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Impacts of *Tamarix* (L.) Litter and Mycorrhizal Amendments on *Baccharis salicifolia* (Ruiz & Pav.) Pers. Competitiveness and Mycorrhizal Colonization

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Abstract: *Tamarix* spp. are ecological threats in the Southwest U.S.A. because they displace native vegetation, increase soil salinity, and negatively affect soil microbial communities. After *Tamarix* L. removal, legacy effects often necessitate restoration to improve ecosystem services of *Tamarix*-impacted communities. Commercial mycorrhizae fungal inoculation has been recommended to improve restoration success, although inoculation treatments are rarely tested on lesser-known facultative riparian species. Our study asked two questions: (1) Can a commercial mycorrhizal fungal inoculant increase native *Baccharis salicifolia* (Ruiz & Pav.) Pers. (mule-fat) performance against *Tamarix chinensis* Lour. (i.e., tamarisk) and is this influenced by tamarisk leaf litter? (2) Is mycorrhizal colonization of mule-fat roots influenced by tamarisk stem density and leaf litter? A greenhouse experiment was performed with mule-fat cuttings in soil collected from a tamarisk monoculture. Treatments were factorial combinations of tamarisk stem densities (0, 1, 2, 3, 4 stems pot^{-1}) with or without mycorrhizal inoculation and tamarisk litter. There were five replications and two greenhouse runs. The total biomass of both species was determined and mule-fat arbuscular mycorrhizal colonization rates were determined via the magnified intersection method. Increasing tamarisk biomass negatively affected mule-fat biomass, but there were interactions with tamarisk biomass, litter and mycorrhizal inoculation, with litter and inoculation increasing mule-fat growth at high tamarisk biomass. Arbuscular mycorrhizal colonization was high in all treatments, yet at higher tamarisk stem densities, inoculation and litter improved colonization. Interestingly, litter did not negatively impact mule-fat as predicted. Moreover, litter and mycorrhizal inoculum interacted with tamarisk to improve mule-fat growth at higher tamarisk biomass, suggesting an opportunity to improve restoration success when in competition with tamarisk.

Keywords: mule-fat; mycorrhizal inoculant; riparian restoration; saltcedar; tamarisk

1. Introduction

Many riparian areas in the Southwestern United States are impacted by human-mediated changes in river hydrology [1]. While altered hydrology is not prerequisite for plant invasion, the changed flow regimes may interact with introduced non-indigenous plant species to form ecosystems often dominated by invasive plants [2]. *Tamarix* spp. (*T. ramosissima* Ledeb., *T. chinensis*, and their hybrids, hereafter "tamarisk"), were introduced to the western United States beginning in the mid-1800s as ornamentals, windbreaks, and for erosion control [3] (plant nomenclature follows the USDA Plants database (available at http://plants.usda.gov; accessed 14 August 2019)). Presently, they occupy a vast proportion of riparian habitat throughout the Western United States [4]. Tamarisk-dominated

communities are viewed negatively by the public and many land managers because they are often monotypic [5,6], support less avian [7] and small mammal diversity [8], and promote wildfire and conflict with management goals such as water storage in reservoirs [4].

Reduction of tamarisk abundance is a goal in many riparian areas, and treatments typically include mechanical or chemical removal. Additionally, the tamarisk beetle (*Diorhabda* spp.), a biological control insect that feeds on tamarisk foliage, has been introduced to the Western United States and has spread throughout much of tamarisk's range [9]. *Diorhabda* spp. defoliate tamarisk and can reduce tamarisk density; however, a reduction in tamarisk density does not assure that desirable plant communities return [10,11]. In fact, restoration of these areas after tamarisk removal can be difficult due to a number of factors including soil salinization [12–14], degradation of the native soil mycorrhizal fungi community [15], altered litter quality resulting from *Diorhabda* spp. herbivory [16], and secondary invasion from other invasive species [10,17].

Passive restoration, when no action is taken to restore a plant community, may not be a suitable option in many riparian systems [10]. Consequently, active restoration is likely required if land managers hope to restore native plant diversity and wildlife habitat [17,18]. Extensive research has been conducted on potential plant species for use in riparian restoration [19–21], including a few species within the *Baccharis* spp. genus [22,23].

One potential, but little-studied species, *Baccharis salicifolia* (hereafter "mule-fat") is a native, dioecious, facultative riparian shrub common to the U.S. Southwest [24]. Mule-fat may have higher mean stem densities in both young and old tamarisk stands compared to other native shrubs, and also be present in dry shrubland habitats [25]. This suggests that greenhouse studies showing that mule-fat has a low salinity tolerance, similar to *Salix* L. and *Populus* L. [26,27], may underrepresent mule-fat's growth potential. The potential for mule-fat as a restoration species is also seen in its ability to grow well in saturated soil conditions [26], as first year seedlings (<5 cm) have higher drought survival rates compared to tamarisk [28]. Finally, mule-fat is a valuable floral resource for pollinators [29]. However, it should be noted that mule-fat may not be a suitable species to establish by seed at some sites because of its low tolerance to sedimentation [30].

Over time, tamarisk stands can deposit large accumulations of leaf and stem litter, which can lead to changes in soil chemistry such as increasing the presence of organic acids, changing soil nutrient availability [13,31], and lead to degradation of the native soil biota community [32,33]. The addition of the tamarisk biological control beetle (*Diorhabda* spp.) changes tamarisk litter, resulting in quicker litter decomposition and more rapid release of nitrogen and potassium into the soil [16], which can affect subsequent plant growth. It was demonstrated in [19] that tamarisk litter had a positive impact on the growth of two native grasses, but had an even larger effect on the exotic plants' downy brome (*Bromus tectorum* (L.)) and Russian knapweed, also known as hardheads (*Acroptilon repens* (L.) DC.). Although mule-fat is known to be present in some established tamarisk stands [25], previous greenhouse research has only focused on salinity tolerance [26,27], and no research is available on mule-fat's interaction with tamarisk or tamarisk litter.

Mycorrhizal fungi grow in a symbiotic association with plant roots, a relationship crucial for many plants, facilitating nutrient and water acquisition [21] and enhancing plant defenses [34]. As tamarisk is thought to be non-mycorrhizal, soil amendment with commercial mycorrhizal inoculants has been suggested as a treatment to restore soil biota and enhance the establishment of newly planted species in tamarisk-impacted sites [17,35]. Although native inoculum may be preferred over a commercial source [33,36,37], in many cases it is difficult to obtain a local source due to a limited number of non-tamarisk-impacted reference sites, and budgetary and logistical constraints [21]. Furthermore, [34] demonstrated that commercial and native inoculants provided similar plant growth. Results of previous studies conducted on commercial and native mycorrhizae inoculants on tamarisk and native plants vary. Tamarisk monocultures were not affected by native inoculum, but when in coexistence with *Populus* species in inoculated pots in a greenhouse, tamarisk biomass was reduced [15]. In another study with a native inoculum source, the amendment increased *Sporobolus wrightii* Munro ex Scribn.

survival and tiller production [36]. The use of a local or commercial inoculum may only be justified if soil phosphorus and initial arbuscular mycorrhizae fungi (AMF) colonization are low [38]. To date, no studies have been conducted on mule-fat in relation to competition with tamarisk and the addition of a commercial soil mycorrhizal inoculant.

We conducted a greenhouse study to address gaps in knowledge about how mule-fat, a known mycorrhizal species [39], responds to tamarisk litter and mycorrhizal soil fungi amendment. This study aimed to assess the performance of mule-fat against tamarisk under different soil restoration practices. Our objectives were to assess the impacts of tamarisk litter, commercial mycorrhizal inoculants, and their interaction on (1) mule-fat success against increasing tamarisk stem density and biomass, and (2) mycorrhizal colonization of mule-fat.

2. Materials and Methods

2.1. Soil and Plant Material Collection and Preparation

Soil was collected at the Caballo Reservoir (32.92° N, −107.29° W, Sierra County, New Mexico) within a tamarisk (*Tamarix chinensis* (L.)) monoculture, and soil was collected separately for each run. Collection locations were haphazardly selected from within a 40-m-diameter section within the larger tamarisk monoculture. Soil was placed into 25 cm diameter × 15 cm deep plastic pots, with care taken to preserve soil structure and hyphal networks. Pots were transported to the Leyendecker Plant Science Research Center (PSRC) (32.20° N, −106.74° W, Doña Ana, New Mexico) where they were placed in a greenhouse. Hardwood cuttings of mule-fat were taken from two separate populations near Caballo Reservoir in early March 2017. Tamarisk cuttings were collected at PSRC due to extensive defoliation by the tamarisk beetle (*Diorhabda sublineata* Lucas) and limited regrowth at Caballo Reservoir. Fresh cuttings of both species were stripped of foliage material before cold storage (4 °C) to reduce transpiration, and soaked in water for 48 h in separate bins by species prior to weighing and planting. Mule-fat cuttings were trimmed to 15 cm and tamarisk to 10 cm. Desiccated litter from beetle-affected tamarisk plants was gathered by hand from two locations at Caballo Reservoir in summer 2016 and stored at room temperature until use.

2.2. Experimental Setup

The experiment was a randomized complete block design with factorial combinations of two soil treatments (non-inoculated soil or mycorrhizal-inoculated), two litter treatments (litter applied or no litter applied) and five tamarisk density treatments (0, 1, 2, 3 and 4 cuttings pot^{-1}) for a total of twenty treatments. Experimental units were single 25-cm-diameter pots with six replications. Tamarisk and mule-fat cuttings were fresh weighed to the nearest one gram before planting. A duplicate set of cuttings, grouped into fresh weight classes, was oven dried at 65 °C until constant weight to obtain surrogate measure of starting dry weight. Cuttings of both species were then planted by inserting them into the soil to a depth of 8 cm for mule-fat and 5 cm for tamarisk. Mule-fat cuttings were planted in pairs and, once established, thinned to the desired density of 1 cutting pot^{-1}. Tamarisk cuttings were planted at twice the desired density to ensure establishment and subsequently thinned after survival was ensured. After cuttings were planted, MycoApply Soluble MAXX (Mycorrhizal Applications, Grants Pass, OR, USA) was applied at the recommended rate of 29.5 ml per 37.3 L of water. Finally, 20 g of air-dried tamarisk litter was placed in pots receiving the litter treatment.

2.3. Growing Conditions

Two experimental runs were conducted: 26 August to 5 December, 2016 and 1 April to 14 June, 2017. A 13 h photoperiod was imposed for both runs with a light-sensitive supplementary lighting system (one overhead 400-watt bulb per bench) when sunlight was below 13 h. Greenhouse temperatures ranged from 25.6 to 40.5 °C during the first run and 22.2 to 36.7 °C during the second run. Temperatures were collected from a central temperature gauge above benches at a height of six

feet above ground. Two blocks were placed on a bench (3.65 × 1.5 m) with pot spacing averaging 6 cm apart. Pots were individually watered daily until establishment and once established, watered when soil surface layer appeared dry (~500 mL per pot^{-1}).

2.4. Measurements

During harvest, aboveground biomass was clipped and separated from belowground biomass. Aboveground biomass of each species separately was dried at 65 °C until constant weight. Roots were washed of soil by hand and thoroughly rinsed of any attached debris and separated by species into different bags. Roots were readily distinguishable by species due to differences in root color (mule-fat roots were light beige; tamarisk roots were deep brown). After washing, a 10 cm section of mule-fat root sample from each pot was placed in a 50% ethanol mixture and stored at 4 °C until processed for later mycorrhizae colonization analysis. Mule-fat relative growth rate was calculated as listed below, where Dry Weight 1 was the initial starting dry weight and Dry Weight 2 was the oven-dried harvest weight per pot^{-1}.

$$\frac{\ln(\text{Dry Weight 2}) - \ln(\text{Dry Weight 1})}{\text{Time (weeks)}} \quad (1)$$

2.5. Mycorrhizal Root Preparation and Analysis

Mule-fat roots were stained using a method adapted from [40]. Roots were placed in 2.5% KOH overnight and rinsed with tap water. Rinsed root segments were treated with an alkaline H_2O_2 solution for 30 min and subsequently washed using three complete changes of tap water to remove any residual H_2O_2 solution. They were then acidified by soaking in 1% HCl for 1 h before and stained with an acidic glycerol solution containing 0.05% trypan blue (Biological Industries, Cromwell, CT, USA) [40] at room temperature for 3 h. Once the stain was drained and rinsed with tap water, the sample was left to de-stain at 4 °C for a week in the acidic glycerol solution. Multiple 2 -cm root segments were laid parallel across on the microscope slide and root samples were analyzed under a compound microscope using the magnified intersection method [41].

2.6. Data Analysis

Both greenhouse runs were combined for analysis. Mule-fat biomass data were analyzed using generalized linear mixed effects models with a gamma distribution in R version 3.4.3 [42] using packages *lme4* [43], *lmerTest* [44], and *lsmeans* [45]. Biomass was the dependent variable and independent variables of tamarisk biomass, litter and inoculation, and all possible two and three-way interactions were included as fixed effects. Run and block were included as random effects. If interactions were not significant, models were simplified as appropriate. Post hoc multiple comparison tests used *lsmeans*. *P*-values less than 0.05 were considered significant.

Mycorrhizal colonization data were only analyzed from the second greenhouse run, as the first run was used for training on fungal structure identification. Colonization was evaluated as a function of tamarisk cutting per pot^{-1}, litter, inoculation, and the two - and three - way interactions to identify mycorrhizal colonization differences within/among treatments. Total microscope slide intersections were used as weights in the generalized linear model, with the family of "binomial." Post hoc multiple comparison tests utilized *lsmeans* to identify differences among treatments. Linear relationships between AMF colonization and mule-fat biomass were tested using *lmer*.

3. Results

3.1. Mule-fat Growth under Different Soil-Litter Treatments in Competition with Tamarisk

The first greenhouse run resulted in high mule-fat mortality across all treatments with plants in thirty-six pots (30% of pots in run) not surviving to harvest. In the second run, mule-fat mortality occurred in only five pots (4.2% of pots in run). Mortality was not a result of the treatments (X^2 (3) = 1.96,

$p = 0.58$), and thus, plants that died were not included in the analysis. The random effects of run and block explained 9.2% and 1.1%, respectively, of the variation in the biomass data.

There was a significant three-way interaction ($p = 0.01$) between tamarisk biomass, inoculation and litter. While mule-fat biomass decreased with increasing tamarisk biomass, both litter and mycorrhizal inoculation moderated the decline (Figure 1). The effects of tamarisk biomass and litter on mule-fat biomass were negatively correlated (−0.300), such that litter had an increasingly positive effect on mule-fat as tamarisk biomass increased. Likewise, tamarisk biomass and inoculation were negatively correlated (−0.195), indicating that at higher tamarisk biomass, inoculation had a greater positive effect on mule-fat. Tamarisk biomass reduced mule-fat RGR ($p < 0.001$), and there was an interaction between mycorrhizal inoculation and litter ($p = 0.018$) (Figure 2). Mule-fat RGR was lower in inoculated pots without litter compared to inoculated pots with litter.

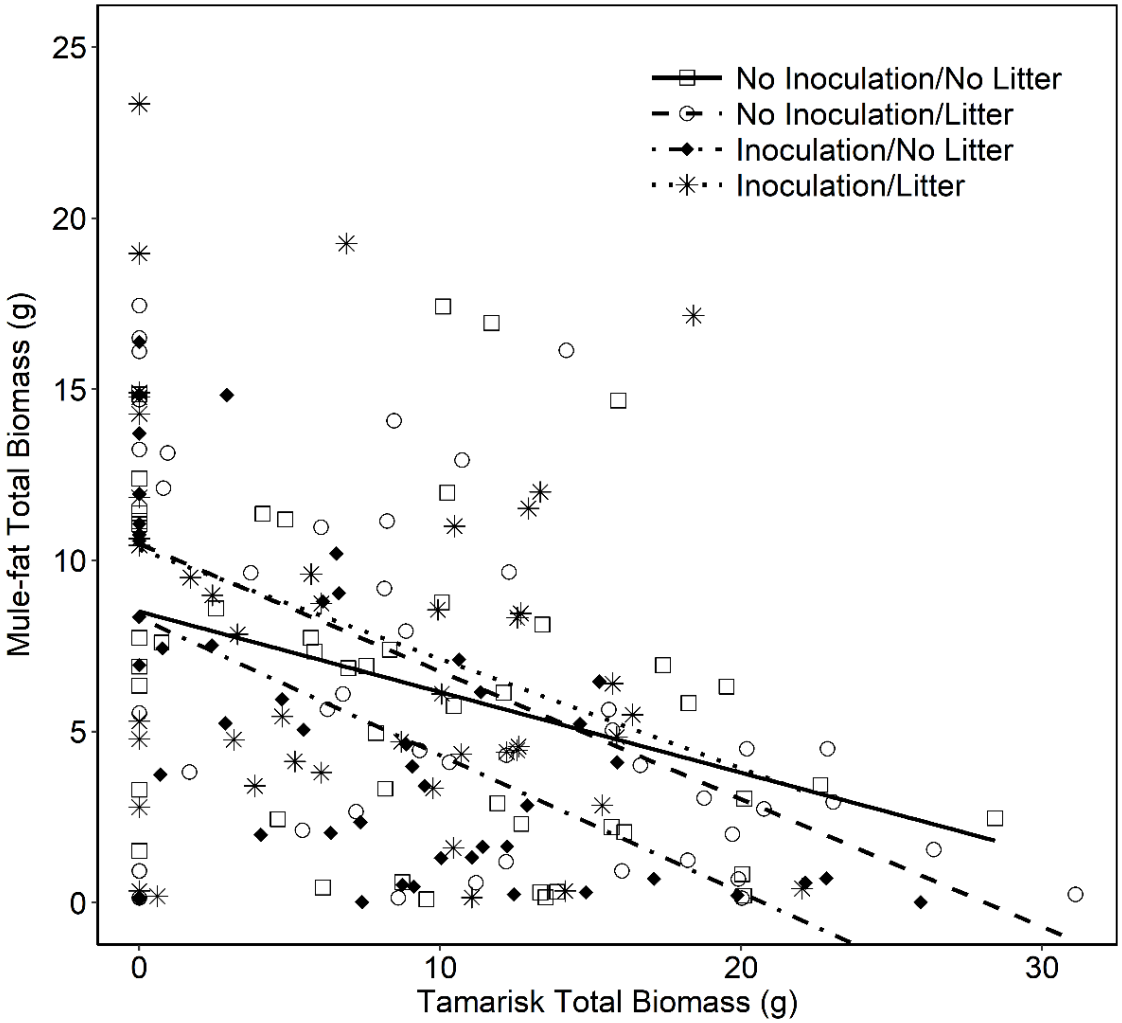

Figure 1. Mule-fat (*Baccharis salicifolia*) biomass response to tamarisk (*Tamarix chinensis*) biomass in competition experiments, with and without a mycorrhizal inoculant and tamarisk litter. Regression lines are based on final measured biomass of each species.

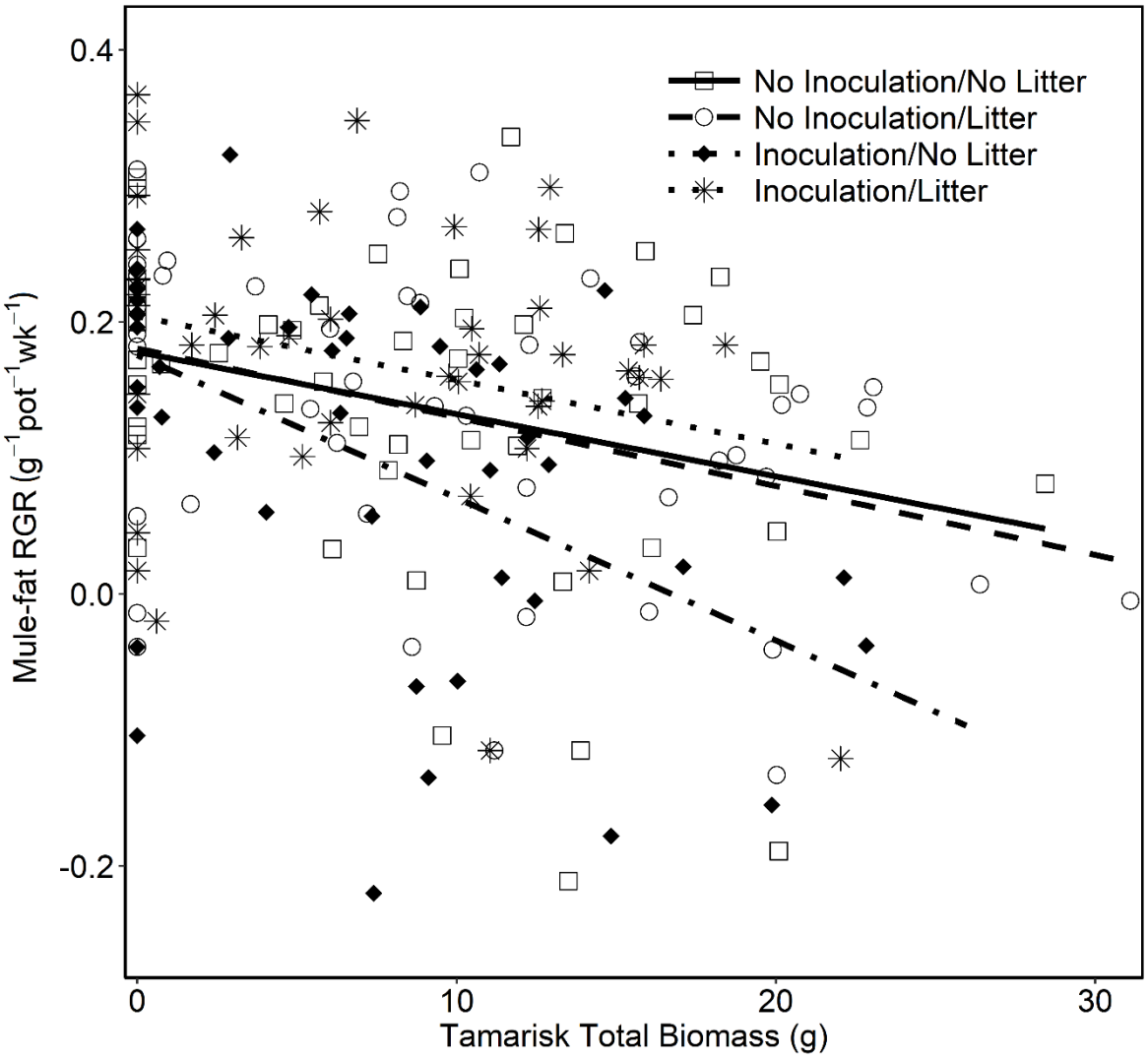

Figure 2. Mule-fat (*Baccharis salicifolia*) relative growth rate response to tamarisk (*Tamarix chinensis*) biomass in competition experiments, with and without a mycorrhizal inoculant and tamarisk litter. Regression lines are based on the calculated mule-fat relative growth rate and final measured tamarisk biomass.

3.2. Arbuscular Mycorrhizal Fungi Colonization of Mule-Fat

Arbuscular mycorrhizal colonization was not influenced by inoculation ($Z = -1.33$, $p = 0.18$), tamarisk abundance within the pots ($Z = 1.46$, $p = 0.15$) or litter ($Z = 0.51$, $p = 0.61$), although there was a significant interaction between inoculation and litter ($Z = 5.74$, $p < 0.001$) (Figure 3). At stem densities of 3 and 4 tamarisk pot^{-1}, there was greater AMF colonization in inoculated pots with litter compared to those without. Arbuscular mycorrhizal colonization did not affect mule-fat biomass ($Z = 0.93$, $p = 0.35$).

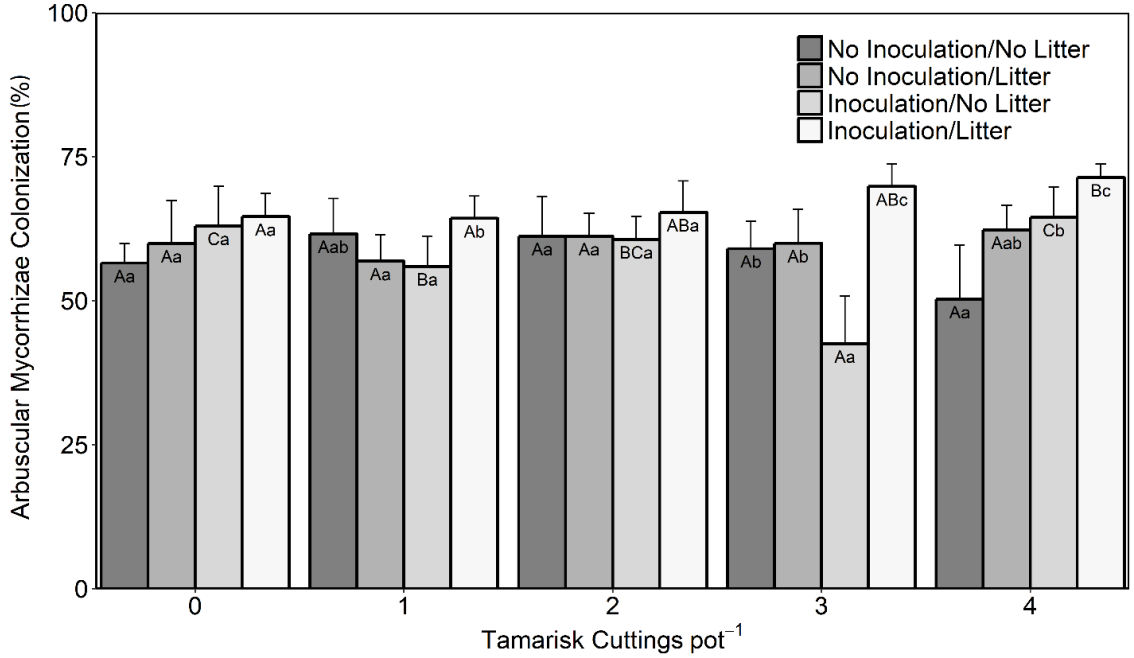

Figure 3. The influence of tamarisk stem density, soil inoculation and tamarisk litter on arbuscular mycorrhizae colonization of mule-fat roots. Data are means with n = 5. Error bars indicate +SE. Differences within tamarisk stem density and within soil treatment were analyzed separately by ANOVA followed by *lsmeans* post hoc tests incorporating run and block as random effects. Different uppercase letters indicate differences within an inoculation-litter treatment across stem densities (p-value < 0.05). Different lowercase letters indicate differences between inoculation-litter treatments within a stem density (p-value < 0.05).

4. Discussion

Restoration of degraded riparian areas after invasive plant removal is complicated by many factors, including poor plant establishment, colonization by other undesirable plants, and both chemical and biological legacy effects of the invasive plant [17,46]. The primary legacy effects from tamarisk are salinity and nutrients leached from accumulated litter and degradation of the beneficial soil fungal community. These factors may be overcome through management by litter removal and addition of a commercial mycorrhizal soil amendment, but these practices can add substantially to the cost of restoration. Our study tested the impact of litter and a mycorrhizal fungi soil amendment on the growth of the desired species, mule-fat, and we found that neither litter removal nor a mycorrhizal soil amendment independently led to consistent increased performance success of mule-fat against tamarisk. However, our research identified complex interactions between the biomass of the tamarisk, mycorrhizal inoculation, and the presence of tamarisk litter, with both inoculation and litter generally increasing mule-fat growth at higher tamarisk biomass. This suggests that tamarisk litter, likely through nutrient release, may have a beneficial impact on subsequent species growth, especially when combined with mycorrhizae and when tamarisk is present at higher densities. However, during the early phases of restoration after tamarisk has been removed, it is unlikely that mule-fat would be competing with tamarisk in high densities. Furthermore, it should be noted that while not tested explicitly, the lack of differences in colonization between pots with and without inoculum indicated that there may have been sufficient mycorrhizal inoculant in the field soils. Therefore, the level of inoculant in field soils should be considered prior to restoration, and the additional expense of a mycorrhizal amendment should be considered for restoration projects.

Previous greenhouse research indicated that mule-fat has low salinity tolerance (less than 8 g L^{-1}) [26,27]; however, in our study tamarisk litter had no negative effect on mule-fat biomass production. No differences were recorded in final soil electrical conductivity (EC) (dS cm^{-1}) analysis

from the control and pots with litter additions [19]. The tamarisk litter treatments applied in our experiment were meant to increase soil salinity, but over time with multiple weekly waterings, it is possible salts may have slowly leached out of the pots. The mycorrhizal amendment–litter interaction may have been the result of both frequent weekly watering, leading to a reduction in soil salinity, and decomposition of beetle-affected litter. Prior research found increased tamarisk litter decomposition rates with daily watering compared to water-limited conditions, leading to more available soil nutrients [47]. Further, beetle-affected litter can result in increased leaf litter decomposition rates [16]. Quicker decomposition rates led to greater nutrient releases of nitrogen, potassium, and phosphorus concentrations in the soil, even within a short time (48 days) [16], compared to our experimental runs of 101 and 74 days.

Although few mule-fat cuttings reached heights above 120 cm, at termination date roots of both species (particularly mule-fat) did not appear root-bound in the planting container. Longer greenhouse growth times and higher planted densities of tamarisk in our greenhouse pots may have resulted in more intense competition and greater differences between treatments, particularly with the inoculation–litter interaction.

There were no tamarisk density effects on arbuscular mycorrhizal fungi (AMF) colonization of mule-fat roots. As noted in previous research, non-mycorrhizal tamarisk and its foliage litter can suppress arbuscular mycorrhizal colonization [15,32,48,49]. Our study showed no clear trend in AMF colonization rates between non-inoculated and inoculated treatments. There are two potential reasons for the relatively high arbuscular colonization rates and no consistent pattern between inoculation treatments. First, AMF has been observed in tamarisk-degraded soils [49–51] and thus tamarisk presence does not necessarily indicate a complete absence of AMF colonization. This suggests our non-inoculated soil may have already contained an adequate source of native fungi inoculum. Second, *Baccharis* spp. inconsistently responds to AMF colonization [21,22]. Previous work on *Baccharis hamifolia* L. recorded positive growth in treatments with an AMF/ectomycorrhizal inoculant [22]. Although overall AMF colonization rates were similar between this and previous research [22], noted ectomycorrhizal colonization rates between 10% and 20% of roots, whereas no ectomycorrhizal colonization was observed during our analysis.

Our research should be considered preliminary work which could provide useful information for designing further studies. Nonetheless, this research has illuminated interesting interactions between tamarisk litter, mycorrhizal inoculation, and the amount of tamarisk present with respect to the growth of mule-fat. Future restoration with this species, and perhaps others in the *Baccharis* genus, could benefit from additional research on these relationships. Specifically, additional greenhouse studies could help elucidate the mechanisms by which tamarisk litter and mycorrhizal inoculum facilitate mule-fat competition with tamarisk. Similarly, field studies are needed to determine if trends noted in the greenhouse translate to restoration success in degraded riparian areas.

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