). When grown in monoculture, the growth of cheatgrass was inhibited by VAM fungi (Schwab and Loomis 1987, Benjamin and Allen 1987). When grown in a mixture where bluebunch wheatgrass was most numerous, cheatgrass shoot biomass and phosphorus content was greater in mycorrhizal than non-mycorrhizal treatments, but in mixtures where cheatgrass was most abundant, VAM fungi inhibited shoot growth of cheatgrass and phosphorus content was lower (Schwab and Loomis 1987). Cheatgrass did not benefit from mycorrhizal colonization except when the relative density of mycorrhizal competitors was high. If cheatgrass is able to inhibit colonization of its roots by VAM fungi, carbon that would flow to symbionts could instead support vegetative growth. It may be that cheatgrass allocates its carbon to growth (i.e., space capture) during the period when the native perennials are dormant, and becomes a significant sink for soil resources taken up by VAM fungi only late in its development, when growth is most rapid. That is, cheatgrass may function as a sink for resources captured by mycorrhizae when doing so denies resources to the native perennials, and may otherwise minimize carbon allocated to mycorrhizal fungi.

Mycorrhizae and Seedling Establishment

It has been demonstrated that nutrient transfer via VAM mycelium from mature plants to seedlings occurs and is sufficient to increase seedling growth (Whittingham and Read 1982, Francis *et al.* 1986). One possible mechanism by which native perennial bunchgrasses could replace alien weeds would be the preferential flow of assimilates from mature plants to their progeny through the mycorrhizal network. Coevolved mutualists may exchange nutrients, water, and carbon more efficiently than would a profiteering alien, such as cheatgrass, and any measure of host specificity (McGonigle and Fitter 1990, Anderson 1988) could compound the effect. If this asymmetry of benefit were the case, the asymmetry of competition between seedlings and larger or mature plants would be reduced or

even eliminated. Mature plants could subsidize the growth of seedlings, increasing the probability of seedling survival (Grime *et al.* 1987). Once a long-lived perennial bunchgrass became established, the probability of successful establishment of additional individuals of that species could be enhanced.

Since seed density generally declines exponentially with increasing distance from the parent plant, it follows that seedling density should be greatest near the parent. If assimilates flowing from mature plants into the mycorrhizal network were taken up by nearest neighbors, a mature plant could, indirectly, increase the chances of successful establishment of its progeny. This type of seedling subsidization does not appear to necessarily be the case, however. Chiariello *et al.* (1982) found the movement of labeled phosphorus from donor plants to receivers could not be predicted on the basis of proximity, size, or taxon in a serpentine annual grassland. Patterns of translocation could be different in a perennial grassland featuring a mix of established plants and seedlings; growth form and phenology could also affect translocation patterns.

Assimilates do tend to move through the hyphal network from sources to sinks. Heavily shaded seedlings accumulated up to six times more labeled carbon than partially shaded seedlings (Francis and Read 1984). Thus, the transfer of assimilates may reduce asymmetrical competition and increase seedling survival. Eissenstat and Newman (1990) investigated mycorrhizal mediation of competition between seedlings and large plants. The investigators compared the growth of unshaded seedlings of buckhorn plantain (*Plantago lanceolata*), a forb, in soils with and without both VAM fungi and large plants of the same species. The presence of large plants stimulated colonization of seedlings by VAM fungi, and mycorrhizal seedlings obtained more nitrogen and achieved greater growth than nonmycorrhizal seedlings. However, both mycorrhizal and nonmycorrhizal large plants were equally effective in suppressing seedling growth. Though the mechanism was not demonstrated, the study suggests the intensity of competition between large plants and seedlings is not lessened by mycorrhizal fungi.

Contrasting results were obtained using a mixture of grasses and forbs, however (Grime *et al.* 1987). In this experiment, mycorrhizal and nonmycorrhizal *Festuca ovina* seedlings were transferred to flats and allowed to establish. Seeds of a mixture of grasses and forbs which commonly

occur together were then added. Biomass of mycorrhizae-hosting (mycotrophic) seedlings was significantly greater in the mycorrhizal treatments, whereas biomass of the mycorrhizal canopy dominant, *F. ovina*, was significantly reduced. The biomass of nonhost (nonmycotrophic) plants was unchanged. Additionally, VAM allowed greater species diversity; seedlings which died in the treatments lacking mycorrhizae survived given VAM.

Future Research

Study of the role of mycorrhizal fungi in rangeland systems is needed. The growth response of rangeland grasses to colonization by VAM fungi depends upon the severity of environmental stress and intensity of interference, the plant species, the species of fungal symbionts, and their phenologies. Until this research is completed, little more than speculation is possible.

The mycorrhizal dependence of cheatgrass and especially the native perennial grasses needs to be determined. Patterns of variation in this dependence should be studied. Successional, seasonal, phenological, and density changes may all affect interactions among symbionts. Additionally, seasonal and successional changes in the composition and abundance of the community of VAM fungi in rangelands needs greater study. The rates of colonization of cheatgrass and native bunchgrass seedlings may provide insights into the timing of competitive interactions among these species and also their allocation patterns. Patterns of soil resource transfer via VAM mycelium in semiarid perennial grasslands need to be investigated. This could be accomplished by repeating the experiment of Chiariello *et al.* (1982) in suitable locations.

The relative competitive abilities of cheatgrass and native perennial grasses given mycorrhizal fungi, particularly over the long term, require study. There is a possibility of differential benefit among species (e.g., Allen and Allen 1986). Evolution of the ruderal strategy in plants is correlated with a reduction in mycorrhizal dependence (Trappe 1987). Fitter (1977) showed that velvetgrass derived more benefit from a mycorrhizal symbiont than did perennial ryegrass, despite the facts that both species hosted VAM fungi and the two species were equal competitors in the absence of mycorrhizae. Other experimental results have shown later emerging seedlings to derive greater benefit from the mycorrhizal symbiosis than did

already established plants (Grime *et al.* 1987). In stress-tolerant species, plasticity of the root system (the capacity to respond to and exploit transient nutrient-rich microsites) may be largely a function of the fungal symbiont.

Though benefit to mycorrhizal seedlings has been demonstrated (Whittingham and Read 1982, Francis *et al.* 1986), VAM mediated transfers from mature plants to juveniles under conditions of interspecific competition have received scant study. Repeating Eissenstat and Newman's (1990) experiment using a mature native bunchgrass and shaded and unshaded seedlings of both cheatgrass and the native would be one way to investigate the role of VAM fungi in rangelands. The microcosm approach of Grime *et al.* (1987) would be another excellent method of study. In sagebrush-grass communities, both shrub and grass seedlings are found primarily beneath the canopies of larger plants (Eckert *et al.* 1986, Miller 1987). In this situation, asymmetrical competition may be reduced as a result of assimilate transfer from sources to sinks.

Conclusions

Community dynamics in sagebrush-grass systems were radically altered with the introduction of domestic livestock and alien annuals and by fire suppression. Community composition through succession is now fundamentally different, with alien annuals comprising the early seral stages and inhibiting the re-establishment of native bunchgrasses. Mycorrhizal fungi appear to play an important role in succession in rangeland systems. Alien pioneer species are nonmycorrhizal and growth is inhibited in these species given colonization of their roots by VAM fungi. The establishment of native grass species is aided by mycorrhizal fungi, as VAM fungi increase the efficiency with which the soil volume is exploited by host plants and can inhibit nonmycorrhizal plants. Rangeland plants hosting VAM fungi generally have improved water relations, and water is the most limiting factor in the rangeland environment.

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However, cheatgrass may derive more benefit from fungal symbionts than do native bunchgrasses. Cheatgrass grows rapidly, belowground in winter and aboveground in spring, providing a strong sink for nutrients, water, and carbon translocated via the hyphal network. Native perennial grasses become quiescent during the cold of winter; rapid growth by the natives is usually limited to spring. The competitive relationship described by Harris (1967), where cheatgrass was much more effective in sequestering soil moisture than was a native bunchgrass, is probably not altered by mycorrhizal fungi. Cheatgrass remains a highly effective competitor for soil moisture due to its phenology, rapid growth, and ability to host VAM fungi.

If, however, assimilates tend to flow from source to sink and to nearest neighbors, a mature plant could effectively subsidize the growth of its nearby seedlings. This could be an important mechanism for reoccupation of a site by native bunchgrasses. Assimilates may be more efficiently transferred among cocolved mutualists than to a facultative alien host. If assimilates are more efficiently transferred from a native bunchgrass to seedlings of native bunchgrasses, then VAM fungi have an important role to play in the restoration of Intermountain rangelands. Many questions remain unanswered, and additional research is needed. The roles of mycorrhizal fungi in seedling establishment and competitive interactions among the seedlings of native and alien grasses and among plants of different sizes are in need of study.

Acknowledgments

I thank the Northwest Scientific Association for supporting a graduate student research proposal; the awarded grant allowed the literature review which became this manuscript. Thanks also to Paul Doescher and Jim Trappe for constructive comments and suggestions.

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Received 1 August 1991

Accepted for publication 30 April 1992