

Germination and Growth of Native and Invasive Plants on Soil Associated with Biological Control of Tamarisk (*Tamarix* spp.)

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Introductions of biocontrol beetles (tamarisk beetles) are causing dieback of exotic tamarisk in riparian zones across the western United States, yet factors that determine plant communities that follow tamarisk dieback are poorly understood. Tamarisk-dominated soils are generally higher in nutrients, organic matter, and salts than nearby soils, and these soil attributes might influence the trajectory of community change. To assess physical and chemical drivers of plant colonization after beetle-induced tamarisk dieback, we conducted separate germination and growth experiments using soil and litter collected beneath defoliated tamarisk trees. Focal species were two common native (red threeawn, sand dropseed) and two common invasive exotic plants (Russian knapweed, downy brome), planted alone and in combination. Nutrient, salinity, wood chip, and litter manipulations examined how tamarisk litter affects the growth of other species in a context of riparian zone management. Tamarisk litter, tamarisk litter leachate, and fertilization with inorganic nutrients increased growth in all species, but the effect was larger on the exotic plants. Salinity of 4 dS m⁻¹ benefitted Russian knapweed, which also showed the largest positive responses to added nutrients. Litter and wood chips generally delayed and decreased germination; however, a thinner layer of wood chips increased growth slightly. Time to germination was lengthened by most treatments for natives, was not affected in exotic Russian knapweed, and was sometimes decreased in downy brome. Because natives showed only small positive responses to litter and fertilization and large negative responses to competition, Russian knapweed and downy brome are likely to perform better than these two native species following tamarisk dieback.

Nomenclature: Downy brome, *Bromus tectorum* L.; Russian knapweed, *Acroptilon repens* (L.) DC.; tamarisk, *Tamarix* spp.; red threeawn, *Aristida purpurea* Nutt. var. *longiseta* (Steud.) Vasey; sand dropseed, *Sporobolus cryptandrus* (Torr.) Gray.

Key words: *Acroptilon repens*, *Aristida purpurea*, biological control, *Bromus tectorum*, legacy effects, secondary invasion, *Sporobolus cryptandrus*, *Tamarix*.

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Control of invasive plant species can have unexpected consequences. In particular, if an invasive plant species has come to serve key roles in the ecosystem, its removal can affect carbon (C), nitrogen (N), and water cycles; eliminate a major producer from the trophic web; deprive an endangered species of food or shelter (Seastedt 2014); and/or create space for possible colonization or expansion of other exotic species (“secondary invasion,” Buckley et al. 2007; D’Antonio and Meyerson 2002). Revegetation is sometimes omitted from invasive species control efforts, leaving native plant communities to recover passively (Kettering and Adams 2011). However, research has shown that native plant communities do not always recover when left alone after control of invasive species and can become susceptible to secondary exotic plant invasion (Carson et al.

Management Implications

Following control of tamarisk, riparian land managers often seek to establish a native plant community, but secondary weed invasions can thwart such efforts. Soil conditions are among the factors that determine plant community composition following tamarisk die-back after biocontrol by tamarisk beetles. Soils that have been dominated by tamarisk for decades generally have a thick layer of tamarisk leaf litter and are higher in nutrients, organic matter, and salts than nearby soils. Mechanical removal of dead or dying tamarisk can leave behind wood chips or debris. Greenhouse experiments showed that such soils are not harmful to two native species, red threeawn and sand dropseed, but generally had positive effects on the growth of two common invasive exotic plants, Russian knapweed and downy brome, when plants were grown alone or in competition. Russian knapweed even showed a slight positive growth response to small increases in salinity. A thick layer of tamarisk wood chips was detrimental to plant germination, but a thin layer of wood chips increased growth slightly.

Russian knapweed and downy brome are likely to do well after tamarisk dieback where soils are enriched in nutrients from tamarisk litter and beetle frass, so managers should be prepared for secondary invasion by these species following tamarisk removal if they occur nearby. Further experimentation should elucidate when a thin layer of wood chips might benefit plant growth. However, soil conditions vary from site to site. Soil testing and assessment of which native species grow nearby could suggest desirable native species to plant to facilitate establishment of the plant community of interest.

2008; Denslow and D'Antonio 2005; Suding et al. 2004). Indeed, secondary exotic plant invasion is common, whether the initial exotic plant was reduced by traditional mechanical or chemical methods (D'Antonio and Meyerson 2002; Hulme and Bremner 2006; Yelnick and D'Antonio 2013) or by biological control (Blossey et al. 2001; Bush et al. 2007; Denslow and D'Antonio 2005). Active revegetation might be necessary if the goal is to have a native plant community following the removal of exotics (Kettering and Adams 2011). However, this type of intensive restoration following the removal of an exotic species can be impossible at large spatial scales, and an improved understanding of the factors that determine plant community succession following exotic removal could help in the development of less-intensive management techniques or in the identification and prioritization of sites where more or less intensive approaches might be warranted.

Eurasian riparian trees and shrubs of the genus *Tamarix* spp. (tamarisk) were planted for erosion control and as ornamentals in North America beginning in the 19th century. Since then, *Tamarix* has been notably successful in colonizing riparian areas, particularly in the western United States, often forming dense monocultures along lakes, rivers, and streams (Nagler et al. 2011). However, *Tamarix* spp. are now experiencing widespread defoliation in much

of their North American range as the result of a biological control agent, beetles in the genus *Diorhabda* (tamarisk beetles, *Diorhabda* spp.), first released in 2004 (Hultine et al. 2014; Nagler et al. 2014). Past restoration efforts have shown that removal of *Tamarix* alone does not ensure native vegetation will return to a site (Belote et al. 2010; Harms and Hiebert 2006; Ostoja et al. 2014), raising concerns about which plant species will replace *Tamarix* when it dies and what management actions might be warranted (Bay 2013; Shafroth et al. 2008). Undesirable species that can dominate after *Tamarix* removal include bromegrasses (*Bromus* spp.), perennial pepperweed (*Lepidium latifolium* L.), Russian knapweed [*Acroptilon repens* (L.) DC], as well as tumbleweeds (*Kochia* and *Salsola* spp.) (McDaniel and Taylor 2003; Ostoja et al. 2014; Weeks et al. 1987).

Secondary invasion is more likely if the removed species occupied a large area, had legacy effects on soil properties and community composition, and/or if abiotic conditions favorable to native replacement species have changed (Hultine et al. 2010; Seastedt et al. 2008). Riparian zones occupied by *Tamarix* in the western United States typically meet these conditions. *Tamarix*-affected areas often have altered flow regimes and increased soil salinity (Merritt and Shafroth 2012), which influence both the establishment and survival of other plant species (Beauchamp et al. 2009; Glenn et al. 1998; Merritt and Poff 2010; Stromberg et al. 2007). Large, dense *Tamarix* stands that have existed for decades likely have a depleted native soil seed bank and large accumulations of leaf and stem litter. The annual input of *Tamarix* litter can influence soil chemistry by enriching organic matter, micro- and macronutrients, and sometimes changing pH and electrical conductivity (Ladenburger et al. 2006; Lesica and DeLuca 2004; Merritt and Shafroth 2012; Yin et al. 2010; Zhaoyong et al. 2006). *Tamarix*-affected soils can also hold less of the beneficial fungal associates needed for optimal growth of some native species such as cottonwoods and willows (Gehring et al. 2006; Meinhardt and Gehring 2012). These types of soil-legacy effects develop over long time scales and can be difficult to reverse (Elgersma et al. 2011).

Beetle herbivory brings further changes to *Tamarix*-dominated ecosystems, some temporary and others long-lasting. Beetle herbivory on *Tamarix* opens up the canopy, thus increasing light reaching the ground, increasing temperature, decreasing humidity (Bateman et al. 2013), and causing increased green litterfall during the spring and summer, which contains elevated N and phosphorus (P) compared to senesced leaves typically shed in the fall (Conrad et al. 2013; Uselman et al. 2011). This litter decomposes faster, releasing more N and P into soils (Uselman et al. 2011), although this is likely to be a short-term effect (Uselman et al. 2013). Litter from beetle defoliation is additionally enriched by beetle frass. Because

alluvial sediments in riparian zones of the semiarid West tend to be nutrient-poor, this soil enrichment can give exotic species, which are often annual plants, an advantage over the often perennial native species typically adapted to nutrient-poor soils (Alpert and Maron 2000; Newingham and Belnap 2006). Defoliation can also decrease the overall C flux from the stand or change its annual pattern of exchange with the atmosphere (Hultine et al. 2010; Snyder et al. 2012). If dead trees are chipped and left on site after control, they can have additional effects on the soil physical and chemical environment. Tree mortality can decrease stability of banks and floodplains, increasing the potential for erosion (Vincent et al. 2009). Taken together, these ecosystem consequences of biocontrol of *Tamarix* could strongly influence the resultant plant community composition.

To explore plant responses to conditions following *Tamarix* biocontrol, we investigated responses of native and exotic species on soil from mature *Tamarix* stands currently undergoing beetle defoliation. In separate germination and growth experiments, we compared the performance of four species common to xeric riparian sites in the western United States: one annual and one perennial native grass, red three-awn [*Aristida purpurea* Nutt. var. *longisetata* (Steud.) Vasey] and sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], respectively, and one exotic annual grass and one perennial exotic forb, downy brome (*Bromus tectorum* L.) and Russian knapweed [*Acroptilon repens* (L.) DC.], respectively. We included treatments designed to simulate some of the effects of beetle defoliation and common restoration practices with and without competition from other plant species, including treatments intended to identify possible mechanisms of response to these post-*Tamarix* conditions.

Materials and Methods

Species Selection, Soil, Seed, and Greenhouse Facilities.

Annual surveys of 60 transects, 10 to 100 m (32.8 to 328 ft) long, perpendicular to the Colorado River near Moab, UT, (R.A. Sherry, unpublished data) show that *A. repens* and *B. tectorum* are the most common nonnative plants in and adjacent to *Tamarix* stands in the area. *S. cryptandrus* is one of the top three, equally common native perennial grasses along the transects. *A. purpurea* was the most common native annual grass. These taxa also occur at other riparian sites across the interior western United States (Beauchamp and Shafroth 2011; Dela Cruz et al. 2014; Reynolds and Cooper 2011).

Germination and growth experiments were conducted separately, but both used the same soil, seed, and greenhouse facilities. Soil and *Tamarix* leaf litter were collected from under 24 beetle-defoliated *Tamarix* tree

canopies within stands along the Colorado River near Moab, UT. A summary of the treatments is presented in Table 1. Characteristics of the soil and the composition of treatment solutions are presented in Table 2. The soil was a silty loam with $25.7 \pm 1.5\%$ sand, $54.2 \pm 2.5\%$ silt, and $20.1 \pm 1.0\%$ clay.

After shipment to greenhouse facilities on the campus of Colorado State University, (Fort Collins, CO), the soil was homogenized and mixed with an equal volume of coarse horticultural perlite (Supreme Perlite Company, Portland, OR). The greenhouses maintained 16 : 8 h day/night cycles year-round with supplemental lighting. Minimum and maximum temperatures recorded on our bench were 16.6 C and 30 C (62 and 86 F), respectively, although daily highs and lows varied within this range and were correlated with ambient outdoor temperatures. Seeds of *Bromus tectorum* and *Acroptilon repens* were collected from areas adjacent to *Tamarix* stands near Moab, UT. Seed of *Sporobolus cryptandrus* and *Aristida purpurea* was purchased from Native American Seed (Junction, TX).

Experimental Design, Hypotheses, and Rationale.

Twelve treatments and a control addressed how germination and growth of different plant species respond to various conditions associated with *Tamarix* soil, litter, and wood chips (see Table 1). All treatments and the control received the same amount of tap water. In the growth experiment, species were planted either alone or in a combination of all four species to address questions involving competition.

In the Control, seeds and plants received only tap water. Two *Tamarix* Chips treatments consisted of a 1 cm- (0.39 in-) (Chips 1) or 4 cm- (1.57 in-) (Chips 2) deep layer of *Tamarix* wood chips (≤ 2.5 cm in length) on top of the soil. Two Nutrient Addition treatments used 0.72% (+Nutrs) and 1.44% (+2× Nutrs) solutions of Jack's Professional LX 15–5–15 water-soluble fertilizer (JR Peters Inc., Allentown, PA). In two Carbon (C) Addition treatments, sugar was sprinkled on the soil surface at a rate of 91.8 g C m^{-2} ($0.30 \text{ oz C ft}^{-2}$) (+C) or 275.4 g C m^{-2} ($0.90 \text{ oz C ft}^{-2}$) (+3× C) 1 wk before the beginning of each experiment. Two Salinity treatments consisted of 0.103 g KSO_4 , 0.050 g CaSO_4 , 0.500 g NaSO_4 , 0.257 g MgCl , 0.460 g NaHCO_3 , and 0.717 g NaCl L^{-1} of water for the +Salts treatment (equivalent to an EC [electrical conductivity] of 4 dS m^{-1} [0.12 mho ft^{-1}]) and double each of those salt concentrations for the +2× Salts treatment (equivalent to 8 dS m^{-1} [0.24 mho ft^{-1}]). For two *Tamarix* Leachate treatments, we soaked 550 g (19.4 oz) of air-dried *Tamarix* litter in 20 L (0.53 gal) of water for 24 h, removed the litter, and diluted the leachate to 16.4% (+Tam Leachate) or 32.8% (+2× Tam Leachate) of its original concentration. Two *Tamarix* Litter treatments

Table 1. Descriptions of the 12 treatments and control used in the germination and growth experiments.

| Label | Description | Details | Question(s) addressed | Rationale |
|------------------|--|---|--|---|
| Control | Control | No chips or litter added. Water was the only liquid addition. | Do natives and invasive differ in performance on <i>Tamarix</i> soils? | A baseline with which to evaluate the effects of the other treatments. |
| Chips 1 | 1 cm <i>Tamarix</i> chips | 1-cm depth of <i>Tamarix</i> wood chips added on soil surface. | What is the effect of <i>Tamarix</i> wood chips on germination and growth of natives and invasives? | Dead or removed <i>Tamarix</i> is often chipped and left at restoration sites. This might inhibit germination, or leach salts, or improve soil water retention. |
| Chips 2 | 4 cm <i>Tamarix</i> chips | 4-cm depth of <i>Tamarix</i> wood chips added on soil surface. | | |
| +Nutrs | Nutrient addition | Watered with 0.72% solution of Jack's Professional LX 15–5–15 water-soluble fertilizer. | Are effects of <i>Tamarix</i> litter due to extra nutrients? Do additional nutrients help invasives more than natives? | Greater growth than control indicates nutrient limitation. |
| +2× Nutrs | 2× Nutrient addition | Watered with a 1.44% solution of the above fertilizer. | | |
| +C | C addition | Sugar sprinkled on soil surface at 91.8 g C m ⁻² 1 wk before experiment began. | What is the effect of reduced nutrient availability? Does it affect natives and invasives differently? | Addition of carbon reduces nutrient availability via microbial immobilization. Helps determine if litter or leachate effects are due to nutrients. |
| +3× C | 3× C addition | Sugar sprinkled on the soil surface at 275.4 g C m ⁻² 1 wk before experiment began. | | |
| +Salts | Salt solution | Watered with a 4 dS cm ⁻¹ salt solution (see methods for composition). | Are effects of <i>Tamarix</i> litter and leachate due to salts (as opposed to nutrients)? | What is the effect of additional salinity (as from <i>Tamarix</i> litter or concentration due to lack of flooding)? |
| +2× Salts | 2× Solution | Watered with a 8 dS cm ⁻¹ salt solution (double concentration of the above salt solution). | | |
| +Tam Leachate | <i>Tamarix</i> Litter leachate solution | Watered with <i>Tamarix</i> litter leachate (see methods). | Are litter effects due to leachate or to physical presence of litter? | Nutrients, salts, and other compounds in <i>Tamarix</i> litter might affect restoration efforts. |
| +2× Tam Leachate | 2× <i>Tamarix</i> Litter leachate solution | Watered with double concentration of the above <i>Tamarix</i> litter leachate. | | |
| Tam Litt 1 | 1 cm <i>Tamarix</i> litter | 1-cm depth <i>Tamarix</i> litter added on soil surface. | How does <i>Tamarix</i> litter affect the germination and growth of native and invasive plant species? | <i>Tamarix</i> leaf litter and beetle frass might affect plant community recovery by adding nutrients and/or salts. |
| Tam Litt 2 | 4 cm <i>Tamarix</i> litter | 4-cm depth <i>Tamarix</i> litter added on soil surface. | | |

had 1-cm (1.57-in) (Tam Litt 1) or 4-cm depth (Tam Litt 2) of leaf litter placed on the soil surface. Seeds were sown on the surface of the litter for the germination experiment. In the growth experiment, litter was placed around the seedlings. A more detailed account of rationales for the treatments and the hypotheses they address is presented in supplementary materials (Supplementary Material; [http://](http://dx.doi.org/IPSM-D-16-00034.S1)

dx.doi.org/IPSM-D-16-00034.S1, <http://dx.doi.org/IPSM-D-16-00034.S2>).

Germination Experiment. Seeds were sown in 6.1 by 6.1 by 5.66 cm pots in packs of four (“804 standard 1020 inserts,” McConkey, Sumner, WA). 1,040 pots (260 inserts) were filled with 65 g (2.29 oz) of the prepared

Table 2. Characteristics of the initial soil and solutions used in the germination and growth experiment. Values are means \pm SE. Inorganic N and available P and K were assessed from soil extracts, whereas the remaining elements represent total soil pools as determined by nitric-perchloric acid digestions.^a

| Initial soil or solution | pH | EC dS m ⁻¹ | NO ₃ ⁻ -N ppm | NH ₄ ⁺ -N ppm | avail P ppm | avail K ppm | Ca SAR ppm | Mg SAR ppm | Na SAR ppm |
|------------------------------|---------------|--------------------------|--|--|-----------------|----------------|----------------|---------------|----------------|
| Initial soil | 7.7 \pm 0.0 | 4.1 \pm 0.01 | 12.7 \pm 1.5 | 6.3 \pm 0.7 | 14.7 \pm 0.5 | 650 \pm 1 | 500 \pm 10 | 88 \pm 31 | 21.1 \pm 0.2 |
| Tam leachate | 6.7 \pm 0.1 | 0.1 \pm 0.0 | 0.04 \pm 0.0 | 4.0 \pm 0.1 | 1.41 \pm 0.0 | 12.4 \pm 1.7 | 13.8 \pm 0.2 | 4.2 \pm 0 | 5.0 \pm 0.2 |
| 2 \times Tam leachate | 6.7 \pm 0.1 | 0.3 \pm 0.01 | 0.08 \pm 0.01 | 8.1 \pm 0.1 | 2.81 \pm 0.01 | 24.9 \pm 1.7 | 27.7 \pm 0.2 | 8.4 \pm 0 | 10.0 \pm 0.2 |
| Nutrient solution | | | 85.7 | 21.4 | 35.7 | 107.1 | 28.6 | 14.39 | |
| 2 \times Nutrient solution | | 4 | 171.4 | 42.9 | 71.4 | 214.3 | 57.1 | 28.6 | 1,680 |
| Salt solution | | | | | | 100 | 515 | 250 | 3,360 |
| +2 \times Salt solution | | 8 | | | | 200 | 1,030 | 500 | |

^aAbbreviations: EC, electrical conductivity; SAR, sodium adsorption rate; Tam, Tamarisk.

soil. Four inserts were placed in a single standard 10 by 20 in (25.40 by 50.80 cm) greenhouse tray, spaced widely apart, resulting in 65 trays of 16 pots each. Each tray was randomly assigned to one of the 13 treatments (5 trays or 80 pots treatment⁻¹). For the *Tamarix* litter and chips treatments, either 1- or 4-cm depth of litter or chips was placed on top of the soil. One week before seed planting, sugar was applied to pots in the trays of the C addition treatments. On the second, fifth, and seventh d before planting, pots and soil were “prewatered” with 30 ml (1.01 oz) of either tap water or their assigned treatment solution. Pots were then planted with 10 seeds of a single species such that each cell of four pots contained one pot of each species (making 20 replicates treatment⁻¹). Following planting, each pot was hand misted daily with either 5 ml (on cooler days) or 10 ml (on warmer days) of water or its assigned treatment solution using a misting bottle. Pots were checked daily for seed germination. Radicle emergence was counted as germination. No fungus was observed on the seeds. Seedlings were removed as they were counted to reduce competition between seedlings and ensure an accurate count. Temperature on the greenhouse benches averaged 20.1 \pm 0.1 C during the course of the experiment. One end of the bench, occupied by the Chips 2 treatment, averaged 0.7 \pm 0.1 C cooler than the rest of the bench. The Chips 2 treatment was left out of the analysis of the germination experiment for this reason.

Growth Experiment. Prior to starting treatments, seedlings were first grown in the *Tamarix* soil mix in 6.5-cm-diam by 25-cm-deep cone-shaped pots, each with a volume of 656 cm³ (D40 Deepots, Stuewe & Sons, Tangent, OR). Preliminary experiments showed that most of the *Aristida* seed germinated in 1 to 2 d and *Bromus* in 3 to 5 d, whereas the bulk of the *Acrpoptilon* seed took over 1 wk and the *Sporobolus* seed over 2 wk to germinate. Because we could not replicate seasonal phenological differences in seed dispersal and germination and account for differences in time to germination and ensure that plants of different species were at approximately the same developmental stage at the start of the experiment, planting was staggered over a 2-wk period. In the field, *Bromus*, a winter annual, would have an even greater germination advantage because it gets its start in the fall.

About 4 wk later, when grass seedlings were approximately 10 cm tall or rosettes had at least four leaves, every seedling was transplanted into another pot with the same soil mix that had been pretreated once with sugar or treatment solutions. For each treatment, we established 20

pots of each species alone and 20 pots with all four species planted together in a single pot (to evaluate the effects of the treatments under competition), totaling 100 pots treatment⁻¹ and 1,300 pots overall. After transplanting was finished, *Tamarix* litter or chips at 1- or 4-cm depth were placed on top of the soil around the base of seedlings in the litter or chips treatments. Pots were placed in 65 trays with 20 pots per tray. Each tray contained four pots of each species and four pots with all four species together. Pots were randomized within trays and the five trays assigned to each treatment were randomized on the greenhouse bench. Beginning 3 d after transplanting, 30 ml of the assigned treatment solution (water, nutrient solution, salt solution, or *Tamarix* leachate) was applied 3 d wk⁻¹. Trays were rotated around the greenhouse bench and turned end-to-end once a week. Plant height was measured at time of transplanting, 1 mo later, and at the end of the experiment.

A separate set of 10 plants of each species was harvested at the same time as transplantation. Aboveground portions were cut and roots were gently washed free of soil. Shoots and roots were dried for 72 h in a 65 C oven and weighed. For each species, power equations were fitted to the relationships between plant height and shoot weight, and between plant height and root weight. The equations were used to calculate initial shoot and root weight for each plant in the experiment. The R² values of these equations ranged from 0.80 to 0.92.

In addition, five pots of the soil mix without any plants were watered with each of the treatment solutions (including a control set watered with tap water) at the same rate as the experimental plants. At the end of the experiment, samples of these soils were sent to the Environmental Analytical Laboratory of Brigham Young University in Provo, UT, where soils were assessed for: soil NO₃⁻ and NH₄⁺ concentrations in KCl extractions (Kenny and Nelson 1982); pH; electrical conductivity (EC) determined with a saturated paste (Rhoades 1982); available P and potassium (K) extracted in sodium bicarbonate (Olsen et al. 1954; Schoenau and Karamonos 1993); and a suite of total element pools (not available pools) measured by nitric-perchloric acid digestion followed by assessment using inductively coupled plasma mass spectrometry (ICP-MS, Johnson and Ulrich 1959).

The experiment was halted for all plants about 6 wk later at the first sign of bud formation, because natural pollination and seed set was not possible in the greenhouse. At the end of the experiment, plant height was measured again; the aboveground portions of each plant were clipped and dried in a 65 C oven for 72 h and weighed. For plants in the noncompetition pots only, soil and roots were carefully removed from each pot and stored in a 4 C cold room until analysis.

To assess belowground growth, roots from a subset of plants were carefully washed clean of soil, collected in a

series of sieves, dried in a 65 C oven for 48 h, and weighed. Because small pieces of root that broke off during washing proved difficult to separate from the perlite in the soil mix, we collected both main root mass and broken root pieces from only five of the treatments (seven plants of each species from Control, +2× Nutrs, +Salts, +2× Salts, and +Tam Leachate). When analysis showed no statistically significant differences among treatments in the relationship between the weight of the main root mass and the weight of the broken root pieces, the remaining eight treatments were sampled for main root mass only and total root mass was estimated using the allometric relationships.

Response Ratios. Response ratios were calculated for percent germination, number of days to germination, shoot biomass, root biomass, total biomass, and root:shoot ratio (R:S), where each value was divided by the average value of the control for each species. For shoot biomass, response ratios for plants grown under competition were calculated in two ways: (1) with the denominator being the average for control plants grown under control conditions *without* competition to indicate the effect of competition under treatment conditions, and (2) with the denominator being the average for control plants grown under control conditions *with* competition to indicate the effect of treatments under competitive conditions.

Analyses. The response ratios of all germination and growth parameters were log (x + 1) transformed prior to analysis to ensure normality of residuals. For the germination experiment, the response ratio of percent germination and average number of days to germination were analyzed in separate mixed-model ANOVAs with treatment and species as fixed effects and tray (within treatment) as a random effect. When the ANOVA indicated significant effects of species or treatment, pairwise Bonferroni-adjusted Tukey's t posthoc tests were consulted to determine which species-treatment combinations were significantly different from each other.

For the growth experiment, the response ratios of shoot biomass, root biomass, total biomass, and R:S were analyzed in separate mixed-model ANCOVAs with initial shoot, root, or total biomass as a covariate. Treatment and species were designated as fixed effects, and tray (within treatment) a random effect. Competition was an additional fixed effect in the ANCOVA for shoot biomass. When higher order (3- or 4-way) interactions were not significant, they were left out of the final model. When the ANCOVA indicated significant main effects or interactions, pairwise Bonferroni-adjusted Tukey's t posthoc tests determined which treatment-competition-species combinations were significantly different from each other.

Table 3. Type 3 tests of fixed effects from ANOVA on ln response ratio (RR) of days to germination and on percent germination. Tray was included in the models as a random effect.

| Effect | ln RR days to germination | | | ln RR percent germination | | |
|---------------------|---------------------------|---------|----------|---------------------------|---------|----------|
| | df | F value | Pr > F | df | F value | Pr > F |
| Treatment | 11 | 8.19 | < 0.0001 | 11 | 20.53 | < 0.0001 |
| Species | 3 | 30.33 | < 0.0001 | 3 | 38.42 | < 0.0001 |
| Treatment * Species | 33 | 4.83 | < 0.0001 | 33 | 5.65 | < 0.0001 |

Although many correlations, positive and negative, were found among the soil traits measured at the end of the experiment (from soil that received treatments but had no plants), no particular pattern emerged. Therefore, all traits were included in a one-way MANOVA to test for soil differences among treatments. When the MANOVA proved significant, pairwise Tukey's t-tests with Bonferroni adjustment determined which treatments were significantly different from each other for which soil characteristics.

Results and Discussion

Germination Experiment. Days to germination and percent germination were both significantly affected by

treatment, species, and treatment by species interactions (Table 3). *Acroptilon* showed no response of germination time to any treatment (Figure 1A). Chips 1, +C and +3× C delayed germination in *Aristida*, *Bromus*, and *Sporobolus* (Figure 1B–D). +Nutrs and +2× Nutrs delayed *Sporobolus* germination but advanced *Bromus*. +Salts and +2× Salts advanced germination in *Bromus*, whereas +2× Salts delayed *Sporobolus*. Tam Leachate delayed germination in *Aristida*, and +2× Tam Leachate delayed germination in all three species. Tam Litt 1 and Tam Litt 2 delayed germination only in *Aristida* (Figure 1B). *Bromus* was the only species that showed any advanced germination in response to any treatment (Figure 1C). *Sporobolus* was the

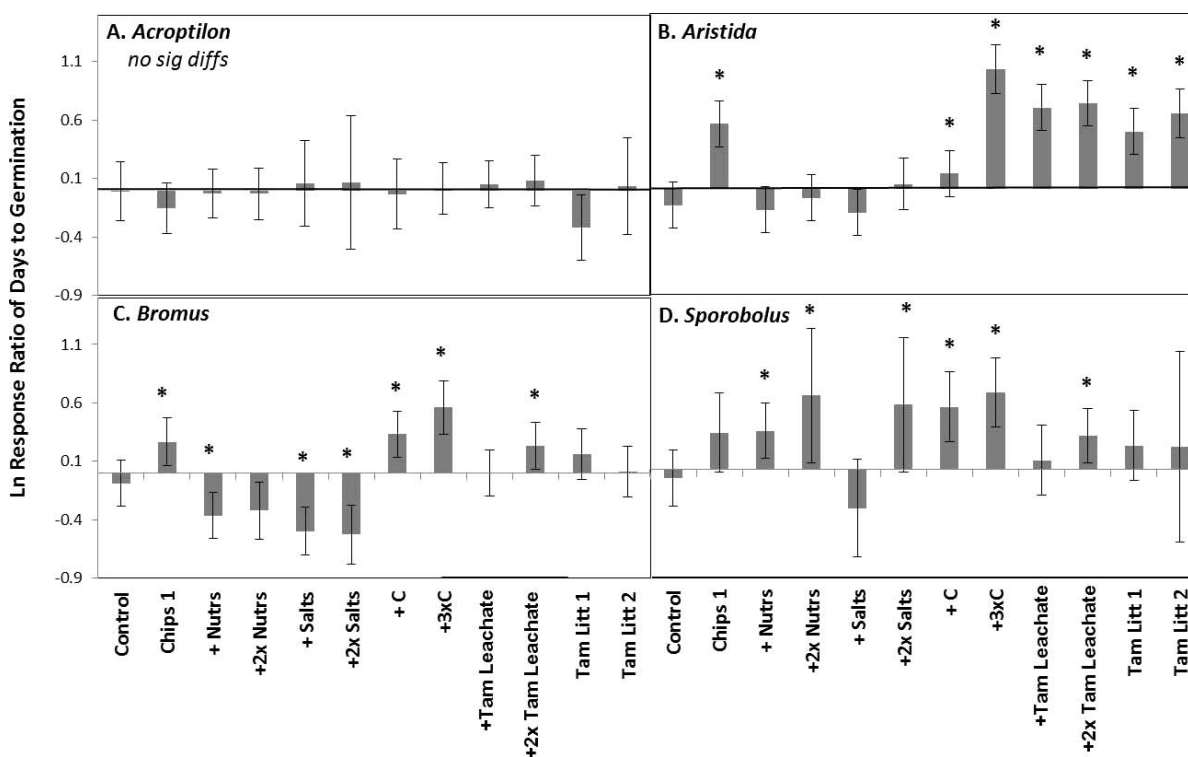


Figure 1. The natural log of response ratio for days to germination calculated relative to the control of each species, least-square means \pm 95% confidence interval. * Indicates treatments that differ significantly from the control at $P < 0.05$. For treatment abbreviations, see Table 1.

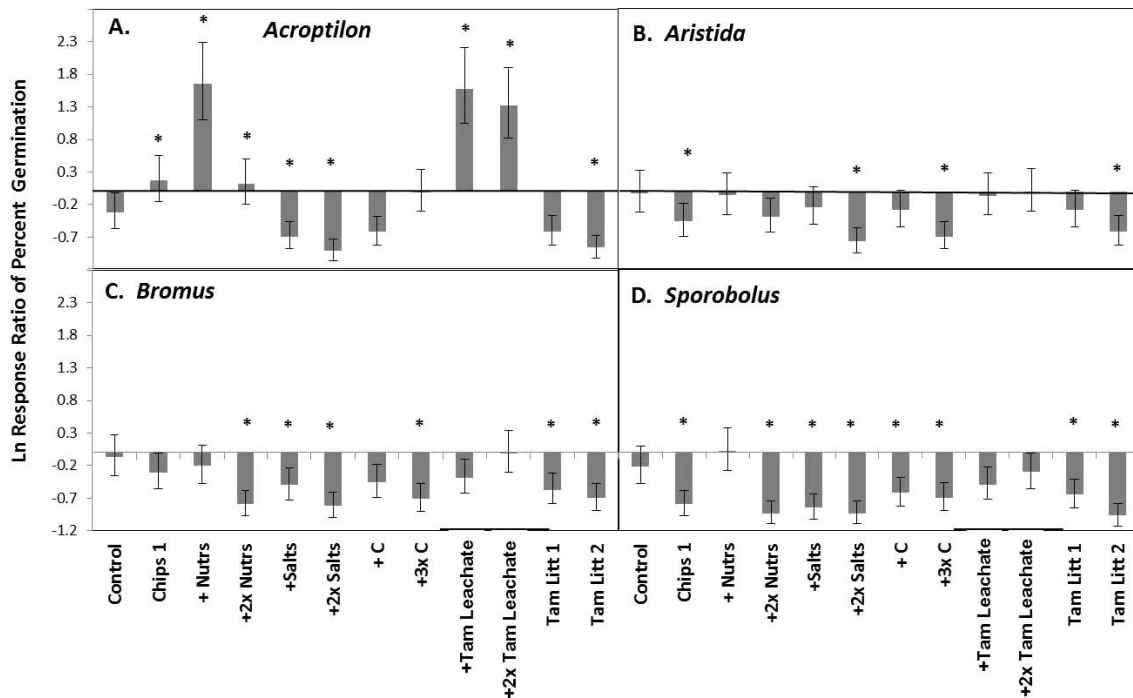


Figure 2. The natural log of response ratio for percent germination, least-square means \pm 95% confidence interval. Average response of each species to all treatments averaged. * Indicates treatments that differ significantly from the control at $P < 0.05$. For treatment abbreviations, see Table 1.

only species to respond negatively to the +Nutrs and +Salts treatments (Figure 1D).

For percent germination, only *Acroptilon* showed positive responses to any treatment, with +2 \times Nutrs, +Tam Leachate, and +2 \times Tam Leachate increasing germination by 120% on average, and +Salts, +2 \times Salts, and Tam Litt 2 decreasing germination by an average of 73.6% (Figure 2A). In the three other species (Figure 2B–D), treatments at the higher solute levels (+2 \times Nutrs, +2 \times Salts, +3 \times C) either reduced germination or had no effect, and smaller additions had even less impact.

Overall, when treatments had an effect, they generally delayed germination and reduced percent germination. The Tam Litter and Chips treatments might have decreased germination because the seeds, perched on the surface of these materials and not in contact with the soil, dried out faster than those in the control (R.A. Sherry, personal observations), despite more abundant water than under field conditions. Similarly, Jensen and Gutekunst (2003) found that of 35 grassland species, 33 had lower recruitment when litter was present, with the largest impacts on early successional species. Cycles of grazing and/or fire in grasslands reduce thatch, allow new plant establishment (particularly of annuals), and greatly increase productivity (Knapp et al. 1998). In riparian systems, erosion and deposition associated with flooding can remove or promote faster decomposition of litter (Andersen and

Nelson 2006; Ellis et al. 1999). Thus, our observations of delayed germination with increased litter is in line with responses observed in other systems, and suggests that the massive litter drop that occurs with defoliation could hinder establishment of the subsequent plant community. However, Dela Cruz et al. (2014) found that mulch increased germination in both native species and *Bromus* species, so under natural conditions, where wind or rain can allow seed to fall between the chips or pieces of litter, and where effects of increased moisture within or under the litter can confer a larger advantage, a thin layer of litter or chips might benefit germination. In general, positive effects of mulch or litter are generally seen when the plants of interest are already established or can become established in openings in the litter.

The effects of other treatments on time to germination and on germination rate varied by species, demonstrating the species-specific nature of nutrient effects on germination and the negative effects of osmotic agents in general on germination (Vincent and Roberts 1977; Williams 1983). In general, lower levels of osmotic stress delay germination and higher levels also reduced germination rates (Bajji et al. 2002), and any ion, including nutrients, can function as an osmotic agent and reduce the rate of water imbibition into the seed.

Although small amounts of salts can sometimes have positive effects on germination, at least in some halophytes

Table 4. Ending soil characteristics from pots with no plants that received treatment solutions over the course of the experiment (included petlite). Values are means \pm SE. Values in boldface are significantly different from the control, $P < 0.05$, Bonferroni-adjusted Tukey's test.^a

| Ending soil by treatment | pH | EC dS cm ⁻¹ | NO ₃ ⁻ -N ppm | NH ₄ ⁺ -N ppm | avail P ppm | avail K ppm | Ca ppm | Mg ppm | Na ppm |
|--------------------------|-----------------------------|-----------------------------|--|--|------------------------------|----------------------------|--------------------|-----------------|-------------------------------|
| Control | 7.3 \pm 0.1 | 1.2 \pm 0.2 | 22.7 \pm 7.5 | 3.6 \pm 0.8 | 12.5 \pm 1.2 | 408 \pm 26 | 29,615 \pm 1,051 | 7,788 \pm 326 | 1,777 \pm 193 |
| Chips 2 | 7.4 \pm 0.1 | 0.7 \pm 0.2 | 13.0 \pm 7.5 | 2.5 \pm 0.8 | 11.1 \pm 1.2 | 281 \pm 26 | 29,509 \pm 1,051 | 7,685 \pm 326 | 1,631 \pm 193 |
| +Nutrients | 7.4 \pm 0.1 | 2.2 \pm 0.2 | 81.6 \pm 7.5 | 2.6 \pm 0.8 | 19.7 \pm 1.2 | 368 \pm 26 | 28,349 \pm 1,051 | 7,487 \pm 326 | 1,614 \pm 193 |
| +2 \times Nutrients | 7.3 \pm 0.1 | 3.0 \pm 0.2 | 132.4 \pm 7.5 | 4.3 \pm 0.8 | 29.6 \pm 1.2 | 481 \pm 26 | 27,487 \pm 1,051 | 7,112 \pm 326 | 1,750 \pm 193 |
| +Salts | 7.5 \pm 0.1 | 4.5 \pm 0.2 | 26.5 \pm 7.5 | 3.9 \pm 0.8 | 14.1 \pm 1.2 | 445 \pm 26 | 28,683 \pm 1,051 | 7,515 \pm 326 | 2,277 \pm 193 |
| +2 \times Salts | 7.7 \pm 0.1 | 4.4 \pm 0.2 | 23.4 \pm 7.5 | 3.6 \pm 0.8 | 13.3 \pm 1.2 | 462 \pm 26 | 29,254 \pm 1,051 | 7,910 \pm 326 | 2,465 \pm 193 |
| +C | 7.6 \pm 0.1 | 0.9 \pm 0.2 | 12.7 \pm 7.5 | 3.3 \pm 0.8 | 9.2 \pm 1.2 | 302 \pm 26 | 28,715 \pm 1,051 | 7,841 \pm 326 | 2,073 \pm 193 |
| +3 \times C | 7.4 \pm 0.1 | 0.8 \pm 0.2 | 13.5 \pm 7.5 | 2.9 \pm 0.8 | 10.4 \pm 1.2 | 344 \pm 26 | 28,351 \pm 1,051 | 7,804 \pm 326 | 2,039 \pm 193 |
| +Tam leachate | 7.4 \pm 0.1 | 1.3 \pm 0.2 | 26.5 \pm 7.5 | 2.2 \pm 0.8 | 13.7 \pm 1.2 | 402 \pm 26 | 28,309 \pm 1,051 | 7,815 \pm 326 | 2,131 \pm 193 |
| +2 \times Tam leachate | 7.5 \pm 0.1 | 0.9 \pm 0.2 | 20.1 \pm 7.5 | 2.5 \pm 0.8 | 13.0 \pm 1.2 | 405 \pm 26 | 29,487 \pm 1,051 | 8,148 \pm 326 | 2,030 \pm 193 |
| Tam Litt 1 | 7.5 \pm 0.1 | 0.9 \pm 0.2 | 30.2 \pm 7.5 | 2.0 \pm 0.8 | 12.8 \pm 1.2 | 375 \pm 26 | 3,0316 \pm 1,051 | 8,321 \pm 326 | 2,002 \pm 193 |
| Tam Litt 2 | 7.4 \pm 0.1 | 1.2 \pm 0.2 | 36.8 \pm 7.5 | 2.0 \pm 0.8 | 12.4 \pm 1.2 | 367 \pm 26 | 28,761 \pm 1,051 | 7,814 \pm 326 | 1,936 \pm 193 |

^aAbbreviations: C, carbon; Chips 2, treatment of 4 cm *Tamarix* wood chips; EC, electrical conductivity; Tam, tamarisk; Tam Litt 1, treatment of 1 cm *Tamarix* leaf litter; Tam Litt 2, treatment of 4 cm *Tamarix* leaf litter.

(Bajji et al. 1998; Matoh et al. 1986), the effects of NaCl on plant germination and growth are usually overwhelmingly negative, due both to direct osmotic effects and to ion-specific interactions with cell membranes and with other ions (i.e., excess Cl⁻ leads to Ca⁺ deficiency in many species, Almansouri et al. 2001; Keiser et al. 1995). The degree of salt tolerance of *Bromus* and *Acroptilon* seen in this experiment is generally in line with the literature. Ecotypic variability in salt tolerance in *Bromus tectorum* has been observed before (Haubensak et al. 2014; Rasmuson and Anderson 2002; Scott et al. 2010), and Belnap et al. (2003) noted that NaCl additions had only moderate effects on its germination. Likewise, although *Acroptilon repens* is not widely known to be salt tolerant, it does grow on a wide variety of soil types, and the related genus *Centaurea* is salt tolerant (Radić et al. 2005; Ussal et al. 2006; Yildiztugay et al. 2011). Taken together, the data suggest that, even when adding relatively low concentrations of C, nutrients, and salts, plant germination can respond negatively. Because of the high likelihood of such inputs following defoliation and *Tamarix* mortality, these results suggest that the chemistry of the riparian zone might interact with species-specific responses to influence the composition of the vegetation that initially replaces *Tamarix*.

Growth Experiment. Treatments had significant cumulative effects on soil chemistry during the growth experiment (Table 4). Available K showed a large decrease in the Chips 2 treatment relative to the control. Soil that received added nutrients was enriched in NO₃⁻-N and available P, but salinity was also increased. NH₄⁺-N did not increase. Soils that received salt solutions were higher in EC and Na. Soils with +1 \times C additions had less available P and K, and an increase in pH, although the +3 \times C showed no effects. Effects of Tam Leachate on nutrient concentrations were not significant. Tam Litter increased the concentration of NO₃⁻-N.

Shoot, Root, and Total Biomass without Competition. Shoot biomass was significantly affected by all factors (treatment, initial shoot biomass, species, and competition) and all second- and third-order interactions (Table 5). Root and total biomass were significantly affected by treatment, initial biomass and all second-order interactions, but not by species identity (Table 6).

Carbon addition, whether in the form of wood chips or sugar, generally decreased growth (Figure 3A–D). Chips 2 decreased shoot biomass in all species, and +3 \times C decreased shoot biomass in all species except *Aristida*. The thicker layer of chips had larger negative effects on *Acroptilon* and *Sporobolus* than on *Aristida* and *Bromus*. All

Table 5. Type 3 tests of fixed effects from ANCOVA on ln response ratio of shoot biomass. Tray was included in the model as a random effect and initial biomass was a covariate. The four-way interaction was not significant and was left out of the final model.

| Effect | df | F value | Pr > F |
|---|----|---------|----------|
| Treatment | 12 | 5.57 | < 0.0001 |
| Initial shoot biomass | 1 | 375.90 | < 0.0001 |
| Competition | 1 | 13.73 | 0.0002 |
| Species | 3 | 6.17 | 0.0004 |
| Initial shoot biomass * Treatment | 12 | 3.82 | < 0.0001 |
| Treatment * Competition | 12 | 6.97 | < 0.0001 |
| Treatment * Species | 36 | 2.25 | < 0.0001 |
| Initial shoot biomass * Competition | 1 | 32.63 | < 0.0001 |
| Initial shoot biomass * Species | 3 | 38.03 | < 0.0001 |
| Species * Competition | 3 | 150.01 | < 0.0001 |
| Treatment * Species * Competition | 36 | 2.49 | < 0.0001 |
| Initial shoot biomass * Treatment * Species | 36 | 2.42 | < 0.0001 |

species responded positively to at least one of the Tam Leachate or Litter additions, and all but *Aristida* responded positively to a nutrient addition (Figure 3A–D). *Acroptilon* was the most responsive to treatments, with accelerated growth in six treatments, including +Salt and +2× Salt, the only species with any response to salinity. Shoot, root and total biomass all tended to respond similarly to treatments; however, response of roots to +Nutrs, +2× Nutrs, and +Tam Litt 2 was not as large as the response of shoot and total biomass in *Acroptilon*, *Bromus*, and *Sporobolus*.

Effects of Nutrients and Salts. Although effects on germination rate were consistently negative, treatments that added nutrients generally did have positive effects on growth (except *Aristida* only had significant positive responses to Tam Litt 1). In turn, treatments that reduced

nutrients decreased growth, confirming that this soil is nutrient-limited. Thus, the data suggest that the effects of nutrients on germination and growth were effectively decoupled; soil conditions might reduce germination success but, after germination, can facilitate plant growth. The invasive plants showed greater positive responses to increased nutrients than the natives, supporting ideas that invasive plants grow faster and respond more positively to increased nutrient supply compared to natives (Blank 2010; Drenovsky et al. 2012; Evans et al. 2001). High intrinsic relative growth rates that allow them to take advantage of increased nutrients may be a common trait of invasive species (Grotkopp and Rejmánek 2007; Pyšek and Richardson 2007). The tested invasive species also had smaller negative responses than natives to decreased nutrients, which contradicts hypotheses about invasive species performing more poorly than natives under low fertility conditions (Jonasson et al. 1996; Perry et al. 2010). The results suggest that nutrient availability in *Tamarix*-affected soils might play an important role in both individual plant growth and in competitive interactions, and suggest that invasive plants might benefit from nutrient inputs from defoliation and insect frass.

Added salts did not decrease growth in any species and increased growth in *Acroptilon*. However, the salinity levels in our treatments were lower than those reported in other riparian systems (e.g., Merritt and Shafroth 2012). Also, there is considerable variation in the response of different plant species to soil salinity (Beauchamp et al. 2009; Shafroth et al. 2008); thus, other taxa might show greater responses than ours.

Effects of Tamarix Litter, Leachate, and Wood Chips. The significant $\text{NH}_4^+\text{-N}$ in Tam Litter (Table 4) might explain its positive effect on plant growth. Tam Leachate did not significantly increase soil nutrient concentrations by the

Table 6. Type 3 tests of fixed effects from ANCOVA on ln response ratio of root biomass, total biomass, and R:S. Tray was included in the model as a random effect and initial total biomass was a covariate. F values and probabilities for significant effects and interactions are in bold type. The three-way interaction was not significant and was left out of the final model.

| Effect | df | Root biomass | | Total biomass | | R:S ratio | |
|-----------------------------------|----|--------------|-----------------|---------------|-----------------|--------------|-----------------|
| | | F value | Pr > F | F value | Pr > F | F value | Pr > F |
| Treatment | 12 | 2.47 | 0.0130 | 4.48 | < 0.0001 | 2.55 | 0.0103 |
| Species | 3 | 1.06 | 0.3676 | 1.92 | 0.1263 | 7.24 | 0.0001 |
| Initial total biomass | 1 | 18.66 | < 0.0001 | 31.71 | < 0.0001 | 12.73 | 0.0004 |
| Treatment * Species | 36 | 3.13 | < 0.0001 | 3.64 | < 0.0001 | 4.80 | < 0.0001 |
| Initial total biomass * Treatment | 12 | 2.07 | 0.0183 | 2.41 | 0.0053 | 0.99 | 0.4567 |
| Initial total biomass * Species | 3 | 2.04 | 0.1079 | 4.13 | 0.0068 | 10.85 | < 0.0001 |

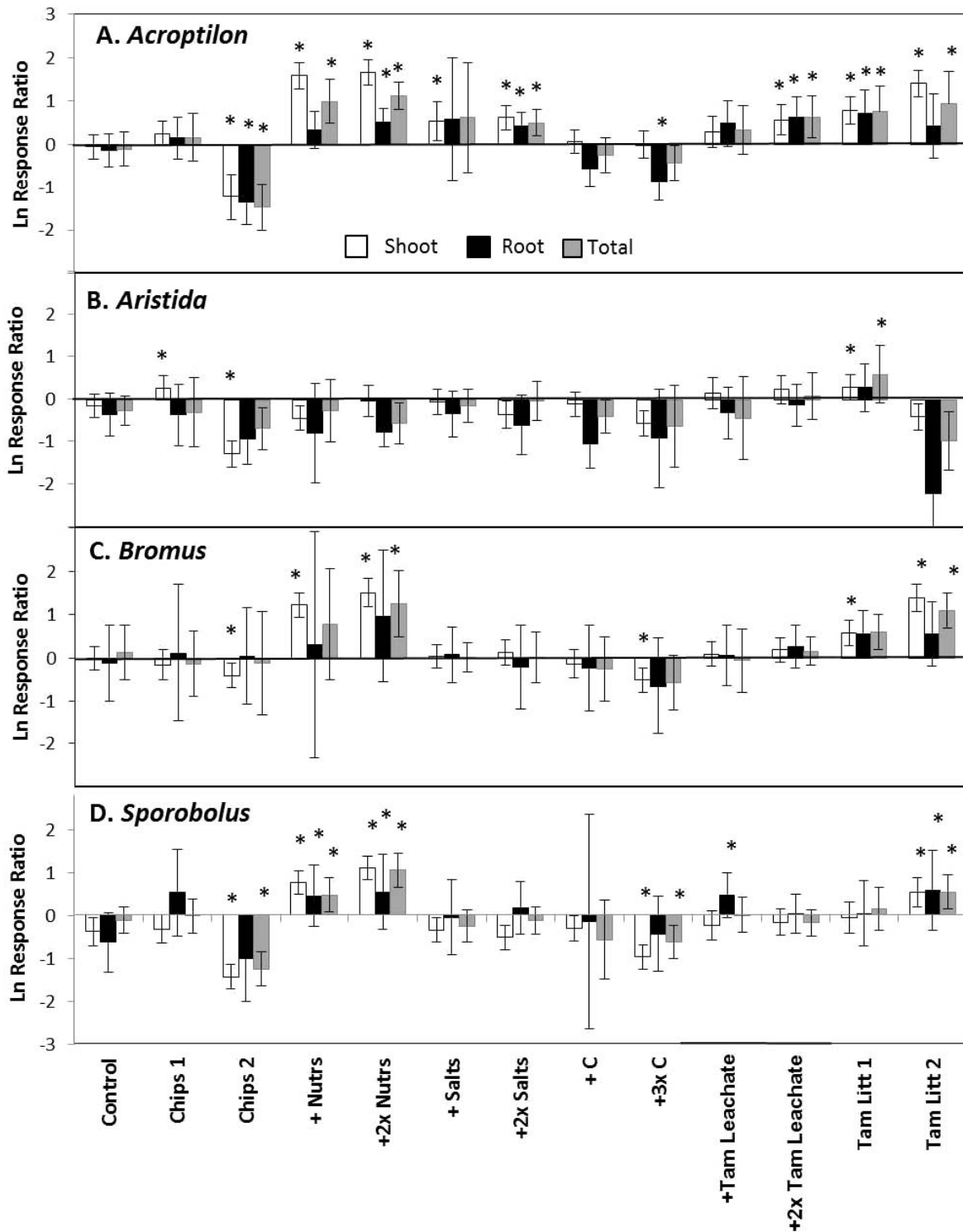


Figure 3. The natural log of the response ratio for shoot (open bars), root (black bars) and total biomass (gray bars) without competition, least square means from ANCOVA with initial shoot, root, or total biomass as a covariate, \pm 95% confidence interval. All response ratios were calculated relative to the control without competition. * Indicates treatments that differ significantly from the control without competition for shoot, root, or total biomass at $P < 0.05$. For treatment abbreviations, see Table 1.

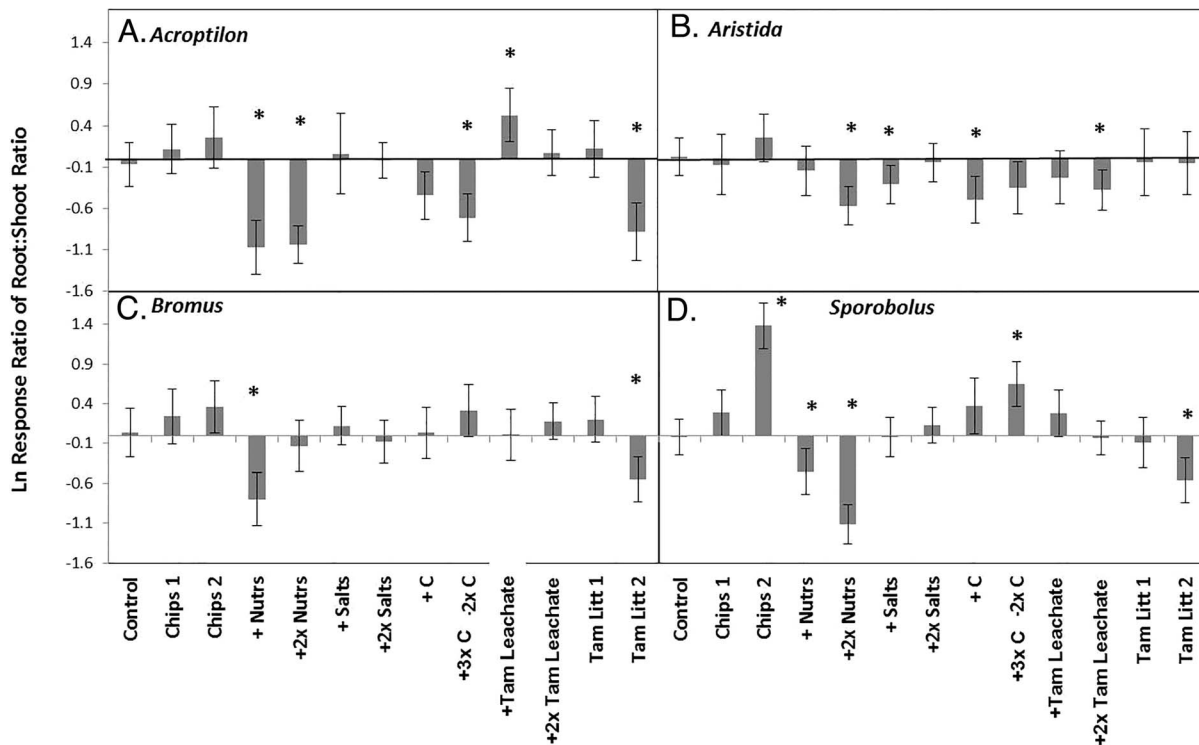


Figure 4. The natural log of the response ratio for R:S (least-square means \pm 95% confidence interval). * Indicates treatments that are significantly different from the control at $P < 0.05$. For treatment abbreviations, see Table 1.

end of the experiment (Table 4), which explains smaller growth responses to leachate than to litter. *Tamarix* leaves have previously been noted to have more biologically available N compounds than co-occurring *Salix*, *Populus*, and *Fraxinus* (Going and Dudley 2008; Kennedy and Hobbie 2004). These results are in line with those of Lehnhoff and Menalled (2013), who showed that eight plant species commonly used in riparian restorations in Montana grew better on *Tamarix*-affected soil than on non-*Tamarix* soil. We also cannot rule out that increased water retention due to litter might have affected plant performance.

The thinner layer of wood chips elicited small positive growth responses, especially under competition, and chips might have increased water retention slightly. However, the effect of the thicker chips layer was always negative. This response is in line with other studies of restoration after removal of woody species, which also show that thin layers of wood chips increase emergence, whereas deeper layers repress emergence (Brockway et al. 2002; Rokich et al. 2002). Because the low stature rosettes of *Acroptilon* were the only seedlings that were actually covered by the chips, the negative effects of the deeper chips might also have to do with nutrient immobilization; for example, pots with chips had significantly less K and nearly half the inorganic

N concentrations than control pots at the end of the experiment (Table 3). If effects of chips in this experiment were due to changes in soil nutrient status, reports of wood chip applications in the field decreasing invasive species could be due to nutrient immobilization (Eldridge et al. 2012). It is also possible that the positive effects of chips on native emergence in the field might be due more to suppression of weed seeds underneath the chips, leading to decreased competition for natives that arrive in seed rain. However, any positive effects of chips or litter on growth are moot if seeds don't germinate, highlighting the potentially contrasting effects of treatments on germination vs. growth, as well as the potentially modifying role of competition.

Root:Shoot Ratio. R:S was significantly affected by treatment, initial total biomass, and species (Table 6). Additionally, there were significant treatment by species interactions, and species by initial total biomass interactions. *Acroptilon* had the highest R:S (1.48 ± 0.11), whereas *Aristida* and *Bromus* had similar R:S (0.89 ± 0.10 and 0.87 ± 0.19 , respectively). *Sporobolus* had the smallest R:S (0.32 ± 0.03).

The Chips 1 treatment did not change R:S (Figure 4A–D). The Chips 2 treatment increased R:S only in *Sporobolus*

(Figure 4D). Nutrient addition generally decreased R:S. Added salts had no effect on R:S except in *Aristida* where the lower concentration decreased R:S. Tam Leachate increased R:S in *Acroptilon* and 2× Tam Leachate decreased R:S in *Aristida*. Tam Litt 1 did not affect R:S, but Tam Litt 2 decreased R:S in three of the four species.

Increased R:S is thought to increase nutrient foraging ability (Cahill 2003). The pattern of R:S response we observed (decreased R:S in treatments that increased nutrients and increased R:S in the treatments that reduced soil nutrients most) is consistent with the theory that allocation to roots increases under low nutrient conditions to maximize nutrient foraging and increases to shoots under higher nutrient conditions to maximize light capture (Poorter and Nagel 2000). It can be difficult to distinguish between adaptive allocation patterns and a simple allometric relationship less than 1, in which smaller plants always have an increasing proportion of their biomass in roots (Cahill 2003). However, our results show *Acroptilon* had a larger R:S in the lower nutrient treatments that could not be attributed to allometry. The R:S ratios were greater than 1; therefore, if allometry was the factor influencing R:S, larger plants would have had the greater R:S ratios, which was not the case.

Our findings are also congruent with previous findings that higher allocation to roots does not necessarily increase competitive ability (Cahill 2003). *Aristida* and *Sporobolus* had similar competitive abilities, but *Aristida* had a higher R:S. Additionally, *Acroptilon* had the highest R:S, much higher than *Bromus*, although *Bromus* was the better competitor. However, we note that our experiment did not cover the period of flowering and seed set, and it is possible that competitive relations between these species could change over time or with life stage. Similar to the other plant metrics, R:S suggests a strong role for *Tamarix* defoliation in regulating the subsequent plant community via effects on soil fertility.

Shoot Biomass with Competition. Competition significantly affected shoot biomass and interacted with species and treatment (Table 5). Competition effects were larger in *Aristida* and *Sporobolus* and smallest in *Bromus* (Figure 5). For *Aristida*, the decrease was significant in all treatments. Competition effects were smallest under nutrient addition and Tam Litter treatments. In *Bromus* under these treatments (+Nutrs, +2× Nutrs, Tam Litt1, Tam Litt 2), shoot biomass under competition was still larger than control shoot biomass without competition. In *Acroptilon*, there was no competition effect under nutrient, salt, and

Tam Litter additions, and largest under Chips 2 and C and Tam Leachate additions.

Treatment responses under competition varied little from the responses without competition (Figure 5). *Aristida* showed the smallest responses to treatments under competition of any species (Figure 5B) and *Sporobolus* had the largest negative responses to treatment when under competition (Figure 5D). When comparing shoot response to treatments with and without competition (Figure 5), plants increased shoot biomass in Chips 1 and +2× Salts with competition but not without, and decreased shoot biomass under Chips 2 and +3× C without competition but not with competition.

The effects of treatments were the same under competition as without it, except that effects were smaller and less often significant. In particular, negative effects of treatments were smaller with competition and were rarely statistically different from the control. This is the expected outcome if a treatment reduced growth overall: as plant size decreased, both roots and shoots would be less likely to come into direct competition with the roots and shoots of other plants, therefore competition effects would be minimized.

It is important to note that the two invasive species had much smaller negative responses to competition than the natives under all treatments. *Bromus* had almost no responses to competition and was the only species that still had positive responses relative to controls grown alone to nutrient addition and Tam Litter when under competitive conditions. This supports the theory that invasive species are better competitors than native species (Blank 2010; Drenovsky et al. 2012; Evans et al. 2001) and suggests that invasive plants might have an inherent advantage. In the same vein, nutrient reductions (e.g., in the C addition treatment) did not decrease the competitive ability of the invasives, which continued to perform better than natives, again contradicting hypotheses about decreased growth advantages of invasives under low fertility conditions (Jonasson et al. 1996; Perry et al. 2010). However, our soil might have already been enriched in nutrients due to the long-term presence of *Tamarix* compared to soil at the site before *Tamarix* invasion, and the nutrient reductions in our experiment might not have been large enough to bring the soil back to pre-*Tamarix* conditions. Thus, although increased native competitiveness under nutrient-poor conditions might hold in other systems, the long-term effects of *Tamarix* dominance might create a nutrient-rich environment where subtle reductions in fertility cannot create condi-

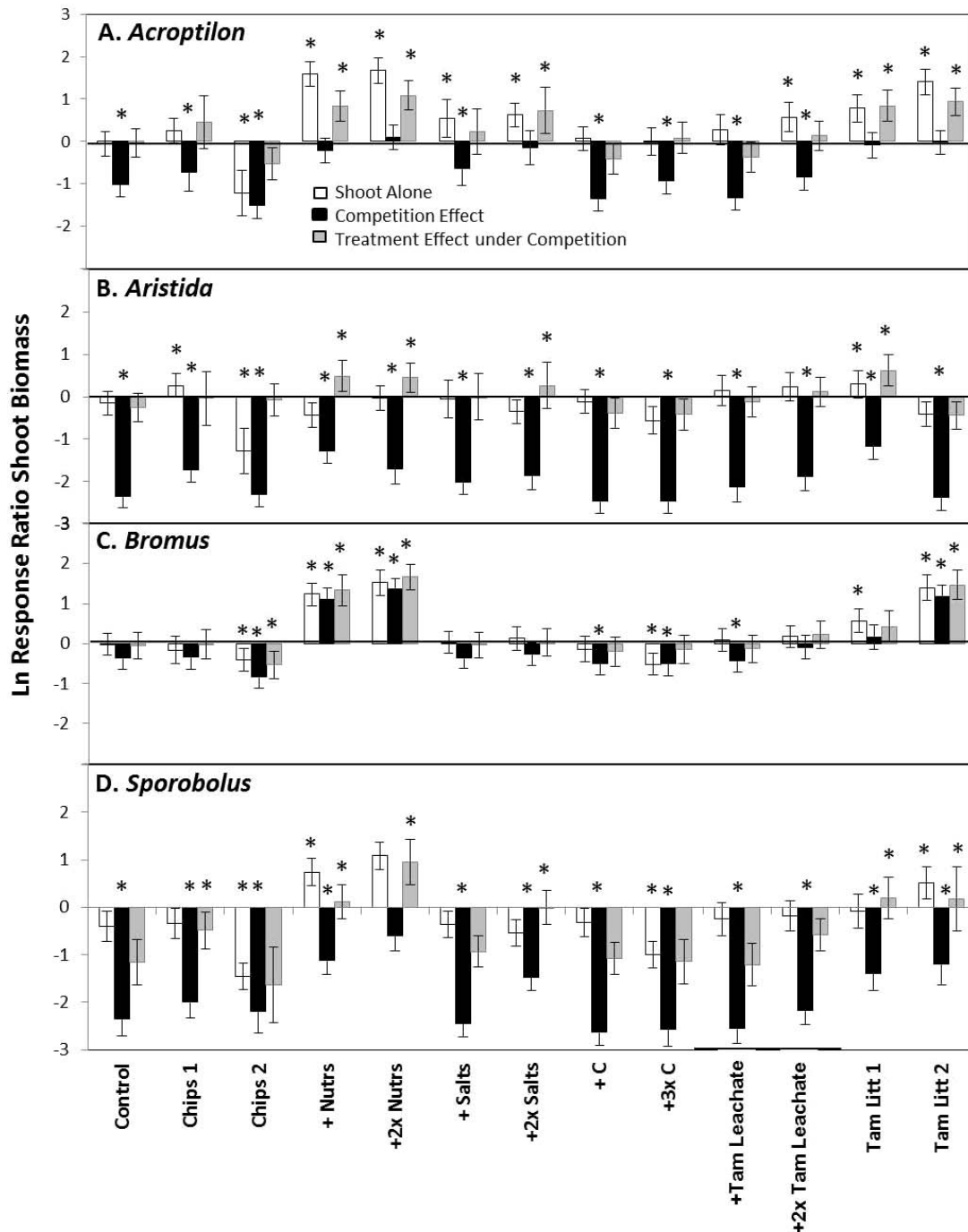


Figure 5. The natural log of the response ratio for shoot biomass with competition calculated relative to the control alone (black bars) or to the control with competition (grey bars). For comparison, the response ratio of shoot biomass without competition is repeated from Figure 3 (open bars). Values are least square means from ANCOVA with initial shoot biomass as a covariate, \pm 95% confidence interval. * Indicates significant difference from the control without competition (open and black bars) or from the control with competition (grey bars), $P < 0.05$. For treatment abbreviations, see Table 1.

tions that are nutrient-poor enough to promote native plant success.

Other explanations for the poorer performance of natives under competition include allelopathy and lack of

symbiotic soil fungi. Allelopathic responses to *Acroptilon repens* are species-specific (Grant et al. 2003; Stevens 1986) and might have affected the native species more than *Bromus*. The long period of *Tamarix* dominance could

have depleted the soil of native symbiotic fungi (Gehring et al. 2006; Meinhardt and Gehring 2012). Both *Sporobolus* and *Aristida* have known mycorrhizal associates (Busso et al. 2001; Khidir et al. 2010), whereas both *Acroptilon* and *Bromus* are known to be fast-growing (DiTomaso 2000; Mosley et al. 1999; Whitson 1999) and are likely to have innately high growth and nutrient acquisition rates (Blank 2010; Evans et al. 2001; Leffler et al. 2011).

Secondary Invasion and Implications for Restoration.

Our greenhouse results suggest that *Acroptilon repens* and *Bromus tectorum*, both common to *Tamarix* sites in the southwestern United States (Beauchamp and Shafroth 2011; McDaniel and Taylor 2003; Reynolds and Cooper 2011), are likely to do well after *Tamarix* dieback, especially in comparison to two common native grasses. Additionally, *Bromus tectorum* was the most abundant seed bank species at *Tamarix* sites near Moab, UT (R.A. Sherry, personal observation). However, if these secondary weeds can be controlled and native propagules introduced, the abundance of natives could increase (Dela Cruz et al. 2014). For example, although in this experiment *Aristida* and *Sporobolus* were poor competitors compared with the exotic species, they both performed adequately and began forming flowers (R.A. Sherry, personal observation). Also, Lehnhoff and Menalled (2013) grew eight noninvasive species commonly used in Montana riparian restorations in *Tamarix* and non-*Tamarix* soils and found no negative effects of the *Tamarix* soils on the natives, despite increased salinity and fertility of the *Tamarix* soil. In some places, often immediately adjacent to water, willows and other native perennials are poised to take advantage of *Tamarix* dieback. Where such species are lacking, especially away from the water's edge, active restoration measures might be needed to avoid secondary invasion.

Our study, like other greenhouse studies, has the advantage of allowing tighter control of individual variables than is typically possible in field experiments or observational studies, but we acknowledge limitations as well. The species we examined are most likely to occur on the drier end of the riparian moisture gradient, such as on high floodplains or terraces. These geomorphic surfaces commonly support *Tamarix* stands, particularly along regulated rivers (Merritt and Shafroth 2012; Ohrtman et al. 2012). However, our results are not likely applicable to areas where "soil" (substrate) conditions are much less stable, such as on more geomorphically active portions of river bottomlands, where flooding can flush salts and nutrients from sediments, and erosion and deposition can lead to turnover of sediments.

Some potential implications for *Tamarix* restoration can be gleaned from this study: (1) The thickness of the litter layer could play an important role, because a thick layer of *Tamarix* wood chips were detrimental to plant germination. Although many *Tamarix* dieback areas are likely to be too large to feasibly apply wood chips, benefits from a thin layer of chips could be possible and warrant further study. (2) Soil chemistry and fertility could represent a very strong control, but this does not mean soil amendments are needed. Our data suggest that, although the levels of nutrients and salts in *Tamarix* soil and litter might provide a greater advantage to the growth of the studied exotics relative to natives, they are not harmful to native plants. (3) Soil conditions do vary from site to site (Beauchamp et al. 2009; Beauchamp and Shafroth 2011; Shafroth et al. 2008). Soil testing and assessment of which native species grow nearby could propose desirable native species to use to facilitate establishment of the plant community of interest.

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