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Salinity tolerance and mycorrhizal responsiveness of native xeroriparian plants in semi-arid western USA

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ABSTRACT

Restoration of salt-affected soils is a global concern. In the western United States, restoration of salinized land, particularly in river valleys, often involves control of *Tamarix*, an introduced species with high salinity tolerance. Revegetation of hydrologically disconnected floodplains and terraces after *Tamarix* removal is often difficult because of limited knowledge regarding the salinity tolerance of candidate native species for revegetation. Additionally, *Tamarix* appears to be non-mycorrhizal. Extended occupation of *Tamarix* may deplete arbuscular mycorrhizal fungi in the soil, further decreasing the success of revegetation efforts. To address these issues, we screened 42 species, races, or ecotypes native to southwestern U.S. for salinity tolerance and mycorrhizal responsiveness. As expected, the taxa tested showed a wide range of responses to salinity and mycorrhizal fungi. This variation also occurred between ecotypes or races of the same species, indicating that seed collected from high-salinity reference systems is likely better adapted to harsh conditions than seed originating from less saline environments. All species tested had a positive or neutral response to mycorrhizal inoculation. We found no clear evidence that mycorrhizae increased salinity tolerance, but some species were so dependent on mycorrhizal fungi that they grew poorly at all salinity levels in pasteurized soil.

1. Introduction

World-wide, over 350 million ha have been classified as saline (EC > 4 dS/m) (Rengasamy, 2006), and restoration of salt-affected soils is becoming a major global concern (Jain et al., 1989; Dixon et al., 1993; Barrett-Lennard, 2002). In the western United States, soils of many riparian areas have become salinized due to the low annual rainfall, which allows salts to accumulate in the soil profile. This is often exacerbated by activities such as flow regulation, groundwater pumping, or channel change that reduce the frequency and intensity of overbank floods which can flush accumulated salts (Jolly et al., 1993). Salinization and hydrologic disconnection of western riparian areas present significant obstacles to restoration or revegetation of these habitats (Shafroth et al., 2008).

Riparian restoration efforts in the western United States commonly include control of *Tamarix* (*T. ramosissima*, *T. chinensis* and their hybrids; tamarisk or saltcedar), an invasive shrub introduced to the western United States in the mid-1880s through the 1930s as an ornamental and for erosion control (Robinson, 1965). Today, *Tamarix* occupies 1–1.6 million acres in the United States (Zavaleta, 2000) and is the third most frequently occurring tree in western riparian areas (Friedman et al., 2005). Unlike native phreatophytes, such as *Populus* spp. and *Salix* spp., *Tamarix* can survive in areas with high levels of soil salinity and deep groundwater (Busch and Smith, 1995; Cleverly et al., 1997; Di Tomaso, 1998; Horton and Clark, 2001; Lite and Stromberg, 2005).

Control of *Tamarix* through a number of methods including biological control (Lewis et al., 2003; DeLoach et al., 2006), herbicide application (Hart et al., 2005) and mechanical clearing (McDaniel and Taylor, 2003) is now proving to be effective. However, active revegetation of these areas, particularly those that have become hydrologically disconnected from fluvial process, is often required to establish a native flora (Harms and Hiebert, 2006; Bay and Sher, 2008). Restoration of native hydromesic vegetation such as *Populus* and *Salix* on these relatively dry, saline sites is often an unrealistic goal. Facultative wetland or xeroriparian plant communities such as savannas, grasslands and shrublands (Johnson et al., 1984) are likely more appropriate restoration targets (Taylor and McDaniel, 2004; Shafroth et al., 2005, 2008). In many instances even active revegetation falls short of meeting restoration goals and scarce

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resources are wasted, usually due to a poor understanding of relationships between site characteristics and the environmental tolerances of the selected replacement vegetation (Briggs et al., 1994; Bay and Sher, 2008; Shafroth et al., 2008).

In some cases, even when site-appropriate plant species are chosen, inoculation of sites with arbuscular mycorrhizal (AM) fungi may be needed when restoring historic floodplain areas and terraces following extended *Tamarix* occupations. AM fungi are soil fungi that associate with the roots of most plant species (Trappe, 1987; Smith and Read, 1997), and in many cases this association results in improved plant survival and growth (Johnson et al., 1997). A few plant species and groups, including the *Tamarix* found in the western United States (Titus et al., 2002; Beauchamp and Stutz, 2005) and most members of the Chenopodiaceae, do not associate with AM fungi (Khan, 1974; Allen et al., 1989; Smith and Read, 1997; Titus et al., 2002). AM fungi may be an important component of riparian ecosystem function (Stutz et al., 2009). In areas with extensive, dense, mature (or long-duration) *Tamarix* occupation, inoculation of the site with AM fungi as part of the restoration plan may increase the performance of native species over new *Tamarix* sprouts or secondary weeds, particularly those in the Chenopodiaceae such as *Kochia* spp. and *Salsola* spp. (Allen and Allen, 1984; Johnson, 1998).

Inoculation of restoration sites with AM fungi may also improve the establishment success of species planted in highly saline or arid soils. AM fungi have been associated with amelioration of salinity and water stress and improved plant performance in many crop plants (Hirrel and Gerdemann, 1980; Ojala et al., 1983; Poss et al., 1985; Bethlenfalvay et al., 1988; Rosendahl and Rosendahl, 1991; Sylvia et al., 1993; Al-Karaki, 2000; Ruiz-Lozano and Azcon, 2000; Cantrell and Linderman, 2001; Feng et al., 2002) and some wild species (Dixon et al., 1993; Giri et al., 2003; Giri and Mukerji, 2004; McHugh and Dighton, 2004). In saline soils, association with AM fungi may improve the supply of mineral nutrients to plants, especially less mobile nutrients (such as P) that tend to precipitate out under high levels of Ca^{2+}, Mg^{2+} and Zn^{2+} (Ojala et al., 1983; Poss et al., 1985; Sylvia et al., 1993; Marschner and Dell, 1994; Al-Karaki et al., 2001). Mycorrhizae can also improve the water absorption capacity of plants by increasing root hydraulic conductivity, the absorptive surface area of the root system, and access to small soil pores (Bethlenfalvay et al., 1988; Ruiz-Lozano and Azcon, 1995; Ruiz-Lozano et al., 1996; Auge, 2001; Feng et al., 2002).

The objective of this study was to address key knowledge gaps regarding the suitability of species native to western USA for revegetation of *Tamarix*-dominated xeroriparian areas. Our work focused on xeroriparian plants of the Rio Grande, the third longest river system in USA; however, most of these taxa have distributions that extend to other rivers throughout semi-arid and arid western North America, and many of the genera and families studied have cosmopolitan distributions. Specifically, our goals were to (1) characterize the effect of salinity on germination, survival and growth for xeroriparian species native to this region; (2) characterize the effect of AM fungal inoculation on survival and growth of xeroriparian species; and (3) determine if AM fungal inoculation increases salinity tolerance for each species tested. We expected to find a range of salinity tolerance and mycorrhizal responsiveness among the plants tested, expressed as differences in germination, survival, and growth between treatments, with members of the Chenopodiaceae being among the most salt tolerant and the least responsive to mycorrhizal fungi. We hypothesized that AM fungi would have the greatest positive effect on plant growth at higher salinity levels and that the most salt-tolerant plants would also have the highest levels of mycorrhizal responsiveness (with the exception of those in the Cheneopodiaceae).

2. Methods

Species tested in this study (Table 1) were selected based on a review of historical and contemporary accounts and floras of the Rio Grande valley and surrounding region (Havard, 1885; Metcalfe, 1903; Bailey, 1905; Watson, 1912; Fosberg, 1940; Lesueur, 1945; Denyes, 1956; Manthey, 1977; Henrickson and Johnston, 1986; Dick-Peddie, 1993), meetings and conversations with land managers and restoration practitioners, and seed availability. With the exception of *Atriplex* spp., we focused our efforts on testing the salinity tolerance of glycophytes or taxa with unknown salt tolerance, rather than studying known halophytes. All species are referred to by the species codes used in the USDA PLANTS database (USDA and NRCS 2008).

2.1. Germination

To determine germination requirements, and germination percentages and vigor for planting in the greenhouse, we sowed between 10 and 200 seeds per species (depending on results of germination pilot studies) into Petri dishes lined with thick filter paper (Whatman 3 qualitative paper) and saturated with 6 mL of tap water (0.10 dS/m). Three replicate dishes were prepared for each species. Each dish was sealed with Parafilm and placed in a growth chamber at 25 °C and 16 h of light per day. Germination was recorded at the end of 7 or 14 days, depending on species.

To determine the effects of salinity on germination, species were also germinated in salt water in a growth chamber using the above methods. Each dish received 6 mL of 1.3 dS/m, 8 dS/m or 15 dS/m salt solution, which was designed to match the ionic composition of water in the Rio Grande near San Marcial, NM and consisted of 38% $CaSO_4$, 37% $NaHCO_3$, 15% MgCl, 9% NaCl and 2% K_2SO_4 (Shafroth et al., 1995). For each species, five dishes were prepared at each salinity level. Germination trials were not conducted for *Atriplex* species because they require repeated leaching with tap water (D. Dreesen, NRCS, personal communication, 2006).

2.2. Survival and growth

Experiments examining the effects of salinity and fungal inoculation on plant survival and growth were conducted in a greenhouse at Colorado State University with temperatures kept between 20 °C and 24 °C, 70% humidity and ambient day length. Species were tested in three batches due to space limitations. All trials lasted for 10 weeks. Trial 1 ran from May to August 2005, trial 2 ran from September to December 2006 and trial 3 ran from April to July 2007 (Table 1).

Species with rapid germination and vigorous growth in tap water were direct-seeded into pots. Less vigorous species were seeded into trays filled with riverbed soil obtained from a gravel mine near Fort Collins, CO (Loamy sand: 85% sand, 5% silt, 10% clay; NO_3 7.4 ppm, P 2.5 ppm, K 158 ppm; pH 7.4; EC 0.7 dS/m), which had been steamed for 2 h and allowed to cool (Table 1). These trays were watered as needed with tap water and seedlings were transplanted once they had reached sufficient size (typically 2–4 weeks). All species were either direct seeded or transplanted into 650 mL Deepots (Stuewe and Sons, Corvallis, OR). Prior to planting, Deepots were rinsed with a fungicide (Prescription Treatment Green-Shield, 1 Tbsp/Gal (15 mL/3.8 L)), allowed to dry and filled with 600 mL of pasteurized soil. Pots were kept covered with plastic sheeting until planting. At the time of planting, 1.5 mL of AM fungal inoculum or microbial wash mix was added to each pot in the mycorrhizal and non-mycorrhizal treatments, respectively. Mycorrhizal inoculum of *Glomus intraradices* (AM120) was provided by a commercial supplier (Reforestation Technologies

Table 1
Species tested in greenhouse screening for salinity tolerance and mycorrhizal responsiveness.

Scientific name	Code	Common name	Variety or location	Supplier	Trial	Planting method	Fertilizer applied	Pre-treatment
Acacia constricta	ACCO2	White thorn acacia	Mexico	Granite Seed	1	Direct	No	Mechanical scarification[1]
Acacia greggii	ACGR	Catclaw acacia	Mexico	Granite Seed	3	Direct	Yes	Mechanical scarification
Achnatherum hymenoides	ACHY	Indian ricegrass	"Paloma" Colorado	Los Lunas PMC	2	Transplant	Yes	
Aristida purpurea	ARPU9	Purple threeawn	New Mexico	Los Lunas PMC	2	Transplant	Yes	
Atriplex canescens	ATCA2-A	Fourwing saltbush	6X, high salinity site, New Mexico	Los Lunas PMC	3	Direct	Yes	7 days leach with daily water change
Atriplex canescens	ATCA2-B	Fourwing saltbush	6X, low salinity site, New Mexico	Los Lunas PMC	3	Transplant	Yes	7 days leach with daily water change
Atriplex canescens	ATCA2-C	Fourwing saltbush	4X, New Mexico	Los Lunas PMC	3	Transplant	Yes	7 days leach with daily water change
Atriplex polycarpa	ATPO	Desert saltbush	Mexico	Granite Seed	3	Transplant	Yes	7 days leach with daily water change
Baccharis salicina	BASA	Willow baccharis	New Mexico	Los Lunas PMC	2	Transplant	Yes	
Baileya multiradiata	BAMU	Desert marigold	California	Western Native Seed	2	Transplant	Yes	
Berlandiera lyrata	BELY	Chocolate daisy	New Mexico	Plants of the Southwest	2	Transplant	Yes	
Bothriochloa barbinodis	BOBA3	Cane bluestem	"Grant" Arizona and New Mexico	Los Lunas PMC	2	Transplant	Yes	
Bouteloua curtipendula	BOCU	Sideoats grama	"Niner" New Mexico	Los Lunas PMC	2	Transplant	Yes	
Bouteloua eriopoda	BOER4	Black grama	"Nogal" New Mexico	Los Lunas PMC	2	Transplant	Yes	
Bouteloua gracilis	BOGR2	Blue grama	New Mexico	Plants of the Southwest	3	Transplant	Yes	
Chilopsis linearis	CHLI2	Desert willow		Granite Seed	3	Transplant	Yes	
Elymus canadensis	ELCA4	Canada wildrye	"Mandan" Oregon	Western Native Seed	1	Direct	No	
Elymus elymoides	ELEL5	Squirreltail	"Tusas" New Mexico	Los Lunas PMC	2	Transplant	Yes	
Elymus trachycaulus	ELTR7	Slender wheatgrass		Granite Seed	3	Transplant	Yes	
Ericameria nauseosa	ERNA10	Rubber rabbitbrush	New Mexico	Los Lunas PMC	3	Direct	Yes	
Eschscholzia caespitosa	ESCA	Tufted poppy	Oregon	Plants of the Southwest	3	Transplant	Yes	
Forestiera pubescens	FOPU2	New Mexico olive	"Jemez" New Mexico	Los Lunas PMC	3	Transplant	Yes	Cold stratification 40 °C for 60 days
Gaillardia pulchella	GAPU	Blanketflower	New Mexico	Plants of the Southwest	3	Transplant	Yes	
Krascheninnikovia lanata	KRLA2	Winterfat	Colorado	Western Native Seed	2	Transplant	Yes	
Leymus triticoides	LETR5	Beardless wildrye		Granite Seed	3	Transplant	Yes	
Lycium torreyi	LYTO	Squawthorn	New Mexico	Los Lunas PMC	2	Transplant	Yes	
Muhlenbergia asperifolia	MUAS	Scratchgrass	New Mexico	Los Lunas PMC	1	Direct	Yes	
Muhlenbergia pungens	MUPU2	Sandhill muhly	New Mexico	Los Lunas PMC	2	Transplant	No	
Oenothera pallida	OEPA	Pale evening primrose	California	Plants of the Southwest	2	Transplant	Yes	
Panicum obtusum	PAOB	Vine mesquite	New Mexico	Los Lunas PMC	2	Transplant	Yes	
Pascopyrum smithii	PASM	Western wheatgrass	North Dakota	Granite Seed	3	Transplant	Yes	
Pleuraphis jamesii	PLJA	James' galleta	"Viva" New Mexico	Los Lunas PMC	2	Transplant	Yes	
Prosopis glandulosa	PRGL2	Honey mesquite	California	S&S Seeds	3	Direct	Yes	Mechanical scarification
Prosopis pubescens	PRPU	Screwbean mesquite	Arizona	Granite Seed	3	Direct	Yes	Mechanical scarification
Psorothamnus scoparius	PSSC6	Broom dalea	"Mesa" New Mexico	Los Lunas PMC	3	Transplant	Yes	
Ratibida columnifera	RACO3	Mexican hat	California	Plants of the Southwest	3	Direct	Yes	
Sorghastrum nutans	SONU2	Indiangrass	"Llano" New Mexico	Los Lunas PMC	3	Transplant	Yes	
Sporobolus airoides	SPAI	Alkail sacaton	"Salado" New Mexico	Los Lunas PMC	2	Transplant	Yes	
Sporobolus cryptandrus	SPCR	Sand dropseed	Colorado	Western Native Seed	1	Direct	No	
Sporobolus flexuosus	SPFL2	Mesa dropseed	New Mexico	Los Lunas PMC	3	Direct	Yes	
Sporobolus wrightii	SPWR2-A	Big sacaton	Arizona	Research Ranch	1	Direct	No	
Sporobolus wrightii	SPWR2-B	Big sacaton	New Mexico	Los Lunas PMC	2	Transplant	Yes	

[1] Mechanical scarification was accomplished by nicking the seed coat with a razor blade.

International; Salinas, CA). A microbial wash for the uninoculated treatment was made by homogenizing a sufficient amount (1.5 mL per pot) of live inoculum in a blender, sieving this blend three times through a 45 μm sieve to remove fungal spores and hyphae, and mixing the filtrate with a sterile clay inoculum base (baked at 140 °C for 3 h), provided by the inoculum supplier.

To germinate and establish seedlings, all pots were watered twice weekly with tap water to flow-through. Once seedlings were large enough to be measured without damage, all pots were thinned to one seedling per pot, the height of all remaining plants was measured, and salt treatments were initiated. Woody species were measured from the soil surface to the apical meristem. Herbaceous species were measured from the soil surface to the tip of the longest leaf. Salt treatments consisted of a 50 mL dose of 1.3 dS/m, 8 dS/m or 15 dS/m salt solution per pot applied twice per week for 10 weeks. The 1.3 dS/m treatment was chosen to represent exposure to low salinity soils as we lacked a deionized water source capable of producing sufficient quantities of water for a 0 dS/m control treatment. Each salinity/fungal combination was replicated 10 times for a total of 60 pots per species. Pots for each trial were organized in a randomized-block design to account for any environmental differences along the greenhouse bench. Each replicate formed a block on the greenhouse bench and all treatments and species were randomized within each block. In some cases not all 60 plants survived to the beginning of the salt treatments. In these cases, the surviving plants were divided as evenly as possible between the salt treatments. Seedlings in trials 2 and 3 were watered with 100 mL of phosphorus-free fertilizer solution (100 ppm; 0.65 g/L; 15–0–15) one week prior to the initiation of salt treatments and halfway through the experiment (week 5). For each round of fertilization, the fertilizer solution was applied as two 50 mL doses given five days apart.

Dead plants were harvested twice weekly throughout the experiment. An individual was determined to be dead when no green tissue remained on the plant. At the end of the experiment, or upon death, roots and shoots were harvested, dried to a constant weight in a 40 °C oven and weighed. Plant biomass is expressed as the sum of the dry root and shoot weights. At the end of trial 1, soil

was collected from a subset of pots in each salinity treatment and analyzed for pH and EC by the Colorado State University Soil, Water & Plant Testing Laboratory (Fort Collins, CO).

2.3. Verification of colonization

Roots from three randomly selected individuals from the inoculated and uninoculated treatments for each species were placed in tissue capsules and stained with trypan blue to highlight fungal structures (Koske and Gemma, 1989). Stained roots were cut in to 1 cm segments and placed in a Petri dish with a gridded bottom. The gridlines were used to scan each sample for colonization (*sensu* Giovannetti and Mosse, 1980), but the number of colonized intersections was not recorded. Roots of BASA, OEPA, ESCA and BELY were not checked due to poor root growth. This effort checked the roots of 10% of the plants (230 samples) grown for this experiment.

2.4. Data analysis

Percent germination was compared between the three salinity levels for each species using the Kruskal–Wallis test with Dunn's test used for post hoc pairwise comparisons. Because of the differences in sample size between the tap water and salt water germination trials (originally, these were not intended to be compared), we did not include the tap water treatment in the statistical tests, but highlight instances where germination in tap water was at least 120% greater than the maximum amount of germination achieved in salt water.

Survival analysis was used to compare survival curves between salinity levels and mycorrhizal treatments for each species. Survival analysis was run twice, once to test for the effect of salinity while controlling for mycorrhizae and again to test for the effect of mycorrhizae while controlling for the effect of salinity (Allison, 1995).

The effects of salinity and mycorrhizae on plant growth (biomass) were examined using a two-way ANOVA with block (position in greenhouse) included as a main effect. Original plant height (measured at the initiation of salt treatments) was included as a covariate to account for any influence starting size may have had on plant response. Due to deaths before the initiation of the salt treatment, some species had unbalanced numbers of replicates between treatments. In these cases, we used the P values associated with the type III sums of squares. Values for each species were tested for normality and homogeneity of variance, and were transformed as necessary to meet these assumptions before analysis. In some cases, species grew very poorly in the uninoculated treatment and showed a significant response to mycorrhizae, but not salinity. In these cases, we also used a one-way ANOVA, with block as an effect and original height as a covariate, to test the effect of salinity in only the mycorrhizal treatment. Statistical analyses were conducted using SAS version 8.2 (SAS Institute, 2001). In all analyses, we accepted $P < 0.05$ as indicating a significant difference between groups. To quantify relative mycorrhizal responsiveness of the different species tested, we ranked species by the lower 95% confidence interval of the mean of the ratio between the inoculated and uninoculated treatments for each salinity level in each experimental block.

3. Results

3.1. Germination

Of the species tested, BELY, MUAS and PSSC6 germination was most sensitive to salinity, with germination highest in the tap water treatment and low at all salinity levels (Table 2). Germination of ACHY, BASA, BOER4, CHLI2, ELEL5, ERNA10, MUPU2, OEPA and SPCR also showed low tolerance to salinity with germination affected at intermediate and high levels of salinity and/or germination in tap water at least 120% higher than in any of the salinity treatments (Table 2; Appendix A). Germination of ARPU9, BOBA3, BOCU, ELCA4, ESCA, FOPU2, GAPU, PAOB, SONU2, SPAI, SPFL2 and both ecotypes of SPWR2 was similar between the tap water and two lowest salinity treatments, but was reduced at the highest salinity level. BOGR2, KRLA2, ELTR7, LYTO, PLJA, PRGL2 and PRPU were the most tolerant of salinity at the germination stage, with similar germination rates in tap water and at all three salinity levels (Table 2; Appendix A). Germination of ACCO2, ACGR, BAMU and RACO3 was marginally different between salinity levels ($0.05 < P < 0.10$). While these differences are not statistically significant, which would indicate a high salinity tolerance, these species warrant further investigation to determine if germination is indeed unaffected by salinity.

3.2. Greenhouse experiments

At the conclusion of trial 1, soil EC was 1.3 ± 0.3 dS/m, $6.7 \pm$ dS/m and 10.8 ± 1.0 dS/m in the 1.3 dS/m, 8.0 dS/m and 15.0 dS/m treatments, respectively. Soil pH averaged 8.3 and did not differ across treatments. Growth of BASA, OEPA, ESCA and BELY was poor (<7 mm) in all treatments. We examined these species for survival response to salinity and mycorrhizal fungi, but not for growth responses.

Examination of stained roots showed that roots of BOBA3, BOER4 and PLJA were damaged by harvesting and staining and insufficient cortex tissue remained to assess colonization. Of the remaining samples that were examined, only one sample in the uninoculated treatment was colonized. Of the samples from the inoculated treatment, all ATPO, KRLA2 ATCA2-A, B and C, ACGR, ELEL5, ELTR7 and PAOB samples showed no evidence of mycorrhizal colonization, and least one of the three samples from the inoculated treatment examined for ACCO, ACHY, ARPU9, BOCU, LYTO, PSSC6, SPAI, and SPWR2-B was not colonized.

3.2.1. Response to salinity

Survival of 23 of the 42 species or ecotypes tested was negatively affected by the salinity treatments. Salinity had a positive effect on survival of ELEL5 with three plants dying in 1.3 dS/m treatment and all others surviving at the higher salinity levels (Table 2; Appendix B).

Based on total biomass, ACCO2, BAMU, BOER4, BOGR2, ELTR7, LYTO, MUAS, PAOB, PSSC6, RACO3, SPCR and SPWR2-B had low salinity tolerance, with biomass significantly decreased at the two highest salinity levels (Table 2; Appendix C). ACHY, ATCA2-B, KRLA2, CHLI2, ELCA4, ELEL5, FOPU2, LETR5, MUPU2, PASM, PRPU, SPFL2 and SPWR2-A showed intermediate tolerance to salinity with biomass depressed at the highest salinity level or significantly different between all levels. ARPU9, ATCA2-A, ATCA2-C, ATPO, BOBA3, ERNA10, PLJA, PRGL2 and SONU2 were the most tolerant of salinity, with biomass not significantly different between any of the salinity levels tested (Table 2, Appendix C). Growth of GAPU, ACGR, BOCU, and SPAI was marginally different between salinity levels ($0.05 < P < 0.10$). Although these differences are not statistically significant (which could be interpreted as indicating a high tolerance to salinity), these species warrant further investigation to determine if they are, indeed, highly tolerant of salinity.

3.2.2. Response to mycorrhizal inoculation

Survival of 10 species was increased by mycorrhizal inoculation (Table 3; Appendix D) and 23 of the 38 species analyzed for

biomass had a positive response to mycorrhizal inoculation (Table 3; Appendix C). FOPU2, GAPU, MUAS, SPFL2 and SPWR2-B had both a positive survival and growth response to mycorrhizal fungi. ACCO2, ATCA2-A, ATCA2-C, ATPO, KRLA2, PSSC6, SPCR and SPWR2-A showed no survival or growth response to mycorrhizal inoculation. All other species tested showed a positive response to inoculation in terms of either survival or growth, but not both. Of the 23 species with a positive growth response to mycorrhizae, nine species had less than a two-fold increase in biomass when inoculated, eight had a two- to three-fold increase, and the biomass of six species increased more than three times when inoculated (Fig. 1).

3.2.3. Interactions between salinity tolerance and AM fungal responsiveness

Of the species with low salinity tolerance (as determined by biomass), 60% were positively affected by mycorrhizae, while 84% of those with intermediate to high tolerances to salinity were positively affected by mycorrhizae (Table 4).

Significant salinity × mycorrhizae interactions occurred for 10 species (BAMU, CHLI2, ELTR7, FOPU2, GAPU, LETR5, PAOB, PRPU, RACO3 and SPWR2-A) (Appendix C). Most of these occurred when biomass in the inoculated treatment decreased sharply as salinity increased, while biomass in the uninoculated treatment was similar and very low across all salinity levels (Fig. 2).

Table 2
Summary table for salinity effects on germination, survival and growth.

Code	Germination[1] (tolerance to salinity)	Survival and growth – greenhouse experiments		
		N	Survival[2] (effect of salinity)	Biomass[3] (tolerance to salinity)
ACCO2	High†	60	Negative****	Low**
ACGR	High†	60	Neutral	High†
ACHY	Low**	60	Neutral	Intermediate****
ARPU9	Medium*	60	Negative***	High
ATCA2-A	NA	59	Negative*	High
ATCA2-B	NA	59	Neutral	Intermediate*
ATCA2-C	NA	58	Neutral	High
ATPO	NA	58	Negative**	High
BASA	Low**	53	Negative*	NA
BAMU	Medium*	58	Negative****	Low*
BELY	High†	47	Neutral	NA
BOBA3	Medium**	59	Neutral	High
BOCU	Medium*	60	Neutral	High†
BOER4	Low*	39	Negative*	Low*
BOGR2	High	59	Negative****	Low****
CHLI2	Low**	60	Negative****	Intermediate****
ELCA4	Medium*	59	Neutral	Intermediate****
ELEL5	Low**	60	Positive*	Intermediate***
ELTR7	High	60	Neutral	Low****
ERNA10	Low**	58	Neutral	High
ESCA	Medium**	57	Negative****	NA
FOPU2	Medium**	60	Negative***	Intermediate**
GAPU	Medium*	60	Negative****	High†
LETR5	NA	60	Neutral	Intermediate****
KRLA2	High	42	Negative*	Intermediate*
LYTO	High	60	Negative**	Low**
MUAS	Very low	59	Negative**	Low*
MUPU2	Low**	59	Negative**	Intermediate****
OEPA	Low**	44	Neutral	NA
PAOB	Medium**	60	Negative****	Low*
PASM	NA	60	Neutral	Intermediate**
PLJA	High	60	Neutral	High
PRGL2	High	59	Neutral	High
PRPU	High	57	Negative*	Intermediate*
PSSC6	Very low	60	Negative**	Low****
RACO3	High†	58	Negative**	Low**
SONU2	Medium**	60	Neutral	High
SPAI	Medium*	60	Neutral	High†
SPCR	Low*	54	Negative**	Low**
SPFL2	Medium*	60	Negative**	Intermediate**
SPWR2-A	Medium**	60	Neutral	Intermediate*
SPWR2-B	Medium*	58	Negative**	Low***

NA: not tested due to poor germination or growth at all salinity levels.

[1] Very low: affected at all salinity levels when compared to tap water (no significant effect of salinity, but germination in tap water at least 120% greater than germination at any salinity level); low: affected at intermediate and high levels of salinity, or at low salinity levels when compared to tap water; medium: affected at the highest salinity level but similar between the tap water and two lowest salinity treatments; high: similar germination rates in tap water and at all three salinity levels (no significant effect of salinity).

[2] Positive: increase in survival as salinity increases; neutral: no significant effect of salinity on survival; negative: decrease in survival as salinity increases.

[3] Low: affected at intermediate and high levels of salinity; medium: affected at the highest salinity level or at all levels ($1.3 > 8.0 > 15.0$); high: similar growth at all three salinity levels (no significant effect of salinity).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

† Marginal difference in response between salinity levels ($0.05 < P < 0.10$) indicating that some effect of salinity may be present.

Table 3
Summary table for effects of AM inoculation on survival and growth.

Code	Survival and growth – greenhouse experiments		
	N	Survival[1] (effect of AM fungi)	Biomass[2] (response to AM fungi)
ACCO2	60	Neutral	Neutral
ACGR	60	Positive*	Neutral
ACHY	60	Neutral	Positive**
ARPU9	60	Neutral	Neutral
ATCA2-A	59	Neutral	Neutral
ATCA2-B	59	Neutral	Positive*
ATCA2-C	58	Neutral	Neutral
ATPO	58	Neutral	Neutral
BASA	53	Neutral	NA
BAMU	58	Positive***	Neutral
BELY	47	Neutral	NA
BOBA3	59	Neutral	Positive*
BOCU	60	Neutral	Positive**
BOER4	39	Positive*	Neutral
BOGR2	59	Positive**	Neutral
CHLI2	60	Neutral	Positive****
ELCA4	59	Neutral	Positive*
ELEL5	60	Neutral	Positive****
ELTR7	60	Neutral	Positive****
ERNA10	58	Neutral	Positive*
ESCA	57	Neutral	NA
FOPU2	60	Positive*	Positive****
GAPU	60	Positive****	Positive****
LETR5	60	Neutral	Positive****
KRLA2	42	Neutral	Neutral
LYTO	60	Neutral	Neutral
MUAS	59	Positive**	Positive****
MUPU2	59	Neutral	Positive**
OEPA	44	Neutral	NA
PAOB	60	Neutral	Positive*
PASM	60	Neutral	Positive****
PLJA	60	Neutral	Positive***
PRGL2	59	Neutral	Positive***
PRPU	57	Neutral	Positive****
PSSC6	60	Neutral	Neutral
RACO3	58	Positive****	Neutral
SONU2	60	Neutral	Positive***
SPAI	60	Neutral	Positive*
SPCR	54	Neutral	Neutral
SPFL2	60	Positive*	Positive*
SPWR2-A	60	Neutral	Neutral
SPWR2-B	58	Positive**	Positive****

NA: not tested due to poor germination or growth at all salinity levels.
[1] Positive: increase in survival with AM fungal inoculation; neutral: no significant effect of AM fungi on survival.
[2] Positive: increase in height or biomass with AM fungal inoculation; neutral: no significant effect of AM fungi inoculation on height or biomass.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

4. Discussion

Salinity tolerance and mycorrhizal responsiveness of crop plants has been widely studied, but much less is known about the responses of wild grass, shrub and herb species to salinity and mycorrhizal inoculation (Shafroth et al., 2008 and references therein). We observed considerable variation in species' tolerance to salinity and response to AM fungi, highlighting the potential utility of this type of study for practitioners who may otherwise be faced with making uninformed decisions about which species to plant (Anderson et al., 2004) or whether or not to use mycorrhizal inoculum in restoration projects.

Examination of stained roots showed that inoculation was successful in the majority of samples examined from the inoculated treatment. None of the samples of ATPO, KRLA2 ATCA2-A, B and C examined were colonized, as expected for members of the Chenopodiace. Lack of colonization in all examined samples of ACGR, ELEL5, ELTR7 and PAOB and in at least one of the three samples examined for ACCO, ACHY, ARPU9, BOCU, LYTO, PSSC6, SPAI, and SPWR2-B may be due to inability of *Glomus intradicies* to colonize a particular plant species, or due to lack of fungal spore germination in a fraction of the samples in the inoculated treatment. Three of the species in which no mycorrhizal colonization could be detected in the subsample examined (ATCA2-B, PAOB and ELEL5) had a positive biomass response to AM fungal inoculation. In the case of ATCA2-B and PAOB, this response was weakly positive. Lack of fungal spore germination in some of the inoculated pots may result in underestimates of mycorrhizal responsiveness for some species. Of the samples from the uninoculated treatment that were examined, only one was colonized. Colonization in this sample was restricted to one root fragment and likely represents transfer of a root fragment from an inoculated sample to this sample at some point during processing.

We hypothesized that species in the Chenopodiaceae would be most tolerant of salinity and least responsive to mycorrhizal fungi. Of the five species or strains of Chenopodiaceae tested in this study, ATCA2-C was the most tolerant of salinity, with survival and growth unaffected at all salinity levels. ATCA2-A and ATPO were also highly tolerant of salinity with survival affected at high salinity levels, but growth unaffected at all levels. KRLA2 and ATCA2-B showed the most sensitivity to salinity, with growth affected at the highest salinity level in ATCA2-B and both growth and survival of KRLA2 affected at the highest salinity level.

These findings also highlight the potential differences in salinity tolerance between strains of the same species. ATCA2 has the broadest distribution of the saltbushes, and is capable of inhabiting a wide range of habitat types and soil salinities. Additionally, this species exhibits high genetic diversity with a variety of chromosomal races of varying ploidy and numerous ecotypes (Glenn et al., 1996; Sanderson and McArthur, 2004). Studies of ATCA2, and other species, have found that salinity tolerance can vary with ploidy (Schachtman et al., 1992), and ecotype (Glenn et al., 1996).

The ATCA2 genotype with the lowest sensitivity to salinity (in terms of both survival and growth) was the tetraploid ATCA2-C. Of the hexaploids tested, ATCA2-A, which was collected from a high salinity site, was least sensitive to salinity (in terms of growth), while ATCA2-B, from a low salinity site, had the most sensitivity to salinity, indicating that site conditions can influence selection for traits such as salinity tolerance. In situations where genotypes with high salinity tolerance are desired for revegetation, the best strategy may be to collect seed from nearby reference sites with high salinity, rather than collecting seed from known lower salinity sites or purchasing seed of unknown origin from a commercial supplier (Glenn et al., 1996; Sanderson and McArthur, 2004).

Our hypothesis that members of the Chenopodiaceae would not respond to inoculation with mycorrhizal fungi was supported for four of the five species or genotypes tested. Inoculation with AM fungi had no effect on survival of any of the species tested, and only ATCA2-B showed a growth response to AM fungal inoculation. While members of the Chenopodiceae are typically considered non-mycorrhizal, and certain species within this family can actively reject infection by the fungus (Allen et al., 1989), there is evidence that some species of *Atriplex* form functioning mycorrhizas for short periods (Allen, 1983; Plenchette and Duponnois, 2005). When checked for colonization, all samples of Chenopodiceae examined were not colonized. The slight (<2-fold) growth increase in the colonized treatment of ATCA2-B may represent a Type I error, or may have occurred if individuals other than those examined were colonized.

Ecotype-level differences in response to salinity and mycorrhizal fungi were also evident in SPWR2. This bunchgrass is a major component of semi-arid grasslands associated with riparian areas

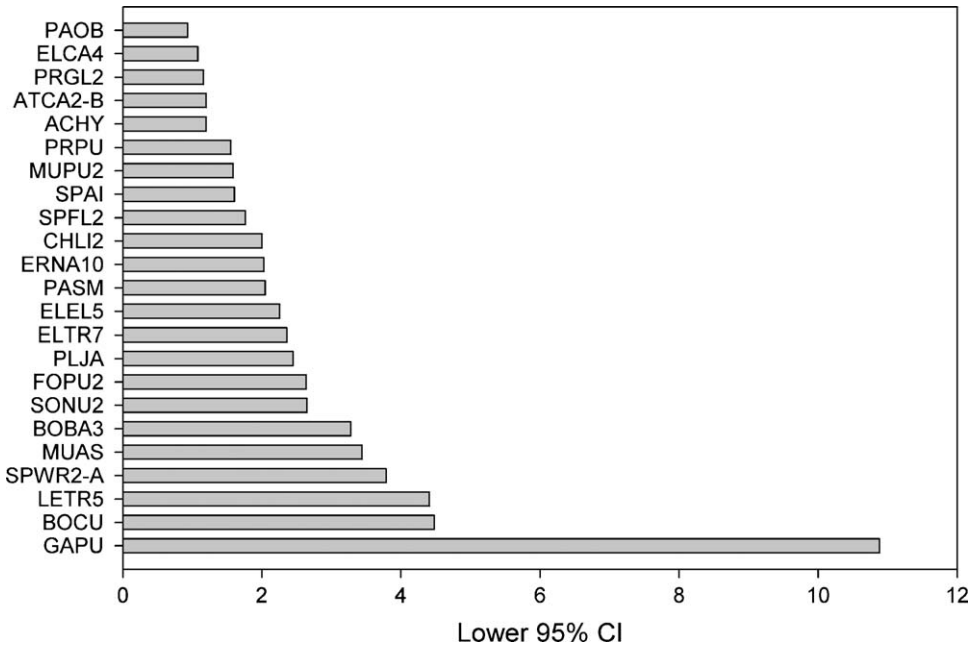

Fig. 1. Mycorrhizal responsiveness of native xeroriparian species. Value shown is the lower 95% CI of the mean of the biomass ratio between mycorrhizal and non-mycorrhizal plants for each species. Only species with a statistically significant response to mycorrhizal fungi ($P < 0.05$) are shown.

in the southwestern United States and Sonora, Mexico. Previous work with this species found that SPWR2 associates with mycorrhizal fungi (Kennedy et al., 2002) and that pre-inoculated plants used in revegetaion projects had greater survival and growth (Richter and Stutz, 2002). In our study, we tested SPWR2 strains from Arizona (AZ) and New Mexico (NM). We found that the AZ strain (SPWR2-A) showed higher tolerance to moderate levels of salinity than the NM strain (SPWR2-B), and that the NM strain had a stronger response to AM fungal inoculation.

Effects of salinity on survival and growth corresponded for many species. Survival of 92% of species with low salinity tolerance (as determined by biomass response) was negatively affected by salinity, while survival of only 46% of species with intermediate and high salinity tolerance was negatively affected by salinity. Conversely, there was very little correspondence between the effect of salinity on germination and on survival and growth, indicating that different factors may be responsible for salinity tolerance at the germination and seedling stages (Norlyn, 1980). Species such as ACHY, ARPU9, BOBA3, CHLI2, ELEL5, ERNA10, MUPU2 and SONU2 that showed low to medium salinity tolerance at the germination stage, but medium to high salinity tolerance at the seedling stage, may survive at high salinity sites if planted as container plants, or otherwise are exposed to reduced salt levels at germination (e.g., via deep-furrow seeding into less saline soil horizons; K. Lair, USBR, personal communication, 2008).

Inoculation with *G. intraradices* (AM120; Reforestation Technologies International, Salinas CA) proved either beneficial or neutral for all species tested, indicating that it can have a positive effect on many species when used in environments where the native inoculum potential is low. In saline soils, association with AM fungi may improve water absorption capacity (Bethlenfalvay et al., 1988; Ruiz-Lozano and Azcon, 1995; Ruiz-Lozano et al., 1996; Auge, 2001; Feng et al., 2002) and increase the supply of mineral nutrients to plants (Ojala et al., 1983; Poss et al., 1985; Sylvia et al., 1993; Marschner and Dell, 1994; Al-Karaki et al., 2001). For species other than those in the Chenopodiaceae, we hypothesized that AM fungi would have the greatest positive effect on plant growth at higher salinity levels, and that the most salt-tolerant plants would also have the highest levels of mycorrhizal responsiveness. Our results show some support for this hypothesis. Of the 10 species with high salinity tolerance (other than plants in the Chenopodiaceae), all showed at least some response to AM fungi, and six showed growth increases of two-fold or more when inoculated.

A significant interaction between salinity tolerance and mycorrhizal responsiveness, where increased salinity had a less negative effect on the inoculated treatment when compared to the uninoculated treatment, would be convincing evidence that inoculation with AM fungi increased salinity tolerance in a particular species (Fig. 2a). We found 10 instances of a significant interaction between salinity and AM fungal inoculation in this study, but the nature of the interaction does not support our hypothesis that AM inoculation would increase salinity tolerance. In the majority of interactions encountered, biomass in the inoculated treatment decreased sharply as salinity increased, while biomass in the uninoculated treatment was similar and very

Table 4
Salinity tolerance and mycorrhizal responsiveness of native xeric riparian species.

Response	Low salinity tolerance*	Intermediate salinity tolerance	High salinity tolerance
No mycorrhizal response	ACCO2, PSSC6, SPCR	KRLA2	ATCA2-A, ATCA2-C, ATPO
Survival response only	BAMU, BOER4, RACO3		ACGR†
Growth increase <2-fold	PAOB	ACHY, ATCA2-B, ELCA4, MUPU2, PRPU, SPFL2, SPWR2-A	ARPU9, PRGL2, SPAI†
Growth increase >2-fold but <3-fold	LYTO, BOGR2, ELTR7	CHLI2, ELEL5, FOPU2, PASM	ERNA10, PLJA, SONU2,
Growth increase >3-fold	MUAS, SPWR2-B	LETR5	BOBA3, BOCU†, GAPU†

* Determined by biomass – see notes for Table 2 for definition of categories.
† Marginal difference in response between salinity levels ($0.05 < P < 0.10$) indicating that some effect of salinity may be present.

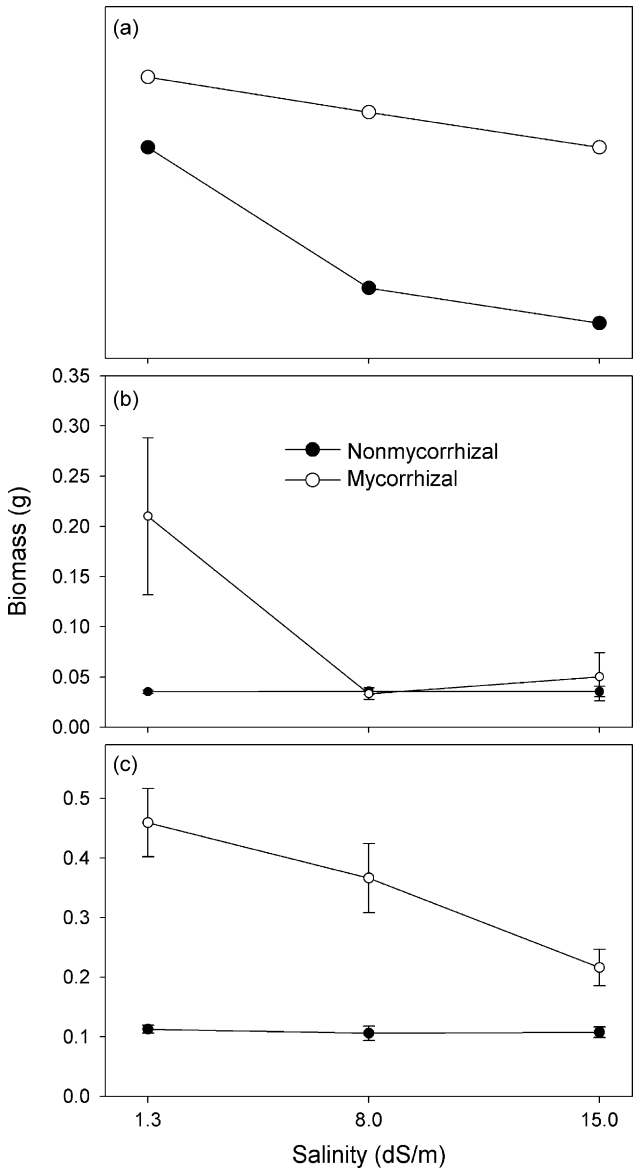

Fig. 2. Salinity × mycorrhizae interactions. Upper panel (a) shows expected relationship where inoculation with mycorrhizal fungi results in increased salinity tolerance. Lower panels show actual relationships between salinity and mycorrhizae for growth of (b) PAOB and (c) FOPU2, which are representative of the salinity × mycorrhizae interactions found in this study.

low across all salinity levels (Fig. 2b and c). While this pattern could be interpreted as increased salinity tolerance due the interaction of the plant with mycorrhizal fungi, the more likely explanation is that some plants are so dependent on AM fungi that they grow poorly, even at low salinity levels, if the fungi are not present. In most cases, the increase in growth seen with inoculation was more pronounced at the low (1.3 dS/m) and intermediate (8 dS/m) salinity levels.

AM fungal inoculation has been used in a number of restoration efforts, including those on mine spoils (Reeves et al., 1979; Noyd et al., 1996; Johnson, 1998; Burke, 2003), desertified areas (Requena et al., 1996, 2001; Palenzuela et al., 2002), abandoned agricultural fields (Richter and Stutz, 2002), tallgrass prairie (Smith et al., 1998) and tropical soils (Cuenca et al., 1998; Allen et al., 2003). Use of AM inoculum can be particularly beneficial in cases where soil disturbance (Jasper et al., 1989; McGonigle and Miller, 2000) or occupation by non-mycorrhizal species has reduced soil inoculum potentials (Lekberg and Koide, 2005). This is likely the case in restoration of long-duration *Tamarix* domination in riparian areas. Removal of *Tamarix* often involves intensive soil plowing and raking to remove root material, and burning of the accumulated woody debris (Taylor and McDaniel, 1998; McDaniel and Taylor, 2003). Intensive soil disturbance can destroy hyphal networks (Jasper et al., 1989; McGonigle and Miller, 2000), and burning can reduce fungal populations (Esquilin et al., 2007), lowering inoculum potential in areas where it may already be suppressed due to extended occupation of non-mycorrhizal *Tamarix*. In our study, all plant species tested had a positive or neutral response to AM fungi, indicating that inoculation of *Tamarix*-dominated sites may increase the success of mycorrhizal species used in restoration efforts (Noyd et al., 1996; Cuenca et al., 1998; Johnson, 1998).

In this study, we tested plant responses to a commercially available isolate of *G. intraradices*, as this is the species of AM fungal inoculum most accessible to restoration practitioners (Schwartz et al., 2006) and is likely already present at southwestern US sites (Stutz and Morton, 1996; Stutz et al., 2000; Kennedy et al., 2002). However, introduction of novel fungal isolates of *G. intraradicies* to the restoration site still remains a concern to some practitioners and ecologists. Our results show that commercial inoculum can have positive effects on plant performance. Other studies suggest, however, that the best strategy is to generate customized inoculum from an adjacent reference site (Douds et al., 2000, 2005; Gianinazzi and Vosatka, 2004). This ensures that novel fungi are not introduced to the site (Diez, 2005; Schwartz et al., 2006; Desprez-Loustau et al., 2007), and that the ecotypes used are the best possible match between the environment and target plant species (Stahl and Smith, 1984; Requena et al., 2001; Palenzuela et al., 2002; Caravaca et al., 2003). This approach is typically not implemented due to budgetary and logistical constraints.

Soil alkalinity, texture and a lack of *Rhizobium* inoculation are other factors that may have significantly affected the growth of species tested in this experiment. Soil salinity and alkalinity are often correlated, as a buildup of ions in the soil can significantly alter the pH, making it difficult to separate plant responses to salinity from the effects of increased pH. Soil pH at the end of the first trial was 8.3, and was not significantly different between salinity treatments. In light of this, we are confident that the results presented here reflect responses to salinity, but they need to be interpreted as occurring in a slightly alkaline environment. Response to salinity may vary with soil texture, as salts tend to accumulate more rapidly and for longer duration in fine textured soils (e.g., silts, clays). For this experiment, we used loamy sand so that all samples would drain well and salts would not accumulate in the pots over the course of the experiment. Poor growth of some species, particularly BASA, OEPA, ESCA and BELY, likely is attributable more to the coarseness of the soil used than to any of the salinity treatments. Finally, five of the species tested (ACCO2, ACGR, PRGL2, PRPU and PSSC6) are members of the Fabaceae. These species would likely be associated with *Rhizobium* bacteria under field conditions. This association may alter their response to mycorrhizal fungi or salinity. We did not inoculate any species with *Rhizobium* in these experiments.

5. Conclusions

Restoration of salt-affected soils is a global concern. In the semi-arid western U.S. much attention has been focused on revegetation of hydrologically disconnected and salinized floodplains dominated by *Tamarix*. Little is known about the salinity tolerance or mycorrhizal responsiveness of potential xeroriparian replacement vegetation for these sites, forcing managers to make uninformed decisions when planning revegetation projects. These types of projects often fail due to a poor understanding of relationships

between site characteristics and the environmental tolerances of the selected replacement vegetation. This study attempted to address some of these knowledge gaps by screening 42 species, races, or ecotypes native to southwestern U.S. for salinity tolerance and mycorrhizal responsiveness.

Salinity tolerance varied widely among species tested. Results from this study show that salinity tolerance can vary between races or ecotypes of the same species. Results also suggest that wherever possible, seed collected from high salinity reference sites may exhibit superior establishment and performance at harsh locations than seed from lower salinity origins.

Mycorrhizal inoculation can improve salinity tolerance by enhancing capture and absorption of water and nutrients for plants; however, our study did not provide clear evidence of this type of interaction between the effects of salinity and mycorrhizal fungi. Many of the species tested grew poorly at all salinity levels in the absence of AM fungi, and inoculation was more likely to increase growth at the lower salinity levels.

Although AM fungal inoculation did not appear to increase salinity tolerance, the majority of plant species with intermediate to high salinity tolerance also showed a strong response to mycorrhizal fungi, and no species tested were negatively affected by inoculation. These results indicate that inoculation may be beneficial on sites with low AM fungal inoculum potential, a common occurrence on sites with high levels of disturbance or extended occupation of a non-mycorrhizal species such as *Tamarix*. However, introduction of a novel (endemically non-native) AM fungal species or isolate to the site should be assessed in relation to site environmental constraints and restoration goals, priorities, and budgets.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2009.07.004.

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