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Effects of Microbiotic Soil Crust Organisms and Mycorrhizal Fungi on Seedling Growth of Blackbrush (Coleogyne ramosissima)

Rosemary L. Pendleton, Burton K. Pendleton, and Gwyn L. Howard



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blackbrush seedlings was enhanced in the presence of mycorrhizal fungi. Inoculation resulted in increased plant biomass, decreased allocation to root systems in general (particularly fine roots), and increased tissue concentrations of both phosphorus and nitrogen. The addition of mycorrhizal fungi also significantly decreased the ability of cheatgrass to compete with blackbrush seedlings when grown at low soil nutrient levels. Revegetation of blackbrush areas would likely benefit from the use of mycorrhizal inoculum. Soil fertilization, however, is detrimental to the establishment of this species and is not recommended.

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Foreword

This study was conducted for Headquarters, U. S. Army Corps of Engineers under 61102ABT25, "Environmental Quality – Corps of Engineers," Work Unit J19, "Cryptogamic Species for Training Land Rehabilitation." The technical monitor was Dr. Victor Diersing, DAIM-ED-N.

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1 Introduction

Background

Blackbrush, or *Coleogyne ramosissima*, occurs as a landscape dominant on over 3 million hectares (ha) in the southwestern United States, occupying the transition zone between hot and cold deserts (Bowns and West 1976: Benson and Darrow 1981). It forms a major vegetational component of many National and State Parks in Utah, Nevada, and California, including Canyonlands, Arches, Valley of the Gods, Lake Powell, and Red Rocks. It also occurs on several military installations including Twentynine Palms, California, and the higher elevations of Fort Irwin. At lower elevations, blackbrush is bounded by creosote (*Larrea tridentata*) and Joshua tree (*Yucca brevifolia*) communities; at higher elevations by juniper (*Juniperus sp.*) and big sagebrush (*Artemisia tridentata*) communities. Blackbrush provides forage for bighorn sheep and wintering deer. The seed is used by both rodents and birds (Pendleton In Press).

Limited attempts at revegetation of blackbrush areas have generally had poor success (Pendleton, Meyer, and Pendelton 1995). Factors that may have been responsible include timing and amount of precipitation, low amounts of seed, and weed competition. A contributing factor is the extremely slow growth of blackbrush. In a study at Arches National Park, average height of 5-year-old seedlings was less than 6 cm (S. E. Meyer and B. K. Pendleton, Research Ecologists, USDA Forest Service, Rocky Mountain Research Station, unpublished data). Slow-growing species such as blackbrush are at a competitive disadvantage in disturbed sites dominated by exotic weeds. Another hypothesis, examined in this paper, is that the soil microflora may play an important part in the successful establishment of this species (Pendleton, Meyer, and Pendelton 1995).

An important but little-studied aspect of arid-zone ecosystems is the role of the soil microflora, including microphytic soil crust organisms and arbuscular mycorrhizal fungi. Microphytic soil crusts (also known as cryptobiotic, microbiotic, and cryptogamic crusts) contribute significantly to ecosystem stability by means of soil stabilization and improved growth and establishment of vascular plant species (Harper and Marble 1988; St. Clair and Johansen 1983). They are formed initially by blue-green algae that fix nitrogen and bond soil particles. Mature crusts also contain a variety of soil lichens and mosses. Arbuscular mycorrhizal fungi are known to aid plants in nutrient acquisition, primarily of phosphorus. In desert systems, however, their role is poorly understood. Root colonization by these fungi can vary widely with season (Allen 1983), possibly corresponding to changes in photosynthetic activity (Bethlenfalvay, Dakessian, and Pacovsky 1984).

Disturbance can have a profound effect on soil microorganisms. Disturbance of the soil crust when it is dry by trampling or off-road vehicle use causes the crust to collapse, leading to erosion of the soil surface (Belnap 1993). The erosion can be significant, exposing 6 inches (15 cm) or more of the shrub root zone (R. Pendelton, personal observation). The ensuing drifting of the sandy soils buries other areas of undisturbed crust, resulting in reduced nitrogen fixation or in the death of the crust. Disturbance also results in decreased numbers of mycorrhizal propagules in the soil (Moorman and Reeves 1979; Powell 1980). Invasive weeds are generally less dependent on mycorrhizal fungi than are climax species (Miller 1979; Reeves et al. 1979; Allen and Allen 1980). Consequently, the lack of mycorrhizal inoculum may increase the time it takes for vegetation to recover.

Objective

The focus of this research was to examine the interaction of arbuscular mycorrhizal fungi with soil crust organisms as it pertains to the successful establishment of native plant species. This report summarizes findings from a series of experiments designed to test the effect of inoculation with arbuscular mycorrhizal fungi, via the use of several inoculant carriers, on the establishment and subsequent growth of blackbrush plants both in the presence and absence of crustforming microorganisms.

Approach

Three individual experiments evaluating growth of blackbrush under varying soil conditions were conducted. In the first experiment, blackbrush seedlings were grown in three soil fertility levels incorporating varying amounts of microbiotic soil crusts; half of the plants were additionally inoculated with mycorrhizal fungi. The second experiment replicated a field restoration attempt. Fill sand was amended to one of three agronomic soil fertility levels using a slow-release 17-7-12 Osmocote fertilizer. The microbiotic inoculum used was derived from pelletized blue-green algae, primarily Schizothrix; cheatgrass was introduced to half of the replicates to mimic natural competition. The third experiment was a modification of the second; only two soil fertility levels were examined and cheatgrass competition was limited to the low fertility replicates.

Mode of Technology Transfer

It is recommended the information in this report be used by installation land managers and training managers while planning approaches to implement rehabilitation of disturbed areas in arid and semi-arid lands with native species.

2 Materials and Methods

Three experiments evaluating growth of blackbrush under different soil conditions and inoculant carriers were undertaken in the years from 1993 to 1997. In the first experiment, we applied three soil fertility levels using mature microphytic soil crusts collected near Moab, UT; blow sand (no crust present), mixed crust (100 percent pulverized crust material), and a crust-over-sand treatment in which we attempted to mimic natural conditions by placing a circle of intact crust material over blow sand. Nitrogen levels varied from 4 parts per million (ppm) in blow sand to 80 ppm in the mixed crust treatment. Mycorrhizal inoculum of the species *Glomus intraradices*, obtained from Native Plants, Inc., was introduced to half of the plants. Ten blackbrush plants, pre-germinated from seed collected in Washington County, UT, were grown in each of the six soil fertility/mycorrhizal treatment levels. Plants were randomized and maintained in a greenhouse for 12 weeks.

In the second experiment, we attempted to establish conditions that would exist in a field restoration activity. A low-fertility bank sand was purchased from Western Sand and Gravel in Spanish Fork, UT. The sand had a pH of 8.5, conductivity of 0.4 mmhos/cm, and plant-available nutrient concentrations of 4.7, 2.9, and 22.4 ppm for nitrate-N, phosphorus, and potassium, respectively. The sand was steamed for 2 hours at 77 C, then amended to one of three agronomic soil fertility levels using a slow-release 17-7-12 Osmocote fertilizer. The low fertility level had no additional fertilizer added. Medium and high treatment levels were amended to low (5 oz [140 g] per cubic foot) and medium (9 oz [252 g] per cubic foot) values recommended by the manufacturer. The mycorrhizal inoculum consisted of spores isolated from soils near Toquerville, UT, where blackbrush was growing. Spores were extracted from the soil by wet-sieving and decanting, followed by sucrose centrifugation (Daniels and Skipper 1982; Walker, Mize, and McNabb 1982). The algal inoculum used was a pelletized blue-green algal inoculum, primarily containing Schizothrix, developed for crust restoration by Jeff Johansen, John Carroll University, University Heights, OH, and Larry St. Clair of Brigham Young University, UT. Pellets were formed by dropping blue-green algae suspension (5g/L [5 ppm]) into calcium alginate and were subsequently airdried. The inoculum was applied at a rate of 75 g/m^2 or approximately 1.6 g [0.056 oz] per pot, sprinkled evenly over the top of the soil at the time of planting. Half of the pots were also planted with one seed of cheatgrass (Bromus

tectorum) to assess the effects of competition. Total treatment number was 24, with three replications per treatment. Plants were grown for 6 months in a walk-in growth chamber programmed to simulate early spring to late summer conditions.

The third experiment was a modification of the second. After performing experiment #2, it was unclear whether the calcium alginate itself had a positive effect on the final results or whether the blue-green algae were solely responsible for the outcome. Two soil fertility levels, low and medium, were established as previously described. Competition with cheatgrass was limited to the low soil fertility level. Ten replicate pots were used for each treatment combination. Pots were randomized and grown for 5 months in a greenhouse that had been cleaned, sprayed with a biocide, and equipped with new evaporative cooling pads.

At the end of each experiment, plants were harvested, dried, and weighed. Shoot biomass was ground and analyzed for nutrient composition at the Soil and Plant Analysis Laboratory at Brigham Young University. Total root length was calculated using a modified line intersect method of Tennant (1975). Data were entered, stored on disk, and analyzed using SAS version 6.11 for the personal computer. Mean separations were accomplished using the Student-Newman-Keuls multiple range test. 9

3 Results

Growth and Allocation Patterns

The addition of mycorrhizal fungi resulted in increased shoot growth of blackbrush plants across all soil treatments. In experiment #1, mycorrhizal plants had a significantly higher average shoot weight (p = 0.0100) and total plant weight (p = 0.0208) than did nonmycorrhizal plants (Figure 1). They also responded more to the higher nutrient content of the crusted soils than did their nonmycorrhizal counterparts. Indeed, mycorrhizal plants growing in blow sand had as much above-ground biomass as did nonmycorrhizal plants growing in the two crusted soils.

Similar results were obtained in experiments #2 and #3, although the means were not statistically different. In experiment #2, shoot weight of mycorrhizal plants grown at low soil fertility averaged 0.187 g as compared with an average of 0.103 g for nonmycorrhizal plants. Poor survival at medium and high soil fertility precluded comparisons for these treatments. In experiment #3, shoots of mycorrhizal plants averaged 0.785 g at medium fertility and 0.152 g at low fertility as compared with 0.682 g and 0.140 g, respectively, for nonmycorrhizal plants (Figure 2).

The addition of mycorrhizal fungi also significantly changed the allocation of plant biomass between shoots and roots. Mycorrhizal plants consistently invested less in root biomass than did nonmycorrhizal plants. In experiment #1, this difference was significant across all soil treatments (Figure 1). In experiment #2, root/shoot ratios averaged 0.574 for mycorrhizal plants and 2.392 for nonmycorrhizal plants. A similar pattern was seen in experiment #3; root/shoot ratios of mycorrhizal plants averaging 0.222 at medium soil fertility and 1.16 at low soil fertility, whereas ratios for nonmycorrhizal plants averaged 0.385 and 1.35, respectively (Figure 2). Specific root lengths (a measure of root architecture) of mycorrhizal plants were also significantly lower (p = 0.0230), indicating less allocation to fine feeder roots as opposed to larger transporting roots. Specific root lengths for mycorrhizal plants in experiment #1 averaged 4544.3 m/g as compared with 5452.1 m/g for nonmycorrhizal plants; a 17 percent decrease.



Figure 1. Mean shoot weights and root/shoot ratios for mycorrhizal and nonmycorrhizal blackbrush plants grown in one of three soils (experiment #1).



Figure 2. Mean shoot weights and root/shoot ratios for mycorrhizal and nonmycorrhizal blackbrush plants grown at low and medium soil fertilization levels (experiment #3).

In general, blackbrush did not respond positively to inoculation with the pelletized algae. In experiment #3, blackbrush plants grown in soils inoculated with the algae had significantly smaller shoot weights than did the control plants (p = 0.0086), especially at medium fertility (Figure 3). Plants with noninoculated soils had a mean shoot weight of 0.893 g at medium fertility and 0.157 g at low fertility, as compared with 0.655 g and 0.135 g for inoculated soils. A similar pattern was seen in experiment #2; plants with noninoculated soils averaged a shoot weight of 0.119 g compared with 0.110 g for plants with inoculated soils.



Figure 3. Effect of soil inoculation with crust-forming algae on shoot growth of blackbrush plants grown at low and medium soil fertilization levels (experiment #3).

Elemental Tissue Analysis

The addition of mycorrhizal inoculum had a notable effect on the elemental tissue concentrations of various plant nutrients. Mycorrhizal plants in experiment #1 had a significantly higher concentration of immobile elements, including Zn, Cu, and P (Table 1). The plant-fungal association was particularly beneficial in increasing tissue concentrations of phosphorus under low nutrient conditions typical of blackbrush habitat (Figure 4). When percent phosphorus is multiplied by plant biomass to obtain total phosphorus uptake, the highest phosphorus uptake was found in mycorrhizal plants growing in the crust-over-sand treatment, suggesting that greatest efficiency in nutrient uptake may occur where mycorrhizae and healthy mature microphytic crusts co-occur. Mycorrhizal blackbrush plants also tended to have a higher nitrogen content in their tissues, although the statistical significance was marginal for this element (p = 0.1008).

Table 1. Means and attained significance values from ANOVA of leaf and stem tissue concentrations of mycorrhizal and nonmycorrhizal plants grown in three soils; mixed crust, crust over sand, and blow sand.*

	%P	%N	ppm Zn	ppm Cu
With mycorrhizae	0.21	1.34	32.04	4.82
Without mycorrhizae	0.09	1.23	23.96	3.27
p value	0.0001	0.1008	0.0067	0.0041

Competitive Ability

Although shoot growth of blackbrush plants was increased by the addition of fertilizer (Figure 2), the ability of blackbrush to survive and compete was greatly reduced in the higher nutrient soils. In the absence of competition from cheatgrass, survival of shrubs was lower under fertilization in both experiment #2 and #3 (Table 2). When grown with cheatgrass, no shrubs survived in fertilized soils (experiment #2).



Figure 4. Nitrogen and phosphorous content of stem and leaf tissue of blackbrush plants grown in three soils; mixed crust, crust over sand, and blow sand.*

* Nitrogen content was determined using the Kjeldahl digestion method. A technician Auto Analyzer (Technicon Instrument Corp, Terrytown, NY) was used to determine phosphorus content. Three composite samples of three plants each were used in the analysis.

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ligh fertility	Medium fertility	Low fertility
		_
	0	9
	8	7
		40
	14	40

Table 2. Blackbrush survival as affected by	soil fertility and con	petition with cheatgrass.*
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In experiment #3, four inoculation treatments were applied to blackbrush plants growing at low soil fertility with and without competition from cheatgrass. Inoculation treatment had a significant effect on blackbrush shoot growth when grown alone (p = 0.0095), but not when grown in the presence of cheatgrass (p = 0.9326). Treatment did, however, affect the growth of the cheatgrass (p = 0.0029). When grown alone, blackbrush shoots grew significantly better when inoculated with mycorrhizae only (Figure 5). This difference in shoot growth disappeared in the presence of cheatgrass. In contrast, cheatgrass grew best when algae were added to the soil, and least with mycorrhizae. The same pattern was observed in experiment #2. In the absence of competition, blackbrush grew better with mycorrhizae only. No treatment differences were observed for the shrub when grown with cheatgrass, whereas the cheatgrass grew best with algae and least with mycorrhizae.

One reason for the observed reduction of blackbrush shoot growth in the presence of both mycorrhizae and cheatgrass may be found in the biomass allocation patterns. Competition resulted in an altered allocation pattern for the shrub, but not the grass. In the absence of competition, root/shoot ratios of mycorrhizal plants were reduced (Figure 1). However, when competition was introduced, the root/shoot ratio of blackbrush actually increased (Figure 6). In contrast, root/shoot ratios for the competing cheatgrass declined with the addition of mycorrhizal fungi.



Figure 5. Effect of soil inoculation treatment on shoot growth of blackbrush plants grown at low soil fertility, alone and in competition with cheatgrass (experiment 3).*

* Cheatgrass weights shown here have been divided by 10 so that shrub and grass weights could be presented on the same graph.



Figure 6. Root/shoot ratios of mycorrhizal and nonmycorrhizal blackbrush plants grown at low soil fertility, alone and in competition with cheatgrass (experiment 3).*

* Root/shoot ratios of the competing grass are also given.

4 Discussion

Nitrogen and phosphorus availability have been implicated as major determinants of community structure and successional dynamics (Tilman 1986; Vitosek and White 1981). Arbuscular mycorrhizal fungi and crust-forming blue-green algae are biological processors of these nutrients. Arbuscular mycorrhizal fungi have demonstrated the ability to enhance nutrient acquisition of many plant species through the formation of mutualistic relationships with plant roots (Allen 1992). The hyphal network essentially provides an extension of the root surface area, increasing plant access to certain immobile elements in exchange for carbon compounds. Beneficial effects are a function of plant root architecture, plant and fungal species interactions, and environmental conditions, including soil nutrient levels, temperature, and moisture.

Blackbrush clearly benefits from a relationship with arbuscular mycorrhizal fungi, and is partially dependent on that relationship for optimal growth. This was evidenced in experiment #1, where blackbrush plants grew larger in the presence of mycorrhizae and had higher tissue concentrations of many nutrients, including nitrogen and phosphorus. Studies documenting increased growth and phosphorus content of mycorrhizal plants are numerous and well-reviewed (Mosse 1973). Several studies have reported an increase in nitrogen uptake as well (Quintero-Ramos et al. 1993; Trent, Svejcar, and Bethlenfalvay 1993). Next to water, nitrogen is the factor most limiting to plant growth in desert ecosystems (Evans and Belnap 1999).

Allocation to root function was also significantly reduced in mycorrhizal blackbrush, indicating that proportionately less root mass was needed to meet the demand for plant growth. Similar reductions in allocation to root function in response to mycorrhizal colonization and increased soil fertility have previously been reported (Chapin 1980; Allen 1991; Redente, Friedlander, and McLendon 1992). Root architecture of blackbrush, as measured by specific root length, further indicates a shift in allocation of mycorrhizal plants away from fine feeder roots. Optimal resource utilization and flexibility in allocation patterns may be particularly important for slow-growing aridland perennials. Plasticity in allocation and root architecture in response to mycorrhizal colonization has been proposed as characteristic of mycorrhizal-dependent plant species (Smith and Smith 1996; Hetrick, Wilson, and Leslie 1991). Growth and allocation trends in experiments #2 and #3 were similar to those in experiment #1; however, in many cases the observed differences were not statistically significant. One reason for this may lie in the inoculum used. Mycorrhizal isolates vary in their ability to increase plant growth (van der Heijden et al. 1998; Trent, Svejcar, and Bethlenfalvay 1993; Bethlenfalvay et al. 1989; Wilson 1988). In the first experiment, the fungal isolate used was one developed and marketed for its superior growth-enhancing capability. In native situations, using a mixture of fungi, the growth response tends to be lower (Trent, Svejcar, and Bethlenfalvay 1993). The consistency of the results obtained from the different experiments does, however, lend credibility to the hypothesis that blackbrush is partially dependent on arbuscular mycorrhizal fungi.

Mycorrhizal fungi may play a part in mediating interspecific plant competition (Francis and Read 1995; Allen 1991; Miller 1987), including interactions between native species and exotic annuals (Goodwin 1992). Exotic annuals and other early seral species are almost always nonmycorrhizal or facultative in nature (Allen 1991). Many of these species show a reduction of yield and survivorship when grown with mycorrhizal fungi (Francis and Read 1995) Later seral species are hypothesized to have more of a competitive advantage when mycorrhizae are present. This has been borne out in limited studies involving native western grasses and a number of chenopod- or mustard-family annuals. (Johnson 1998; Allen and Allen 1986; Allen and Allen 1984).

In this study, blackbrush grew best in the single-inoculation mycorrhizal treatment in the absence of competition. In competition with cheatgrass, the addition of mycorrhizae did not increase plant growth and the allocation to root growth increased, indicating an increase in competitive intensity. Other studies have found that the addition of mycorrhizal fungi increased the intensity of intraspecific competition (Moora and Zobel 1998, and references therein). The cheatgrass, in contrast, showed a decrease in top growth in response to mycorrhizal inoculation, suggesting that its competitive ability declined. These results suggest that, at low soil nutrient levels, the presence of mycorrhizal fungi may give slowgrowing shrubs more of a competitive edge against exotic annuals such as cheatgrass. Further study on this point is needed.

Soil fertility levels may also affect plant interactions. The initial dominance and persistence of annuals on disturbed sites may be related to high nutrient availability, particularly that of nitrogen (Allen 1995; McLendon and Redente 1991). Native perennials displace exotic annuals such as cheatgrass more rapidly on nitrogen deficient soils (Harper 1992). Although a common reclamation practice, fertilization may place slow-growing native species at a competitive disadvantage. In this study, blackbrush demonstrated reduced competitive ability and

survival in fertilized soils when grown in competition with cheatgrass. The rapid growth of the cheatgrass in response to fertilization shaded out the slow-growing blackbrush, resulting in stunted growth or death of the shrub.

Mycorrhizal fungi and biological soil crusts may work synergistically to increase plant establishment and growth. Harper and Pendleton (1993) found greater root colonization by mycorrhizal fungi in soils where microphytic soil crusts were intact. Others report that the presence or limited addition of organic matter can favor the mycorrhizal symbiosis in a way that fertilization does not (Johnson 1998; Hepper and Warner 1983). In this study, the combination of mature soil crust and mycorrhizae provided a better growing environment over that of noncrusted soils. Highest total phosphorus and nitrogen uptake occurred in the crust-over-sand treatment. Harper and Pendleton (1993) reported that tissue concentrations of phosphorus were increased in the presence of soil crusts for mycorrhizal Festuca, but not for the nonmycorrhizae forming Mentzelia. The greatest difference in root/shoot ratios also occurred in the crust-over-sand treatment.

The decreased growth of blackbrush in the algal-inoculated soils of experiments #2 and #3 suggest that competition for soil nutrients may occur during the initial establishment phase of soil-crust formation. Inoculation with the algae also appeared to benefit the growth of cheatgrass. Although these results suggest some negative effects of crust inoculation, other research indicates that the long-term benefits of biological soil crusts to plant establishment and growth are considerable. Once established, mature soil crusts have been shown to improve seedling establishment of several native species, including blackbrush, under field conditions (Harper and Pendleton 1993; Harper and Marble 1988). Tissue concentrations of many plant nutrients, including N, Mg, and Zn, are higher in plants growing on microphytic soil crusts (Belnap and Harper 1995; Harper and Pendleton 1993). Destruction of the soil crust may disrupt the soil nitrogen balance, leading to permanent alterations in plant species composition (Evans and Belnap 1999).

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5 Conclusions

This series of experiments examined the significance and difference of use of microphytic species with and without alginate carriers.

1. Arbuscular mycorrhizal fungi benefit the native blackbrush community by improving growth, reducing investment in fine roots, and enhancing mineral uptake. They may also positively influence the competitive ability of shrub.

2. Fertilization as a restoration technique may increase plant growth, but can reduce shrub survival and result in competitive exclusion of shrubs in the presence of cheatgrass.

3. The presence of a healthy soil crust is essential to soil stability and proper ecosystem function, however there may be some competition with plants for nutrient resources during the initial establishment phase. The effect of crust inoculation on growth and competitive ability of cheatgrass needs further examination.

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