Impacts of *Tamarix*-mediated soil changes on restoration plant growth

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**Abstract**

**Question:** Do soils impacted by *Tamarix* spp. affect the growth of plants used for restoration through altered soil chemistry and/or plant-soil feedbacks?

**Location:** The Bighorn River, the Yellowstone River and the Fort Peck Reservoir, Montana, western USA.

**Methods:** Soil was collected from paired subsites where *Tamarix* was either present or absent along three water bodies. To evaluate chemical and biological soil effects on plant growth, eight plant species (*Achnatherum hymenoides*, *Astragalus cicer*, *Dalea candida*, *Elymus lanceolatus*, *Leymus cinereus*, *Pascopyrum smithii*, *Ratibida columnifera* and *Trifolium pratense*) commonly used in restoration projects at *Tamarix*-invaded sites were grown in the collected soil. Plant-soil feedbacks were evaluated by growing two species (*D. candida* and *P. smithii*) in greenhouse soils inoculated with small amounts of the field soils. Germination, emergence and growth characteristics were compared between *Tamarix*-invaded and un-invaded subsites and across water bodies.

**Results:** Seedling emergence and plant relative growth rate, total biomass production and allocation of resources to roots and shoots were not negatively affected in field soils or in greenhouse soil inoculated with soil from areas where *Tamarix* was present. In fact, overall, plants emerged earlier and produced more biomass in soils affected by *Tamarix* than in soils from where *Tamarix* was not present. These results indicate that for sites in the northern range of *Tamarix*, restoration would not be inhibited by *Tamarix*-induced soil changes.

**Conclusions:** *Tamarix* is a relatively new invader in the northern USA, and little is known about its impacts in this area or the potential implications for restoration. However, our results indicate that neither altered soil chemistry nor plant-soil feedbacks negatively impact native plant growth, and restoration efforts would not be hindered by *Tamarix*-induced changes to soil chemistry or microbiota.

**Introduction**

Restoration of plant communities after the removal of non-indigenous plant species (NIS) is complicated by many factors, including potential changes in soil properties (Weidenhamer & Callaway 2010), depletion of the native species seed bank (French et al. 2011) and increased resource availability that promotes colonization by other NIS (Davis et al. 2000). Also, microbe-mediated plant-soil feedbacks (PSF) may condition the soil in a manner that alters its suitability for the same and other plant species (Bever et al. 1997). Plant-soil feedbacks can determine subsequent plant growth, abundance, persistence and competitive success through changes in decomposition rates (Hobbie 1992; Knops et al. 2002), resource availability (Vinton & Burke 1995; Ehrenfeld et al. 2001; Clark et al. 2005) and/or pathogenic and mutualistic interactions (Hamel et al. 2005; Wolfe et al. 2005). Legacy effects of PSF are important in invaded plant communities as they could either enhance or decrease the performance of plants (Callaway et al. 2004; Kulmatiski & Beard 2011). Positive PSF occur when plants accumulate beneficial microbes in their rhizosphere, including mycorrhizal fungi and nitrogen-fixing bacteria, which enhance the growth and competitive ability of conspecifics relative to other plant species. On the other hand, negative PSF enhance species turnover rates through the accumulation of pathogenic microbes, parasites and herbivores in the...
rhizosphere. In nature, positive and negative PSF seldom occur in isolation, and there is ample evidence that the net effect of these co-occurring events plays a vital role in ecosystem organization, functioning and dynamics (Harrison & Bardgett 2010).

The control of *Tamarix chinensis* and *T. ramosissima*, and hybrids of the two (Gaskin & Schaal 2002), hereafter referred to as *Tamarix*, and restoration of *Tamarix*-invaded sites has recently become the focus of many western land managers (Shafroth & Briggs 2008). *Tamarix* are shrubs or small trees native to Asia that have invaded riparian areas in the southwestern and more recently the northern and northwestern USA (Pearce & Smith 2007; Lehnhoff et al. 2011). Once established in riparian areas, *Tamarix* can limit recruitment of native *Populus* and *Salix* species (Shafroth et al. 1995) and become the dominant tree (Friedman et al. 2005). *Tamarix* can alter soil chemistry by increasing soil salinity and nutrient content (Bagstad et al. 2006; Lehnhoff et al. 2012), reducing soil pH (Ladenburger et al. 2006) and decreasing the abundance of arbuscular mycorrhizal fungi (Beauchamp et al. 2005; Lehnhoff et al. 2012). While the effects of *Tamarix*-altered soil chemistry on native plant establishment have been studied, the impacts of PSF on the success of restoration plants at *Tamarix*-occupied sites have not.

Restoration of *Tamarix*-impacted sites is difficult, and may be unsuccessful because of interacting many factors. *Tamarix* invasion is often closely related to anthropogenic alterations of river hydrology (Stromberg et al. 2007). Because of altered hydrology, simply removing *Tamarix* via burning, herbicide or mechanical means may not lead to the desired changes in plant communities (McDaniel & Taylor 2003; Harms & Hiebert 2006). Invasion by other NIS after *Tamarix* removal is also a concern that affects restoration success. In a review of restoration projects at 28 *Tamarix* sites in the southwestern USA, Bay & Sher (2008) found that 19% of plant species colonizing the sites were NIS. Finally, while it is difficult to decouple *Tamarix*-induced changes to soil properties from the effects of flow alteration, soil chemistry and PSF may have effects on the establishment and growth of restoration plants. Indeed, ecosystems may be altered, either directly by anthropogenic changes or indirectly by NIS through modified soil chemistry or PSF, to the point where they can be considered ‘novel’ (Seastedt et al. 2008), thereby further complicating restoration by making restoration targets ambiguous.

To maximize the probability of successful restoration after NIS management, it is crucial to first understand the implications of such potentially novel ecosystems, including altered soil chemistry and PSF, and second, to select plant species adapted to the conditions present, including both altered soil and hydrology. This study focused on evaluating plant performance in soils altered by the presence of *Tamarix*. The specific objectives of this work were to (1) assess the suitability of eight plant species (seven indigenous and one not indigenous to Montana) for growth at *Tamarix*-invaded sites on three water bodies with different hydrology, and (2) investigate the existence of *Tamarix*-induced PSF. For the first objective, we hypothesized that plant species performance would vary between soils from different water bodies because of differences in soil biological and chemical characteristics. While there is evidence that *Tamarix* increases soil nutrients (Ladenburger et al. 2006; Lehnhoff et al. 2012; Meinhardt & Gehring 2012), which could be beneficial for plant growth, we tested the common assumption that plants would perform worse in soils from where *Tamarix* was present because of increased salinity. For the second objective, no *a priori* hypotheses were developed due to the lack of pre-existing information on the potential impacts of *Tamarix* on PSF. However, previous research has shown a variety of impacts of *Tamarix* on soil biota that could potentially lead to negative PSF. For example, Meinhardt & Gehring (2012) showed that the presence of *Tamarix* reduced the colonization of neighbouring *Populus* trees by beneficial arbuscular mycorrhizal fungi (AMF), and Moseman et al. (2009) found altered diversity and activity of nitrogen-fixing bacteria in *Tamarix*-invaded wetlands.

**Methods**

**Site descriptions and soil collection**

Three replicate sites were selected along each of three water bodies with contrasting hydrology in Montana: the dam-controlled Bighorn River, which experiences annual flooding; the unregulated Yellowstone River, which also floods annually but with higher flow than the Bighorn River; and the Fort Peck Reservoir, which has fluctuating water levels (Fig. 1). The Bighorn River sites included the public access points of Arapooish, General Custer and Grant Marsh. The Yellowstone River sites included the public access points of Bundy Bridge, Duck Creek Bridge and Isaac Homestead. Finally, the Fort Peck Reservoir sites included the Dam, Dry Arm and Sand Arroyo. The oldest living *Tamarix* trees at the Yellowstone, Bighorn River and Fort Peck Reservoir sites were 23, 37 and 15 yr respectively (Lehnhoff et al. 2011). At each of these sites we selected two subsites – one with *Tamarix* present and one without *Tamarix*. Vegetation at the adjacent subsites was similar, with invaded subsites with *Tamarix* simply adding to the species richness but not otherwise changing species composition or diversity (Lehnhoff et al. 2012). At each subsite, 20 aliquots of soil, including the overlying plant litter, were collected with a shovel at randomly located positions to a depth of 15 cm and placed into two 18.9-L plastic
buckets. At the subsites with *Tamarix* present, soil was collected directly under *Tamarix* trees, where there was generally no other vegetation present. Composite soil samples from each subsite were collected from the buckets and analysed for organic matter (OM), nitrate (NO$_3^-$), phosphorus (P) and potassium (K$^+$) concentrations. In a previous study, samples were also collected and analysed for electrical conductivity (EC), pH, calcium (Ca$^{2+}$), K$^+$, sodium (Na$^+$) and magnesium (Mg$^{2+}$), and the sodium adsorption ratio (SAR) was calculated. These data were previously reported in Lehnhoff et al. (2012; Table 1).

Buckets of soil were taken to the Montana State University Plant Growth Center (PGC) and kept in cold storage (12.8 °C) until the experiments began ca. 4 wk later.

**Plant growth in field-collected soils**

The species for this study were all mycorrhizal and included (1) four grasses – *Leymus cinereus* (Scribn. & Merr.) A. Love (basin wildrye), *Achnatherum hymenoides* Roem. & Schult. (Indian ricegrass), *Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould subsp. *Lanceolatus* (thickspike wheatgrass) and *Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass), and (2) four forbs – *Ratibida columnifera* (Nutt.) Woot. & Standl. (stillwater prairie coneflower), *Astragalus cicer* (Cic-er milkvetch), *Trifolium pratense* L. (red clover) and *Dalea candida* (Michx.) ex Willd. (antelope prairie clover). Except for *T. pratense*, all species are indigenous to Montana and all of them are commonly used for restoration. The four grasses are specifically recommended by the Montana Natural Resources Conservation Service for re-vegetation of *Tamarix*-invaded areas in Montana (USDA 2010), and the forbs are commonly used in restoration of prairie sites that are similar to areas above the typical river high water levels and in the reservoir drawdown area. Seeds for all species were obtained from the Bridger Plant Materials Center in Bridger, Montana.

To evaluate the germinability of seeds, 20 seeds of each species were placed on germination paper (regular weight blue paper; Anchor Paper Co., St. Paul, MN, USA) in 11 × 11 × 3.5 cm germination trays, with three replicates for each species. The trays were covered with lids, kept in the greenhouse in ambient light and at temperatures of 21 °C (day, 16 h) and 16.5 °C (night, 8 h), and the germination paper was moistened daily with distilled water. The total number of germinants in each tray was recorded at 11 d.

The growth study evaluated the joint biologically and chemically mediated impacts of *Tamarix* on plant seedling emergence and growth. Eight plant species were grown in soils collected from the nine field sites (18 subsites) as a complete block, randomized design to assess the species’ potential for restoration planting at *Tamarix*-invaded areas. For these experiments, subsite soils were individually placed into 3.8-cm diameter by 21-cm deep pots (Ray Leach ‘Cone-tainer’, model SC10, hereafter ‘conetainer’), with four replicates for each species-subsite combination. Five seeds were planted per conetainer, daily seedling emergence was recorded, and seedlings were subsequently thinned to one per pot. Plants were grown for 10 wk in the PGC with ambient light and temperatures of 21 °C (day, 16 h) and 16.5 °C (night, 8 h), and watered three times daily with an automatic misting system. Plants were then removed from the conetainers, washed over a screen to remove soil from the roots, and the above- and below-ground portions of the plants placed separately into envelopes for drying. Plant material was dried at 40 °C for 1 wk and weighed to the nearest 0.001 g.

Seed germinability was calculated as the mean number of seeds that had germinated at the end of 11 d. For seeds in conetainers, the mean time (days) to >50% emergence was calculated as in Menalled et al. (2005) to provide a relative assessment of species emergence times in different soils, with the assumption that earlier emerging species would have a competitive advantage over undesirable weedy species at restorations sites. Effects of the different soils on seedling emergence were evaluated with a nested ANOVA with subsite nested within water body. The ratio of above- to below-ground biomass, i.e. shoot to root ratio (S:R), was calculated as the shoot biomass divided by root biomass.

![Soil collection locations on the Fort Peck Reservoir, Bighorn River and Yellowstone River sites in Montana, USA.](image-url)
biomass. Nested ANOVA models were also used to evaluate plant biomass and S:R, and data were log transformed prior to analysis to meet the assumptions of normality. All data analyses were performed in R (R version 2.12.1; R Foundation for Statistical Computing, Vienna, AT).

Plant-soil feedback

The PSF study addressed the *Tamarix* biologically mediated effects on plant growth. The study was conducted as a complete block, randomized design with soil from the 18 subsites, two soil treatments, two plant species, two plant harvest times and four replicates. One half of the soil from each subsite was steam-pasteurized (Lindig soil treatment system, 1 h at 70 °C) and the other half was untreated. Pots (10-cm base, 16-cm top, 41-cm high; I.E.M. Plastics, Reidsville, NC, US) were filled with a 1:1:1 mix of mineral soil, Canadian sphagnum peat moss and washed sand, all pasteurized. All pots were then inoculated with the field soil, with half of them randomly receiving steamed soil and the other half untreated soil. Soil inoculation was conducted by mixing 69 cm³ (ca. 1% of the pot volume) of the field-collected soil within the top 2 cm of the greenhouse soil mix and then watering. The small amount of inoculum was used to avoid altering the chemical properties of the greenhouse soil, while adding the soil microbiota occurring at the field subsites. Pots were then planted with seeds of either the forb *D. candida* or the grass *P. smithii*. Greenhouse conditions were maintained at 23.9 °C (day, 16 h) and 20 °C (night, 8 h), with light supplemented with mercury vapour lamps (165 μmol·m⁻²·s⁻¹). To assess changes in relative growth rate as a function of PSF, half of the plants were harvested at 55 d after planting and the remaining plants were harvested at 80 d after planting.

The shoot to root ratio, S:R, was calculated as above, and relative growth rate (RGR) was calculated as:

\[
RGR = \frac{\ln(B_2) - \ln(B_1)}{T_2 - T_1}
\]

where \(B_1\) was the total biomass (both roots and shoots) at the initial harvest, \(B_2\) was the total biomass at the final harvest, \(T_1\) is the number of days until the initial harvest, and \(T_2\) is the number of days until the final harvest. Total biomass and S:R were log transformed prior to analysis to meet the assumptions of normality. Differences in S:R, RGR and total biomass across soil treatments and species with subsites nested within water bodies were evaluated

<table>
<thead>
<tr>
<th>Soil parameter</th>
<th>Tamarix status</th>
<th>Water body</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fort peck reservoir</td>
<td>Bighorn river</td>
</tr>
<tr>
<td>2009 soil samples</td>
<td></td>
<td></td>
</tr>
<tr>
<td>EC (dS·m⁻¹)</td>
<td>Absent</td>
<td>0.48 (0.21)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0.97 (0.78)</td>
</tr>
<tr>
<td>pH (standard units)</td>
<td>Absent</td>
<td>7.84 (0.31)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>7.77 (0.32)</td>
</tr>
<tr>
<td>Ca²⁺ (mmol l⁻¹)</td>
<td>Absent</td>
<td>1.96 (1.37)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>5.32 (6.60)</td>
</tr>
<tr>
<td>K⁺ (mmol l⁻¹)</td>
<td>Absent</td>
<td>0.56 (0.36)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>1.02 (0.75)</td>
</tr>
<tr>
<td>Na⁺ (mmol l⁻¹)</td>
<td>Absent</td>
<td>1.17 (1.25)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0.95 (0.75)</td>
</tr>
<tr>
<td>Mg²⁺ (mmol l⁻¹)</td>
<td>Absent</td>
<td>1.05 (0.61)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>2.89 (3.43)</td>
</tr>
<tr>
<td>SAR</td>
<td>Absent</td>
<td>1.29 (1.79)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0.52 (0.38)</td>
</tr>
</tbody>
</table>

2010 soil samples

| SO₄²⁻ (mg·kg⁻¹) | Absent | 3.50 (1.80) | 11.17 (1.89) | 2.83 (1.53) |
|                | Present | 18.67 (27.15) | 24.67 (2.52) | 14.83 (15.46) |
| K⁺ (mg·kg⁻¹)   | Absent | 229.67 (111.38) | 281.33 (100.07) | 150.33 (51.03) |
|                | Present | 224.67 (57.47) | 530.00 (83.86) | 220.67 (85.34) |
| P (mg·kg⁻¹)    | Absent | 4.00 (2.00) | 6.67 (0.58) | 6.67 (3.06) |
|                | Present | 6.33 (4.93) | 27.00 (4.00) | 9.00 (2.65) |
| OM (%)         | Absent | 1.20 (0.36) | 2.50 (0.79) | 0.77 (0.21) |
|                | Present | 1.37 (0.21) | 3.37 (1.66) | 1.07 (0.64) |

Means are presented with SD in parentheses. Bold indicates significant differences (\(P = 0.05\)) of soil property between *Tamarix*-occupied and unoccupied subsites. Data adapted from: Lehnhoff et al. (2012).
with generalized linear models (GLMs) because of missing values (i.e. plants that did not grow). Model simplification was implemented by removing non-significant terms and conducting ANOVA between the models with a Chi-squared distribution. If the P-value was >0.05, the test indicated that removing the terms did not decrease the model’s explanatory power, and the simpler model was retained.

Results

Plant growth in field-collected soil

From the germination test, the percentage (±SD) of seeds that germinated for each species at 11 d was: L. cinerex, 41.7 ± 17.6; A. hymenoides, 0.0 ± 0.0; E. lanceolatus, 30.0 ± 13.2; P. smithii, 28.3 ± 7.6; D. candida, 45.0 ± 0.0; A. cicer, 3.3 ± 2.9; T. pratense, 58.3 ± 7.6; and R. columnifera, 95.0 ± 0.0. The fact that A. hymenoides did not germinate in the germination test (which was conducted on germination paper rather than soil) indicated that the seeds were either dormant or had very low viability. A. hymenoides also exhibited very poor emergence across all subsites in subsequent experiments; therefore, data for this species were not included in further analysis. A. cicer also had low germination at 11 d, but more seeds germinated over time (data not shown); therefore it was included in further analysis.

For the number of days to 50% emergence of seedlings in the containers, the three-way interaction of species, water body and subsite (i.e. the presence or absence of Tamarix) was significant ($F_{18,462} = 2.43, P = 0.001$). To investigate these complex interactions, the species at individual water bodies were examined separately. Only L. cinerex ($F_{1,22} = 337.5, P = 0.011$) and D. candida ($F_{1,22} = 580.2, P = 0.004$) at the Bighorn River, and D. candida ($F_{1,22} = 408.4, P = 0.023$) at Fort Peck Reservoir exhibited differences in emergence time between subsites, emerging a mean of 7.5, 9.8 and 8.3 d earlier, respectively, in soil from subsites with Tamarix present.

Plants grown in soil from sites where Tamarix was present generally had a higher S:R and produced more total biomass than those grown in soil from subsites where Tamarix was absent (Table 2), although there were interactions between species and water bodies (Table 3). Again, to explore these interactions, species at individual water bodies were examined separately. At the Bighorn River, D. candida ($F_{1,20} = 7.76, P = 0.011$) and T. pratense ($F_{1,22} = 12.75, P = 0.002$) allocated more resources to above-ground biomass in soil collected from subsites with Tamarix present, while the allocation pattern was the opposite for A. cicer ($F_{1,21} = 5.12, P = 0.034$) at the Yellowstone River. At Fort Peck Reservoir, all species except T. pratense ($F_{1,21} = 0.17, P = 0.684$) allocated more resources to above-ground biomass in soils from subsites with Tamarix.

At the water body level, with all species included, more biomass was produced in soil from subsites where Tamarix was present than where it was absent for all three water bodies, but the difference was higher at Fort Peck Reservoir (+147%) than at the Bighorn (+68%) or Yellowstone Rivers (+50%) (Table 2). At Fort Peck Reservoir, S:R was also higher at the subsites with Tamarix than at those without it.

For individual species, more total biomass was produced in soils from subsites with Tamarix at the Bighorn River for L. cinerex ($F_{1,22} = 18.10, P < 0.001$), E. lanceolatus ($F_{1,22} = 7.84, P = 0.010$), P. smithii ($F_{1,22} = 13.05, P = 0.002$) and A. cicer ($F_{1,19} = 17.40, P = 0.001$) than from subsites where Tamarix was absent. At the Yellowstone River, A. cicer ($F_{1,21} = 15.49, P = 0.001$), R. columnifera ($F_{1,21} = 8.80, P = 0.007$), L. cinerex ($F_{1,22} = 18.26, P < 0.001$) and E. lanceolatus ($F_{1,22} = 18.86, P < 0.001$) also produced more biomass in soils from subsites with Tamarix. This same pattern was true at Fort Peck Reservoir for T. pratense, R. columnifera, L. cinerex, E. lanceolatus and P. smithii. For soils only from subsites where Tamarix was present, species biomass production differed by water body ($F_{2,228} = 47.03, P < 0.001$), with biomass generally being the highest at the Bighorn River, although there were interactions between site and species ($F_{12,228} = 4.52, P < 0.001$; Fig. 2). Within water bodies at Tamarix-present subsites, there were few differences in species performance, although T. pratense produced more biomass than the other species at the Bighorn ($F_{6,75} = 7.21, P < 0.001$) and Yellowstone River ($F_{6,77} = 11.86, P < 0.001$) sites, and D. candida produced less biomass than E. lanceolatus or P. smithii ($F_{6,76} = 3.00, P = 0.011$) at Fort Peck Reservoir (Fig. 3).

Plant-soil feedback study

The ANOVA comparisons between RGR models indicated that removing interaction terms between subsite (Tamarix presence or absence) nested within water body and steam pasteurization and species did not reduce the explanatory power of the model ($P = 0.603, d_{full \ model} = 145, d_{reduced \ model} = 160$), and thus the simpler model was retained. Removing steam pasteurization from the simplified model reduced its explanatory power ($P = 0.040, d_{model \ without \ steam} = 162$), indicating that steam pasteurization of soil inoculum affected RGR. Pasteurization of the soil increased RGR ($P = 0.020$) from 0.064 to 0.084 g g$^{-1}$ d$^{-1}$, suggesting that soil microbes negatively affected plant RGR. However, the lack of significance in interaction terms indicated that the presence or absence of Tamarix at subsites did not affect the growth of either species when soil from the subsites was used as inoculum for greenhouse soils. ANOVA results for S:R models showed that neither steam pasteurization ($P = 0.140$,
interaction terms (\(\text{biomass, with non-significant steam pasteurization}\) of cate that soils from subsites with and without the presence
restoration plant species (ANOVA table for shoot to root ratio (S:R) and total biomass of
Table 3. ANOVA table for shoot to root ratio (S:R) and total biomass of
restoration plant species (Dalea candida, Leymus cinereus, Astragalus cicer, Trifolium pratense, Ratibida columnifera, Elymus lanceolatus and
Pascopyrum smithii) grown in soil collected from subsites with or without
Tamarix at three water bodies (Bighorn River, Fort Peck Reservoir and
Yellowstone River).

<table>
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<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum squares</th>
<th>Mean square</th>
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<tr>
<td>S:R</td>
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<td>Species</td>
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<td>Water body × soil</td>
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<td>3,303</td>
<td>1,101</td>
<td>11.935</td>
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<td>Species × soter body</td>
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<td>1,987</td>
<td>0.166</td>
<td>1.795</td>
<td>0.047</td>
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<td>0.126</td>
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<td>41,512</td>
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<td>Total biomass</td>
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<td>Water body × Soil</td>
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<td>Species × water body</td>
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<td>Residuals</td>
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<td>173,325</td>
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</table>

The interaction terms (\(P = 0.626, \text{model without steam} = 145, \text{model } = 160\)) were significant. Results were similar for total biomass, with non-significant steam pasteurization
\((P = 0.893, \text{model with steam} = 160, \text{model without steam} = 162)\) and the interaction
\((P = 0.502, \text{model } = 145, \text{model } = 160)\) terms. These results indicate
that soils from subsites with and without the presence of Tamarix did not have different effects on plant S:R or
total biomass growth.

Discussion

Plant growth results from the conetainer experiment are not consistent with the hypothesis that plants grown in Tamarix-affected soil would grow more poorly than in
non-affected soil; rather, they indicate either that Tamarix conditioned the soil in a manner to make it more suitable
for growth of other plants, or that Tamarix had colonized and occupied more fertile soils. The former possibility is
supported by numerous studies showing that NIS have legacy
effects on soils (Ehrenfeld 2010). For example, N-fixing
NIS can alter ecosystem nutrient dynamics by directly
increasing nutrient levels (Vitousek Walker 1989), litter
decomposition rates can be increased (Liao et al. 2008)
providing more nutrients, and soil chemistry can be
changed through altered pH or redistribution of salts from the
lower soil profile (Vivrette Muller 1977; Conser Connor
2009). Soil samples collected from the subsites
(Table 1) showed that concentrations of NO\(_3^-\), K\(^+\) and P at the
Bighorn River, and Ca\(^{2+}\), K\(^+\) and Mg\(^{2+}\) from the Fort Peck Reservoir,
were over twice as high at subsites with Tamarix
than without it. Yellowstone River soils showed a similar
pattern of nutrient concentrations between Tamarix
present and absent sites, although the results were not statistically
significant. Higher nutrient concentrations under
Tamarix stands have been observed by others (Bagstad et al. 2006; Xu et al. 2006; Yin et al. 2010) and may
explain differences in plant growth in our conetainer
study. Native plant species germination and growth in
Tamarix-affected soils may be negatively affected by elevated
soil salinity [measured as electrical conductivity (EC)]. For example, plant communities separated along salinity
gradients (EC up to 15 and 12.8 dS m\(^{-1}\)) in north-central

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Tables

Table 2. Mean ratio of shoots to roots (S:R) and total biomass produced by plants grown in soils from subsites with or without Tamarix present.

<table>
<thead>
<tr>
<th>Species</th>
<th>S:R</th>
<th>Total Biomass [g]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tamarix absent</td>
<td>Tamarix present</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dalea candida</td>
<td>1.27 (0.36)</td>
<td>0.10 (0.05)</td>
</tr>
<tr>
<td>Leymus cinereus</td>
<td>0.92 (0.36)</td>
<td>0.07 (0.05)</td>
</tr>
<tr>
<td>Astragalus cicer</td>
<td>1.41 (0.58)</td>
<td>0.07 (0.05)</td>
</tr>
<tr>
<td>Trifolium pratense</td>
<td>1.25 (0.49)</td>
<td>0.12 (0.09)</td>
</tr>
<tr>
<td>Ratibida columnifera</td>
<td>0.66 (0.22)</td>
<td>0.12 (0.09)</td>
</tr>
<tr>
<td>Elymus lanceolatus</td>
<td>0.91 (0.34)</td>
<td>0.12 (0.08)</td>
</tr>
<tr>
<td>Pascopyrum smithii</td>
<td>0.90 (0.32)</td>
<td>0.10 (0.06)</td>
</tr>
<tr>
<td>Combined vegetation</td>
<td>1.04 (0.46)</td>
<td>0.12 (0.12)</td>
</tr>
<tr>
<td>Water body differences</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bighorn river</td>
<td>1.16 (0.43)</td>
<td>0.19 (0.16)</td>
</tr>
<tr>
<td>Yellowstone river</td>
<td>1.09 (0.50)</td>
<td>0.10 (0.10)</td>
</tr>
<tr>
<td>Fort peck reservoir</td>
<td>0.87 (0.39)</td>
<td>0.07 (0.03)</td>
</tr>
</tbody>
</table>

SD in parentheses; bold indicates significant biomass differences \((P \leq 0.05)\) between Tamarix-occupied and -unoccupied subsites.
Utah and on the Colorado River, respectively (Carman & Brotherson 1982; Busch & Smith 1995). However, EC levels at the water bodies we studied were all less than 2.0 dS·m⁻¹, which is considered below the level at which plants experience detrimental effects (Taylor & McDaniel 1998). In accordance, seedling emergence in our study
soils are more affected by Tamarix invaded soils. Results from the PSF study indicated that negative feedbacks from Tamarix on the growth of native species did not exist. PSF may be observed deeper in the soil profile where soils are more affected by Tamarix roots than by plant litter. However, PSF in the 0–15 cm depth that we investigated are more directly related to restoration, as this is the depth important for initial establishment and subsequent rooting of the forb and grass restoration species. The results generally indicated that any biological differences in the soil between sites where Tamarix was present and absent were not enough to stimulate differences in plant growth. A biological factor that could potentially alter plant growth is the presence or absence of AMF in the soil. Pringle et al. (2009) showed that plant–mycorrhizal symbioses are affected by NIS, with implications for the plant-soil ecosystems including alteration of the microbial community (Mummey & Rillig 2006), influences on nutrient availability, and disruption of symbiosis (Stinson et al. 2006). Beauchamp et al. (2005) showed that Tamarix is non-mycotrophic, suggesting that sites occupied by Tamarix would have lower levels of AMF propagules. Lehnhoff et al. (2012) found that soils with Tamarix present had reduced numbers of mycorrhizal propagules in the soil, although this did not appear to cause differences in plant growth in this study.

Our study addressed Tamarix impacts on soil chemistry and microbially mediated PSF, and results indicated that all species studied (with the exception of A. hymenoides, which had poor germination) would be suitable for restoration planting in Tamarix-impacted soil. However, water body differences in soil and hydrology may also be important in species success. Nutrient concentrations were generally higher at the Bighorn River than at the other water bodies (Lehnhoff et al. 2012), and these differences could be driving the biomass differences observed. Site hydrology, and specifically water availability during the growing season, was not addressed in this study, but should be considered when choosing restoration plant species. Bay & Sher (2008) showed that proximity to perennial water was an important factor in establishment of native species in Tamarix site restoration. In sites located at a considerable distance from perennial water, such as at the Fort Peck Reservoir when the reservoir is in a period of drawdown, drought-tolerant species would be required for restoration. Flood-tolerant species would be necessary for the free-flowing systems such as the Yellowstone River. Along the dam-controlled Bighorn River, where flooding does not occur annually, a mix of drought- and flood-tolerant species may be more appropriate. In future research, the species used in this study should be tested at field sites to evaluate their performance.

Finally, it should be recognized that Tamarix is a relatively new invader in the northern and northwestern USA, being present in Montana for ca. 50 yr, and for only 15–37 yr at the study sites, so the time Tamarix has had to affect soils is limited. Soil impacts, including both chemical and PSF, could be important factors in the future. Nonetheless, with the annual flooding of the Yellowstone River, the periodic flooding of the Bighorn River and the periodic rise and fall of the water level in Fort Peck Reservoir, Tamarix effects on the soil are expected to be minimal as compared with rivers in the southwestern USA where stream flow patterns have been greatly altered and flows reduced (Stromberg et al. 2007). Overall results indicate that Tamarix-affected soil does not inhibit the growth of other plant species at sites in its northern range where it is a relatively new invader.

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