Inocculation Response by Irrigation System Type for Desert Tree Establishment

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Abstract

Revegetation research offers the opportunity to test theories under difficult field conditions. These tests can help improve guidelines for establishing trees on arid and degraded sites. The borrow pit (surface mine) used for this study reflects the most difficult challenges of low fertility, extreme water stress, and harsh microclimate conditions. This set of conditions made it an ideal site to test interactions between irrigation system type and inoculation with rhizobial bacteria and mycorrhizal fungi. The tree chosen for the study, *Prosopis glandulosa* var. *torreyana* (L.D. Benson, M.C. Johnston), (mesquite, honey mesquite), is a small- to medium-sized leguminous tree with considerable value for ecosystem structure and function. It was once much more common in the low desert of California and was widely used as a food by indigenous people. The destruction of mesquite woodlands for fuel wood and agricultural and urban development has reduced once vast stands to isolated remnants. The California Department of Transportation supported research to mitigate mesquite habitat loss caused by ongoing highway construction. It was also expected this research would help nursery managers better prepare plants for difficult sites and assist restoration specialists and foresters in developing better techniques for restoration and agroforestry projects. The soil analyses showed that soil fertility was greatly reduced and inoculation potential was nearly absent in the borrow pit. Deep-pipe and buried-clay-pot irrigation each enhanced survival and growth. The steady moisture of buried clay pots appears to be more favorable for rhizobial inoculation, and deep-pipe irrigation with deeper wetting and greater aeration is better for mycorrhizal inoculation. Double inoculation provided increased survival and growth in the short term, but long-term effects were minimal.

Introduction

The establishment events for many perennial desert plants are poorly understood but often appear to be confined to pulses linked to unique climatic patterns that may occur only a few times a century. Most of the time, plant establishment is limited by very low and variable precipitation, extreme evaporation, wind desiccation and abrasion, low soil fertility, excessive salinity and sodicity, and herbivory by insects and small mammals (McAulliffe 1986, Allen 1989a). Human activities, such as construction and agriculture, can compound these problems by radically altering ecosystem structure and function, limiting or eliminating beneficial microsymbiont propagules, increasing moisture stress, adding soil salinity from irrigation, adversely affecting soil structure, and changing nutrient levels (Bainbridge et al. 1993, Lovich and Bainbridge 1999, Bainbridge 2007). Revegetation research under rigorous field conditions can help develop guidelines for restoring this type of desert ecosystem. The most extreme condition possible is a borrow pit where excavation of a large volume of soil will typically remove microsymbionts, nutrients, seeds, and propagules.

Mesquite (*Prosopis glandulosa* var. *torreyana* [L.D. Benson, M.C. Johnston]), a small- to medium-sized leguminous tree (Burkart and Simpson 1977), once occurred in extensive woodlands in the low deserts of southern California. Its distribution and occurrence has been greatly restricted during the past century by harvesting for fuel wood, intensive agriculture, groundwater overdraft, off-road vehicle activity, and urban development. Only isolated stands now remain. In the Colorado Desert, mesquite is found in washes, along the edges of playas, and in other areas where groundwater reserves are available. Mesquite usually has a fibrous root system near the surface, exploiting moisture from infrequent rains, and a fast-growing tap root that can reach great depths in its search for water (Phillips 1963, Bainbridge et al. 1990).

Mesquite is a good multipurpose tree crop for dry land agroforestry (Meyer 1984, Bainbridge et al. 1990) and was once a critical food resource for indigenous populations who planted, transplanted, and managed this species (Bean and Saubel 1972). Mesquite trees can be a major nitrogen source for desert ecosystems and may play an important role in long-term productivity of desert plant communities through their effect on soil chemical and physical properties (Virginia 1986, 1990). Indigenous people utilized this trait by transferring mesquite soils to gardens to improve fertility (Nabhan 1982). Mesquite also provides valuable habitat for many desert wildlife species.

Mesquite commonly forms symbiotic root associations with nitrogen-fixing rhizobial bacteria (Virginia and Jarrell 1983, Virginia et al. 1984). Research showed that a mesquite stand near Harper's Well (in the Colorado Desert west of the Salton Sea) was fixing approximately 60 percent of its nitrogen supply (Shearer et al. 1983). Mesquite was the most effective N fixer in a comparative study in Riverside, CA (Abrams et al. 1990). Fast-growing *Rhizobium* and slow-growing *Bradyrhizobium* were found associated with mesquite (Jenkins et al.1987, 1989; Waldon et al. 1989). Nodules were found at depths of up to 26 ft (8 m) (Virginia et al. 1986, Jenkins et al. 1988).

Rhizobial associations have nutrient requirements and limitations. High nitrogen levels in soil can inhibit root-hair infection and nodule development (Gibson and Jordan 1983), but added phosphorus may increase nodulation and nitrogen fixation in phosphorus-limited soils (Louis and Lim 1988). Nodules are commonly found in the moist soils of the phreatic zone with limited oxygen exchange.

Mesquite is also mycotrophic and forms a symbiotic association with vesicular-arbuscular mycorrhiza (VAM) fungi (Bethlenfalvay et al. 1984). VAM can enhance plant growth by improving uptake of phosphorus, water, and other nutrients (Allen 1988). Mycorrhizal plants may be more capable of accessing water in dry soil than nonmycorrhizal plants (Allen and Allen 1986). To perform well, the VAM fungi and plant symbiosis require nitrogen (Allen 1992, Azcón-Aguilar and Barea 1992) and benefit from higher oxygen levels and well-aerated soil. High phosphorus levels can inhibit symbiotic formation and persistence (Menge 1984, Louis and Lim 1988).

Dual inoculation with VAM fungi and rhizobia may increase plant survival and growth (Barea et al. 1987, Carpenter and Allen 1988). Rhizobia and VAM fungi may influence each other directly, at the preinfection and early colonization stages, or indirectly, through their effects on plant nutrition (Azcón-Aguilar and Barea 1992). VAM causes changes in plant water relations, hormonal balance, photosynthetic rate, and carbon allocation that can improve the development of the rhizobial symbiosis.

Reestablishing mesquite trees in disturbed and degraded environments may require careful attention to microsymbiont associations through preplant preparation, field inoculation, and irrigation strategies, especially during establishment in infertile soils without symbionts, such as found in borrow pits. The objective of this study was to explore the effects of irrigation type and inoculation strategies with VAM fungi and rhizobia to develop best practices for desert revegetation with mesquite. Plants were established into resource islands intended to act as islands of fertility to improve soil conditions and provide a source of seeds, microsymbionts, and other propagules to speed recovery of the denuded site.

Materials and Methods

Site Description

The borrow pit site for this experiment is located on the western edge of the Sonoran Desert, northwest of the Salton Sea at 66 ft (20 m) elevation in the Coachella Valley of California (33°25.52 N, 116°05.48 W). The ecosystem is a creosote (*Larrea tridentata* [DC.] Coville) desert scrub bajada intercut with washes having palo verde (*Parkinsonia florida* [Benth. ex A. Gray] S. Watson), smoketree (*Psorothamnus spinosus* [A. Gray] Barneby), and a few ocotillo (*Fouquieria splendens* Engelm.). Mesquite was not found in the immediate area but was growing within 1 km (0.6 mi).

At the start of the experiment, the borrow pit was a bit more than 2.5 ac (1.0 ha) in area and was still in use (figure 1). The borrow pit was used as a source of material for highway construction. Up to 26 ft (8 m) of soil had been removed, leaving a compacted, barren gravel and rock alluvium. The borrow pit was also aerial seeded with a mix of 12 native plant species after the resource islands for the study were fenced. Seeds were then worked into the soil by dragging the site with a section of chain link fence between the fenced resource island plots with transplants.

Figure 1. The borrow pit and one of the resource islands where seedlings were planted for this study. (Photo by David A. Bainbridge 1990)

The annual rainfall at Indio, the closest recording station, averages 3.3 in (83.0 mm) (Western Regional Climate Center 2012). Tropical storms that move north from the Gulf of California every 30 to 40 years result in rain equal to the yearly average in a few minutes, however, causing extensive sheet and stream flow and flash floods. These floods recharge the wash soils for as much as a year after a flow event (Virginia and Bainbridge 1987). Winter storms can also bring ecologically significant rain events every 15 to 20 years, with 4 in (10 cm) of rain or more in a month or two. These large rain events are minor, however, compared with evaporation rates, with annual mean evaporation from a class A pan of 105 in (268 cm), more than 32 times the mean annual precipitation (figure 2).

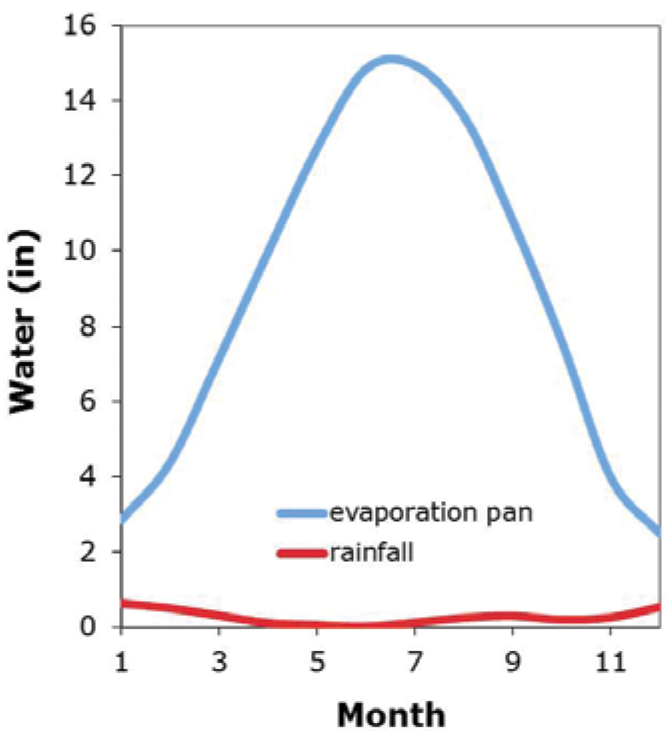

Figure 2. This site water balance graph demonstrates the extremely dry climate as this site by showing evaporation and precipitation. Even in the rainy season, evaporation far exceeds rainfall. Irrigation is essential for initial survival of outplanted seedlings.

Seedlings and Inoculant

Surface sterilized mesquite seeds were sown in 10 in^3 (164 cm^3) Ray Leach SuperCells™ filled with 16-grit silica in the greenhouse at the University of California, Riverside. They were irrigated with tap water as needed for 2 months. No fertilizer was added. Four inoculation treatments were applied: (1) a control (no treatment), (2) rhizobial inoculum, (3) VAM inoculum, and (4) a dual (rhizobia + VAM) inoculation. Seedlings for the rhizobial and dual inoculation treatments were inoculated 1 week before planting by adding a teaspoon of mesquite rhizobia on a peat carrier from Nitragin, Inc. (Milwaukee, WI), to the container surface and watering it in.

Before planting, the site was ripped by a tractor pulling a scarifier. Seedlings were planted as resource islands within the borrow pit site in late March 1990. The seedlings were uniform in size and appearance at the time of planting with roots 4- to 6-in (10- to 15-cm) long and shoots ~1-in (2- to 3-cm) tall with the first pair of true leaves. The seedlings were gently removed from the containers and barerooted into a planting hole made with a KBC tree-planting bar (Ben Meadows™, Janesville, WI) (figure 3). A tablespoon (15 g) of VAM inoculum (*Glomus intraradices* [Nutrilink, NPI, Salt Lake City, UT]) was placed at the bottom of the planting hole. A 3.0-in (7.5-cm) tall section of 3.0-in (7.5-cm) diameter PVC pipe collar was placed around each seedling to protect from sand blast and reduce desiccation. Each plant received 1 qt (0.94 L) of water immediately after planting.

Each resource island started out with a 24-in (60-cm) tall wire mesh fence to limit herbivory, but the fence material was stolen after the second year.

Figure 3. The mesquite seedlings were quite small at outplanting. Also shown is the KBC planting bar. (Photo by David A. Bainbridge 1990)

Irrigation

Three irrigation methods were compared: clay pot, deep pipe, and surface.

Buried-clay-pot irrigation uses an unglazed earthenware pot filled with water to provide controlled irrigation to plants growing adjacent to it. The water moves out of the buried clay pot by capillary action at a rate that is influenced by the adjacent plant's evapotranspiration. This traditional irrigation method is very efficient and effective (Sheik and Shaw 1983, Bainbridge 2001). The clay pots used for this trial were standard 8-in (20-cm) diameter terra cotta nursery pots with the hole in the bottom sealed with silicone caulk. Each pot was covered with an aluminum lid (with holes punched in it to allow rainfall to enter the pot) weighted with a glued-on small rock (figure 4). Four seedlings were planted per pot.

Figure 4. Buried-clay-pot irrigation showing the plant collar, plant protector, and arrangement of seedlings. (Photo by David A. Bainbridge 1990)

Deep-pipe irrigation uses an open vertical pipe to move irrigation water to the deep-root zone (Sawaf 1980, Bainbridge 2006). Deep-pipe irrigation has provided excellent survival and growth in the low desert (Bainbridge and Virginia 1990). The deep-pipe system used in this test consisted of a 16-in (40-cm) length of 2-in (5-cm) diameter PVC pipe (figure 5). Three 0.25-in (6-mm) holes were spaced along the pipe on the sides next to the plants to improve water delivery to roots of the young seedlings. Two seedlings were planted per pipe.

Figure 5. Deep-pipe irrigation showing the plant collar and plant protector. The tall seedling on the right was inoculated and shows the benefit of nitrogen produced in root nodules by rhizobial bacteria. (Photo by David A. Bainbridge 1990)

A surface irrigation treatment with water applied to a shallow basin was used as a control. Two seedlings per basin were planted.

Plants were given 13.5 fl oz (400 ml) of water during each irrigation. This watering occurred approximately every 2 weeks in the summer and tapered off in the fall. Plants received a total of 2.6 gal (10 L) over 2 years. Rainfall in the first growing year, July to June, was 3.3 in (8.4 cm), an average year for this location, and a perfect test for the irrigation systems.

Measurements

A preliminary study of the area soils had been done to explore the effects of site disturbance on soil fertility and soil symbionts (Virginia et al. 1988). Soil samples taken from under plant canopies and barren areas between plants showed that overall soil fertility was low but improved by the presence of plants. Soil saturation percent, soil moisture, and VAM spores were also higher under plant canopies. For the pit site where this study was established, 34 samples were collected and analyzed before planting, 14 in the pit, including one ant mount, and 20 nearby with and without existing plants. Plant roots were excavated, stained, and examined for mycorrhizal infection, and an infection potential bioassay was performed with collected soils. Spores from soils at root collection spots were extracted and counted. Soil samples were taken 5 years after planting from two depths beneath and outside six mesquite tree (from planting) and three creosote bush (from direct seeding) canopies growing in the pit were analyzed for N and P to examine the recovery of soil fertility.

Plant height and survival were recorded several times over the 2 years.

Experimental Design and Analyses

The three by four (inoculation by irrigation) factorial experiment was set up in seven resource islands (replications) within the borrow pit. Each of the 12 treatment combinations included 8 planted seedlings in each resource island. Analysis of variance was done using SuperAnova and Fisher's Least Significant Difference for soils. Duncan's new multiple range test was used to evaluate significance of irrigation and inoculation on plant development.

Results

Soil samples collected before planting revealed that the already low fertility of the desert soils was further reduced by the extensive soil removal from the borrow pit (figure 6). Nitrogen was one-half and phosphorus was about one-tenth that of undisturbed soils. The ant mound sampled at the bottom of the pit had 12 times as much phosphorus and 3 times as much nitrogen as adjacent soils. Previous bioassays of soils with similar disturbance adjacent to the planting site revealed no mycorrhizal infection potential in recently bladed areas (Virginia et al. 1988, Bainbridge and Virginia 1995). After 5 years, soil fertility improved under plant canopies from container plants (mesquite) or direct seeding (creosote bush). Mean total nitrogen levels doubled under mesquite and tripled under creosote bush (table 1).

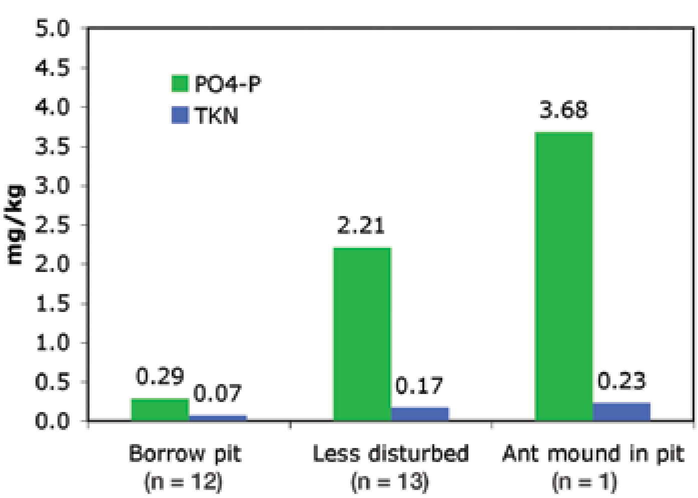

Figure 6. Soil fertility before outplanting from samples taken in the borrow pit, in adjacent less disturbed areas, and in an ant mount in the pit.

Seedling responses to inoculation were minimal. Although early growth effects were observed, survival and growth differences among inoculation treatments were minor over time (table 2, figure 7). All the surface-irrigated plants died by the

Table 1. Mean organic nitrogen concentrations for surface (0.0 to 2.5 cm [0.0 to 1.0 in]) and subsurface (2.5 to 10 cm [1.0 to 4.0 in]) soils sampled beneath and outside mesquite (n = 6) and creosotebush (n = 3) canopies in 1995 increased compared with soil samples collected at the mesquite planting sites before planting in 1990. Within soil layers, means with different letters are significantly different at $p < 0.05$. (1 mg per g = 1,000 ppm).

Sample date and location	Surface layer total organic nitrogen (mg per g)	Subsurface layer total organic nitrogen (mg per g)
1990—open area	0.08 b	0.08 a
1995—beneath mesquite canopy	0.19 a	0.09 a
1995—mesquite open area	0.10 b	0.10 a
1995—beneath creosotebush canopy	0.31 c	0.15 b
1995—creosote bush open area	0.12 ab	0.09 a

Table 2. Growth and survival of mesquite seedlings from each treatment planted in the borrow pit (1.0 cm = 0.39 in).

Irrigation	Inoculation	6-week height (cm)[1]	2-year height (cm)[2]	2-year survival (%)[2]
Surface	None	3.75 A b	—	0
	Rhizobia	3.21 A c	—	0
	VAM	4.31 A c	—	0
	Dual	3.58 A b	—	0
Deep pipe	None	9.36 B a	94.2	79
	Rhizobia	8.38 B b	82.0	86
	VAM	13.32 A a	86.8	86
	Dual	13.84 A a	86	93
Clay pot	None	10.87 B a	70.6	81
	Rhizobia	10.45 B a	72.1	67
	VAM	9.38 B b	50.4	42
	Dual	14.87 A a	52.8	81

[1] For 6-week height, means within each irrigation treatment followed by uppercase letters are significantly different and within each inoculation treatment, means followed by a different lowercase letter are significantly different according to Duncan's new multiple range test.

[2] For 2-year height and survival, plants in the deep-pipe irrigation treatment were significantly greater, but inoculation treatments did not have a significant effect.

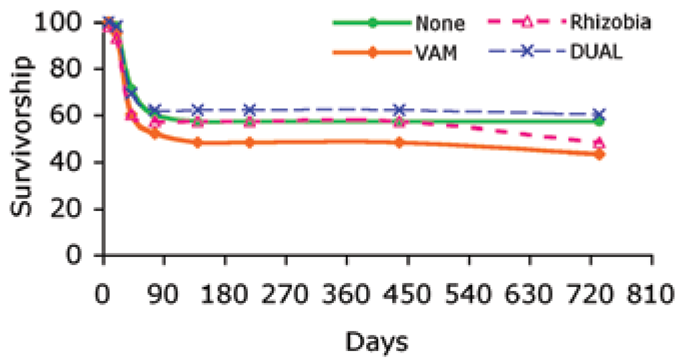

Figure 7. Inoculation treatments did not influence survival significantly over time.

end of the first 5 months, but 86 percent of seedlings irrigated using the deep-pipe method and 68 percent of those irrigated using the buried clay pots remained alive after 2 years (figure 8). Although the growth data have large standard deviations because of high variance in height, differences among the irrigation treatments were significantly different, according to Duncan's new multiple range test. Several trees were more than 3 ft (1 m), while others were only 8-to-16-in (20-to-40-cm) tall after 2 years. The three tallest plants after 2 years were all irrigated using the deep-pipe method. The tallest plant (9.5 ft [2.9 m]) was dual inoculated using deep-pipe irrigation.

Overall, the planted resource islands developed well, due in part to a rain event in spring 1993 (figure 9). This rainfall also led to establishment of a range of other annual and perennial species from the aerial seeding.

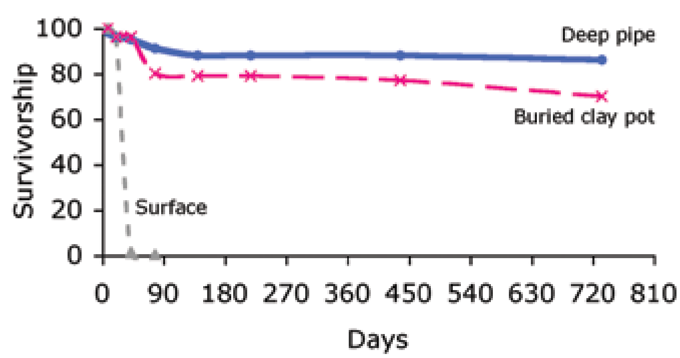

Figure 8. Irrigation method had a significant effect on seedling survival after 2 years.

Discussion

This research clearly demonstrated the changes that severe disturbance can have on site soil fertility and soil ecology. It also confirmed the beneficial effects that plants have on soil fertility and soil moisture. Although we might expect

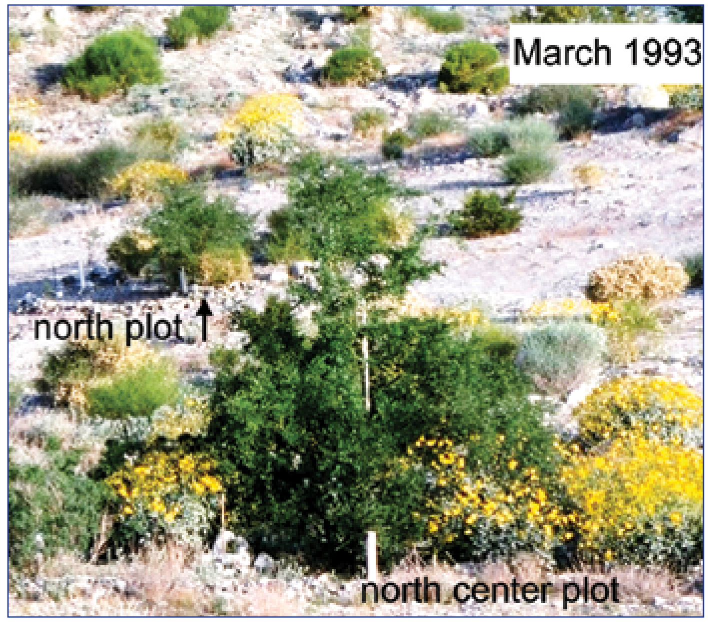

Figure 9. After 2 years, the resource islands were successfully established in the borrow pit. (Photo by David A. Bainbridge 1992)

soil moisture to be depressed under plants, it was increased. This study highlighted also the benefits of deep-pipe and buried-clay-pot irrigation for establishing small seedlings on arid sites (see also Bainbridge 2013). Nearly all the surface-irrigated plants were dead within 78 days, a result all too familiar for many project managers dealing with restoration, revegetation, or reforestation on harsh dry sites, while survival with deep-pipe and buried-clay-pot irrigation was excellent. Mortality in all treatments occurred primarily between July and September of the first year, and more frequent irrigation during this first critical summer may be advantageous. After surviving beyond the critical establishment phase, mesquite seedlings were able to persist.

The very small seedlings used in this study were probably also more vulnerable to drought stress. Larger plants from deep containers with deep-pipe irrigation might survive better and grow faster (Bainbridge 2007, 2012).

The very low soil fertility and limited inoculation potential made this borrow pit an ideal site for an inoculation test, but the benefits of commercial inoculum were modest at best. Inoculation has shown some potential for improving restoration (Allen 1989a, 1989b) but field results have been inconsistent, perhaps because soil ecosystems are complex and not well understood. The interactions between mycorrhizal fungi, rhizobia, and soil fertility are also important. For example, Barea et al. (1987) found that VAM improved nitrogen fixation and uptake. New genetic tools may make it possible to better understand these belowground communities. Koch

(2006) showed large genetic differences between individuals in a mycorrhizal population in an area of 295 by 360 ft (90 by 110 m). Production of effective inoculum for a given site may require much more sophisticated selection and testing.

The soil fertility measurement 5 years after planting and seeding confirmed that plants improve their own microsite by capturing dust and increasing soil fertility. It was surprising to see the increase in soil N under creosote growing in the pit was higher than under mesquite. This result may reflect better capture of litter and dust by creosote. High winds and extensive dust movement may have returned inoculum to these relatively small disturbance sites fairly quickly. Cross infection between treatments may also have occurred. In retrospect, it would have been helpful to sample roots of surviving plants and those that died to see if they had been colonized by symbionts.

The improvement in early performance using clay pots and deep-pipe dual inoculation is instructive. The steady moisture of buried clay pots appears to be more favorable for rhizobial inoculation, deep-pipe irrigation is more favorable with deeper wetting, and greater aeration is better for mycorrhizal inoculation. Deep-pipe plants may also benefit from dust and inoculum falling into the screened open pipe during wind events.

Conclusions

The main goal of this study was to evaluate the effects of inoculation and irrigation treatments on mesquite establishment in the degraded soil of a borrow pit. Inoculation results were mixed and not large. These results might have been different if a locally adapted, site-specific inoculum had been developed. The importance of ants and other microfauna for reestablishing desert soil fertility was also clear (Bainbridge and Virginia 1995, Cammerat et al. 2002).

The value of water-efficient irrigation methods was clearly demonstrated by the excellent survival of clay-pot- and deep-pipe-irrigated trees at the borrow pit. No plants survived using the more traditional surface irrigation.

Preinoculating seedlings is a reasonable strategy for reintroducing symbionts on severely degraded sites but managing root symbiotic associations are complex because of the interactions between soil moisture, soil ecology, and soil chemistry. The management of microsymbionts in containers is not well understood, and inoculation with commercial symbionts is still a developing art even in a controlled nursery setting (Corkidi et al. 2004). Further investigation is needed to determine the optimum inoculum populations, watering regime, irrigation system type, water application rates, nutrient concentrations, growth media, and container size and shape for developing symbiotic associations for mesquite in the greenhouse that will provide long-term benefits in the field. Inoculation of direct seeded plots can also be improved.

Deep-pipe and buried-clay-pot irrigation are each well suited for the most severe sites. Successful revegetation of heavily disturbed arid sites is feasible, but everything must be done well and on time (Allen 1989b, Bainbridge et al. 1993, Bainbridge 2007). Mesquite is a desirable plant for reconstruction because it plays an important role in desert ecosystem function and structure and can provide useful products for animals, birds, and people as well. Funding for long-term research is needed to better determine the best ways for returning mesquite and other multipurpose native trees to degraded drylands.

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