



Original Research

Sodium Chloride Effects on Seed Germination, Growth, and Water Use of *Lepidium alyssoides*, *L. draba*, and *L. latifolium*: Traits of Resistance and Implications for Invasiveness on Saline Soils[☆]

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ABSTRACT

In the semiarid southwestern United States, long-term drought, soil salinity, and land-use intensification have increased the risk of invasive plants that threatens landscape biodiversity. Soil-related factors that regulate plant invasions are not adequately known. We evaluated the salinity responses of three invasive plant species during a 3-mo plant growth period in a greenhouse and during a 2-wk seed germination study in the laboratory. The species included the indigenous *Lepidium alyssoides* A. Gray var. *alyssoides* (mesa pepperwort) and the exotic, invasive *L. draba* L. (whitetop) and *L. latifolium* L. (perennial pepperweed). A NaCl solution at -0.2 MPa reduced germination of *L. alyssoides* by $\approx 20\%$ and had no effect on germination of *L. draba* and *L. latifolium*, merely delaying their mean germination time by a day or less. Reductions in seedling dry matter production and evapotranspiration (ET) were observed following irrigation with NaCl solutions at -0.1 MPa and -0.2 MPa. However, on the basis of ET and total plant dry matter production under common experimental conditions, the salt resistance of these species greatly exceeded that of salt sensitive bean (*Phaseolus vulgaris* L.) and equaled or exceeded that of salt-resistant cotton (*Gossypium hirsutum* L.). Below-ground propagating structures giving rise to clonal shoots were observed for all *Lepidium* spp., consistent with other reports. The results indicate that vegetative propagule pressure and relatively high resistance to salinity at germination and seedling growth stages could contribute to the invasiveness of these species under saline conditions. A broader impact of the findings is in their application to the larger diversity of invasive species to aid in the understanding of soil salinity and how it may govern plant invasions. This dataset could improve risk assessment measures to favor biodiversity in rangelands and natural ecosystems of semiarid regions.

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Introduction

Invasive plants are typically nonindigenous and can displace native vegetation, reduce biodiversity, degrade ecosystems, and infest farmlands (Randall, 1996; DiTomaso, 2000; Sheley et al., 2011). Throughout the western United States, non-native plant species have been reported to occupy about 50% of total land area (Herrick et al., 2010). Anthropogenic disturbances including increased urbanization and land use intensification have increased the risk of invasive plant species in semiarid lands

of the southwestern United States (Abella et al., 2012; Belnap et al., 2012; Hobbs and Huenneke, 1992). In semiarid regions, increased demand for irrigation due to population increases and climate change have increased secondary salinization (Yeo, 1999), which in the southwestern United States may alter plant species diversity (Cox et al., 2006).

To successfully and cost-effectively manage the spread of invasive plants, a preventative strategy that incorporates early detection and prediction of new invasions must be adopted by land managers (Davies and Sheley, 2007; Abella et al., 2009; Davies and Johnson, 2011). However, the biology of the invaders, as well as factors that influence invasions, are not adequately known, which has limited the effectiveness of preventative management strategies (DiTomaso, 2000; Byers et al., 2002; Shea and Chesson, 2002; Suazo et al., 2012). Three herbaceous perennial plant species—*Lepidium alyssoides* A. Gray var. *alyssoides*, *L. draba* L., and *L. latifolium* L.—have been noted for their invasiveness and ability to grow on saline, sodic, or alkali soils (Francis and Warwick, 2007, 2008; Picchioni et al., 2012a, 2012b). *L. alyssoides* is indigenous to the

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southwestern United States (USDA-NRCS, 2017a), whereas *L. latifolium* and *L. draba* are Eurasian introductions to the United States and are considered as noxious, invasive species (Francis and Warwick, 2007; Andrew and Ustin, 2009; Cripps et al., 2009; Renz et al., 2012; USDA-NRCS, 2017b; USDA-NISIC, 2017). *Lepidium latifolium* has been a highly invasive weed species throughout the western United States since the 1980s (Francis and Warwick, 2007) and, as early as 2005, began to invade semiarid New Mexico (Renz and Wilson, 2005). Both *L. draba* and *L. latifolium* are known to infest rangelands (Kiemnec and Larson, 1991; Francis and Warwick, 2007) and are designated as noxious weeds in New Mexico (Cattaneo et al., 2011). The latter species have been described as rhizomatous perennials with significant underground propagule pressure and prolific seed production (Francis and Warwick, 2007, 2008; Leininger and Foin, 2009). Such characteristics of *L. alyssoides* have received no prior study, although based on our observations, this species possesses underground vegetative propagules (Hooks et al., 2018). Both *L. alyssoides* and *L. latifolium* have recently been found harboring an introduced invasive stink bug in New Mexico (Bundy et al., 2012).

L. alyssoides has received little study of any kind, although its ability to aggressively occupy a saline, alkaline, and sodic Chihuahuan Desert shrubland in favor of other indigenous herbaceous species has been demonstrated (Picchioni et al., 2012a, 2012b). This species tolerates a combined Na and Cl accumulation in leaves reaching 10% of dry weight with no signs of leaf injury, which is characteristic of halophyte species (Hooks et al., 2018). Salt tolerance of *L. latifolium* and *L. draba* is not a novel subject, but therein lies a problem. *Lepidium draba* (Mulligan and Findlay, 1974; Lyons, 1998; Francis and Warwick, 2008; Santa Margarita–San Luis Rey Weed Management Area, 2015) and *L. latifolium* (Renz and Blank, 2004; Francis and Warwick, 2007; Zhao et al., 2011) are reported to “be adapted,” to be “common” or “abundant,” or to be “common halophytes” on saline and alkaline soils. *Lepidium latifolium* is mentioned to be “suited to” germinate in sodic conditions (Larson and Kiemnec, 2005). Despite the claims, there is virtually no quantitative data to support these statements about *L. draba* and *L. latifolium*. Some of the reports provide only subjective or anecdotal observations, while others make claims by citing references that provide no quantitative data on salt or alkalinity resistance of *L. latifolium* and *L. draba*, such as in Corns and Frankton (1952), Weber (1989), Blank and Young (2002), Zouhar (2004), and Kadrmas and Johnson (2002).

Identification of habitat characteristics that enable invasive plant species to dominate vegetation communities is essential for developing analytical tools to improve land management practices (Hiebert, 1997). Soil salinity is an underappreciated subject in the vegetation science literature, particularly pertaining to its role in regulating plant invasiveness (Bui, 2013). Thus, assessments of soil salinity and sodicity could serve as analytical tools to predict plant invasions, thereby strengthening preventative measures to aid in management of invasive species. Lack of a quantitative salinity database on *Lepidium* spp. makes this taxon a good research model for understanding the association of soil salinity with plant invasions on semiarid lands. We hypothesize that soil salinity and sodicity may increase susceptibility to invasions by *L. latifolium*, *L. draba*, and *L. alyssoides*. That is, salinity may act as an environmental filter that can favor a species predisposed to rapid spread and aggressive growth (Grace, 2001; Shea and Chesson, 2002; Cox et al., 2006).

Our objective was to evaluate salinity responses of *L. latifolium*, *L. draba*, and *L. alyssoides* to aid in verifying their ability to infest salt-affected lands. Four independent studies were conducted during 2014–2015. Seed germination and plant growth responses of *L. alyssoides*, *L. draba*, and *L. latifolium* were assessed under saline and controlled environmental conditions. Because of a lack of plant salt resistance information on these *Lepidium* spp., we studied salt-sensitive *Phaseolus vulgaris* L. (common bean) and salt-resistant *Gossypium hirsutum* L. (upland cotton) as known agricultural crop standards (Maas and Hoffman, 1977; Francois and Maas, 1994) under common experimental conditions.

Materials and Methods

Seed Collection and Cleaning

Seeds of *L. alyssoides* were collected from a dense stand in southern New Mexico in June 2012 in the town of Mesquite (southern New Mexico; 106°41'W, 32°10'N; 1 200 m elevation). The low-lying site was previously affected by clearing of shrubland vegetation, land grading, road construction, and storm water diversion. Seeds of *L. draba* and *L. latifolium* were collected in July 2013 from plants growing prolifically in suburban agricultural areas near Los Lunas in central New Mexico. The *L. draba* collection site was south of Los Lunas along a weedy fence row (34°43'11"N, 106°43'48"W, 1 472 m elevation) while the *L. latifolium* collection site was north of Los Lunas along a weedy irrigation canal (34°49'47"N, 106°40'33"W, 1 481 m elevation). At the latter two sites, landscape alterations included storm water diversion and close proximity to managed farmland (*L. draba*) and access to surface water along with soil excavation (*L. latifolium*). At each site, seeds were collected from three to five evenly dispersed positions within an approximate 100 m² area densely populated by the parents. We removed the upper one-half of aboveground vegetation that included leaves, stems, flowers, and fruit (siliques) that bore the seeds. The vegetation was dried for 3 mo at room temperature, and the seeds were cleaned and stored following standard methods (Hooks et al., 2018). Seeds of ‘Contender’ common bean and Acala 1517-99 upland cotton required no pretreatment before use.

At each of the *Lepidium* sites, a single soil core (2.5 cm wide × 20 cm deep) was sampled per seed collection position (Hooks et al., 2018). The three to five cores were composited at each site, and the physical and chemical properties were analyzed using the online methods of the New Mexico State University Soil, Water, and Air Testing Laboratory (NMSU-SWAT, 2017). The purpose of the composite soil sampling was to only broadly characterize the edaphic conditions under which the *Lepidium* spp. proliferations were occurring.

Saline Treatments

For all studies, three salt treatments were used, consisting of NaCl at 0 mM (nonsaline control), 24 mM (−0.1 MPa; low salinity), and 48 mM (−0.2 MPa; high salinity). The electrical conductivities (ECs) of the low and high saline solutions met or exceeded soil saturation extract salinities in the previous reports that demonstrated invasiveness of *L. alyssoides* on the salt-affected Chihuahuan Desert shrubland (Picchioni et al., 2012a, 2012b). For the *Lepidium* spp. seed germination study, the salt treatments were prepared with deionized water (< 10 μS m^{−1}; pH 6.0) to provide ECs of 2.7 and 5.2 dS m^{−1} for the −0.1 MPa and −0.2 MPa treatments, respectively. For the plant growth studies, salt treatments were prepared in tap water (0.6 dS m^{−1}; pH 7.8) and included complete Hoagland’s nutrient solution 1 (Hoagland and Arnon, 1950) at half-strength (1.0 dS m^{−1}; pH 5.8). The tap water included (in meq L^{−1}) Na (2.8), Ca (2.4), Mg (1.0), Cl (0.5), SO₄ (4.0), and HCO₃ (1.8). The saline solution characteristics of the plant growth studies are shown in Table 1.

Seed Germination Study

The *Lepidium* spp. seed germination study was designed as a two-way, completely randomized design with four replications. The three salt treatments and three plant species served as the two factors, for a total of 36 experimental units (EUs), each consisting of a single 10-cm-wide × 1-cm-deep petri dish.

On 21 October, 2014, seeds of *L. alyssoides*, *L. draba*, and *L. latifolium* were placed in the petri dishes, each lined with a blotting paper (9-cm diameter, Anchor Steel Blue Seed Germination Blotter, Anchor Paper Co., Saint Paul, MN). The salt treatments were applied to the blotting paper in 5-mL volumes to reach complete saturation, and 50 seeds

Table 1

Composition and properties of the irrigation solution treatments used in greenhouse plant growth studies

Treatment	Concentration	EC	EC	SAR ³
	(mM)	(dS m ⁻¹) ¹	(dS m ⁻¹) ²	
Control	---	---	1.6	1.2
NaCl (-0.1 MPa)	23.8	2.3	3.9	11.7
NaCl (-0.2 MPa)	47.9	4.6	6.2	22.3

¹ Electrical conductivity due to salt (NaCl) only.² Electrical conductivity of irrigation solutions, including NaCl, half-strength Hoagland's complete nutrient solution, and tap water.³ Sodium adsorption ratio calculated as Na/(Ca + Mg)^{1/2}, all ions in mM.

were placed per dish unique to each species. The dishes were sealed with Parafilm (Bemis NA, Neenah, WI) and placed inside a sealed plastic bag to minimize evaporation loss of the treatment solutions throughout the duration of the study. The blotters did not require additional solution after initial wetting. The sealed dishes were then placed in a seed germination chamber (GR41VL, Percival Scientific, Inc., Perry, IA). The chamber provided a 16-hr photoperiod with fluorescent lighting at 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and light/dark temperatures of 26°C/15°C to approximate the greenhouse photoperiod and temperature conditions during the seed germination phase of the plant growth study that is described later. We did not determine the light requirements of *Lepidium* spp. seed, although germination occurred readily under the greenhouse conditions. Successful germination of a seed was determined by the presence of a visible radicle, and observations were made daily at approximately noon for a total of 2 weeks. Germination was recorded, and germinated seeds were removed from each of the dishes, which were then resealed and returned to the chamber.

The 2-wk germination study was terminated on 4 November, when nongerminated seeds were tested for viability using a 0.5% tetrazolium stain procedure (Miller and Peters, 2010). The number of viable seeds that had not germinated was counted in the 50-seed total. The number of nonviable seeds (<6% of total seeds) was deducted from the 50-seed total to provide the final assessments of percentage germination of only viable seed and mean germination time (MT) that was calculated after the methods in Ranal et al. (2009).

Comparative Plant Growth Studies

Three independent plant growth studies (*Lepidium* spp., bean, and cotton) were conducted in a greenhouse at the New Mexico State University Fabian Garcia Agricultural Science Center in Las Cruces from January to August 2014. A shade cloth to exclude 50% of the sunlight was installed atop the roof of the greenhouse on March 27 and remained in place throughout the remainder of the studies. Greenhouse weather data were collected using a Watchdog 2475 weather station and analyzed with SpecWare 9 Professional software (Spectrum Technologies Inc., Aurora, IL). Maximum temperature averaged 27–28°C, minimum temperature averaged 15–21°C, maximum photosynthetically active radiation (PAR) was 2032 $\mu\text{mol m}^{-2} \text{s}^{-1}$ before shade cloth installation and thereafter, maximum PAR was 653–779 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A constant 16-h photoperiod was maintained with supplemental lighting from metal halide lamps during 5–8 a.m. and 5–9 p.m.

On 27 January, seeds of *L. alyssoides*, *L. draba*, *L. latifolium*, and bean were sown in the greenhouse in 107-mL tubular, conical plastic grow cells measuring 3.7 cm in top diameter \times 14 cm in height (SC7 Ray Leach Cone-trainers, Stuewe and Sons Inc., Tangent, OR). The cells contained coarse silica sand that was first acid washed with 0.1 N H₂SO₄ and then thoroughly flushed with tap water. Seeds were sown by hand to a depth of 1 cm. Cotton seeds were sown identically but on 3 June due to a higher minimum temperature requirement for germination. For the *Lepidium* spp., three seeds were sown per cell and the cells were later thinned to a single plant. For bean and cotton, a single seed

was sown per cell. A total of 56 cells were seeded for all species. Small volumes of tap water were added to the sand surface until emergence.

After emergence, seedlings were established in the greenhouse by subirrigation in the nutrient solution without NaCl. The *Lepidium* spp. bore multiple whorls of true leaves 11 wk after sowing. Bean and cotton seedlings supported a well-expanded pair of true leaves within 3 wk and 5 wk, respectively. At these times, 27 established cells of each species were selected for saline irrigation treatments based on total cell weight and aboveground plant size to ensure uniform populations. The *Lepidium* spp. study was arranged as a two-way randomized complete block (RCB) with three replications and split plots, with saline treatment as the main plot and species as the subplot. The bean and cotton studies were laid out as single-factor RCB designs with three replications. Three plants in each of three separate cells represented one EU.

The saline irrigation treatments were applied April 24 to July 22 for the *Lepidium* spp. (89 d), February 18 to April 10 for bean (51 d), and July 9 to August 21 for cotton (43 d). These durations were sufficient to observe significant reductions in growth by salinity for all species. On the first day of irrigation, nine established plants per species that were not used in the saline irrigation treatments were harvested, divided into three, 3-plant groups, and dried at 60°C to determine initial dry weights of underground tissues and shoots per three plants. After weighing the 3-cell EUs, saline irrigation was supplied once daily to the sand surface using a syringe, and in an amount to replenish the depleted water while providing a targeted leaching fraction of 50% determined gravimetrically. In order to avoid water depletion of higher than 50%, irrigation to the *Lepidium* spp. was increased from once to twice daily starting from May 30 until termination of the study. No such adjustment was necessary for the bean and cotton plant growth studies. For the low and high saline solutions, 2-d stepwise increments of -0.05 MPa NaCl were applied initially and for the high saline solution of -0.2 MPa, the final osmotic potential was reached 7 to 8 d after treatment initiation.

The actual leaching fraction in percent (leachate volume divided by irrigation volume, times 100) and leachate EC were determined starting when maximum irrigation water salinity was reached. Leachate was collected at 2-wk intervals for the *Lepidium* study, 7- to 11-d intervals for bean, and 13- to 20-d intervals for cotton. Leachate EC was determined using a TechPro II TPH1 sensor (Myron L Co., Carlsbad, CA). Evapotranspiration (ET) was determined by daily weight change of the three-cell EUs. Cumulative and total ET were determined by summation of daily ET, and cumulative ET was plotted on a weekly basis.

At termination of saline irrigation, the aboveground tissues were cut at the sand surface and rinsed by hand in three consecutive deionized water baths (<30 $\mu\text{S cm}^{-1}$). The shoot tissues were blotted dry, and leaves were separated from stems. Bean plants had produced immature fruiting pods, which were saved along with leaves and stems. Underground tissues were then washed as described earlier for shoot tissues. The underground tissue of the *Lepidium* spp. consisted of true roots plus vegetatively propagating structures giving rise to clonal shoots, which could not be separated at harvest. Several reports on *L. latifolium* and *L. draba* cited previously have described these structures as both rhizomes and creeping roots; thus, we have found some discrepancy on their proper structural name (Hooks et al., 2018). The underground tissues of *Lepidium* were pooled and washed as described earlier. In cases where clonal shoots had egressed from the underground system, they were separated into leaves and stems, and those tissues were pooled with their counterpart aboveground leaf and stem fractions. The fresh tissues of all studies were taken to dryness at 60°C, and the dry weights were determined. The total plant dry weight (TDW) was determined by summation of the individual organ dry weights.

Statistical Analysis and Comparative Seedling Growth Assessments

For the *Lepidium* spp. seed germination, mean germination time, total ET, and tissue dry weights, the analysis of variance (ANOVA) was

performed using PROC GLM in SAS (version 9.3, SAS Institute, Cary, NC). Significance of saline treatment and species main effects, as well as the treatment x species interaction, were determined by F-tests. Where appropriate, main plot (saline solution) treatment means within subplots (species) and subplot means within main plots were separated by Duncan's multiple range test at an alpha of 0.05. For the bean and cotton plant growth studies, the ANOVA was applied for total ET and tissue dry weights, with significance of treatment evaluated by F-tests. Because of different experimental durations and dates for *Lepidium* spp., cotton, and bean, the ANOVAs were not incorporated.

During the plant growth studies of *Lepidium* spp., bean, and cotton, growing degree days (GDDs) were calculated as daily mean greenhouse air temperature ($^{\circ}\text{C}$) minus a base temperature of 10°C . Maintaining a constant base temperature was necessary to establish the same amount of heat accumulation for all species and thus to allow comparisons of total ET among all species. In the high salinity treatment (-0.2 MPa NaCl), bean shoots had expressed severe necrosis by 9 April (1 d before the termination of its experiment), corresponding to 506 GDD. Therefore, we determined the cumulative ET of all three experiments up to 506–508 GDD, which corresponded to 1, 8, and 43 d before the termination of saline irrigation on bean, cotton, and *Lepidium* spp., respectively. We also determined the total plant dry matter production of all studies (TDW) as percentages of the nonsaline (control) solution in the common experimental conditions.

Results

Soil Characteristics at the *Lepidium* spp. Seed Collection Sites

The composite soil samples from the *L. alyssoides* and *L. latifolium* sites had low saturation percentages ranging from ≈ 16 to 18 and low organic matter, from 0.8% to 1.2%, typical of their sandy to loamy sand texture (Table 2). Compositing soil from the *L. draba* site had a higher saturation percentage of 29 and around twice the organic matter (2.2%) as compared with the other two soils, and its texture was a loam. None of the three soils were saline (SSSA, 2008), with soil saturation extract ECs ranging from 1.6 to 2.4 dS m^{-1} , and Cl from 4.1 to 6.5 meq L^{-1} . The soils were slightly basic with pH ranging from 7.2 to 7.4 and were nonsodic (SSSA, 2008), with soil saturation extract SAR no higher than about 2. The *L. draba* site soil composite appeared to be the most fertile with $\text{NO}_3\text{-N}$, Olsen-P, and soluble K concentrations moderate to sufficient, while for the composite samples from the other two sites, there was low to moderate fertility on most agricultural crop standards (R. Flynn, personal communication).

Seed Germination

The treatment interacted with *Lepidium* species on germination percentage of viable seed measured at 2 wk ($P = 0.0029$). Germination of *L. alyssoides* declined from -0.1 MPa to -0.2 MPa , while that of *L. draba* and *L. latifolium* did not (Fig. 1A). Both main effects of species and treatment were significant ($P < 0.0132$), due largely to lower overall germination of *L. alyssoides* and its germination decline with high salinity.

Table 2

Soil characteristics of the seed collection sites of *L. alyssoides*, *L. draba*, and *L. latifolium*. Saturation percentage, pH, EC, SAR, and Cl were determined in the soil saturation extract; $\text{NO}_3\text{-N}$, Soluble K, and Olsen-P are expressed on a dry weight basis

Species	Texture	SP (%) ¹	OM (%) ²	pH	EC (dS m^{-1}) ³	SAR ⁴	Cl (meq L^{-1})	$\text{NO}_3\text{-N}$ (mg kg^{-1})	Soluble K (mg kg^{-1})	Olsen-P (mg kg^{-1})
<i>L. alyssoides</i>	Sand	15.8	1.2	7.2	1.6	1.7	4.1	17.3	76.5	9.4
<i>L. draba</i>	Loam	29.1	2.2	7.2	2.4	1.1	6.5	24.1	155.0	20.9
<i>L. latifolium</i>	Loamy Sand	18.1	0.8	7.4	2.1	1.0	5.3	5.7	107.0	12.3

¹ Saturation percentage.

² Organic matter.

³ Electrical conductivity.

⁴ Sodium adsorption ratio calculated as $\text{Na}/(\text{Ca} + \text{Mg})^{1/2}$, all ions in mM.

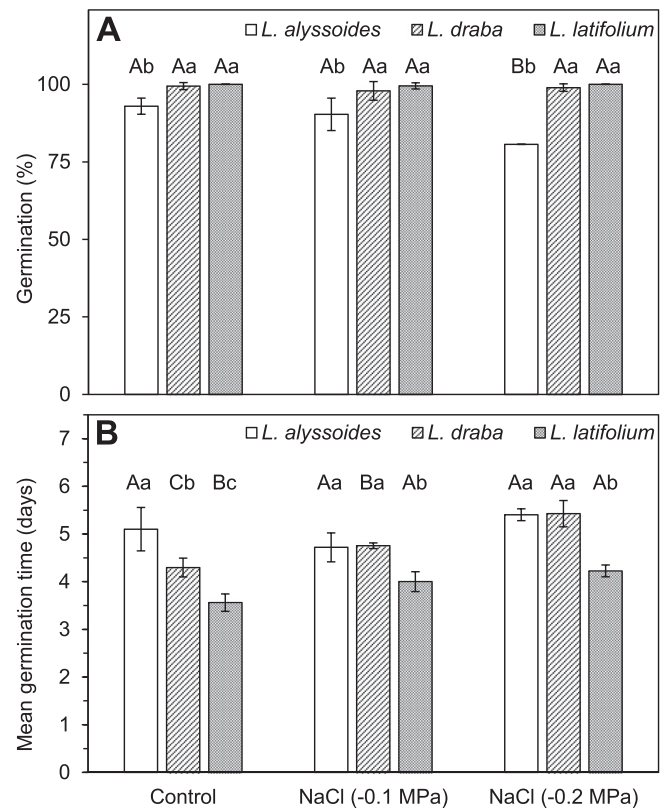


Figure 1. Percentage germination of viable seed (A) and mean germination time (MT; B) of *L. alyssoides*, *L. draba*, and *L. latifolium*. Each observation is the mean \pm SD of three replications; in a few cases (A), the SD is not visible. Within (A) or (B), means followed by different letters indicate significant difference according to Duncan's multiple range test ($P < 0.05$); upper case within species and across treatments, lower case within treatment and across species. For treatment composition and properties, see Table 1.

There was no salinity effect on mean germination time (MT) of *L. alyssoides*, but as salinity was increased, so was MT of *L. draba* and *L. latifolium*. These results contributed to a treatment by species interaction ($P = 0.0210$) and a treatment main effect ($P < 0.0001$; Fig. 1B). A species main effect ($P < 0.0001$) was associated with an overall shorter MT for *L. latifolium* as compared with longer overall MTs for *L. alyssoides* and *L. draba*.

Plant Growth Studies

Leachate Characteristics

For all irrigation solution treatments and experiments, actual (measured) leaching fraction averaged 40–54% across the measurement dates. In the *Lepidium* spp. study, leachate EC in the control, -0.1 MPa , and -0.2 MPa treatments averaged 2.2 ± 0.3 , 8.4 ± 0.8 , and $13.2 \pm 1.8\text{ dS m}^{-1}$, respectively (all species and across measurement dates). The analogous measurements for bean were 1.9 ± 0.1 , 8.0 ± 1.2 , and

10.6 ± 2.2 dS m⁻¹, respectively, and for cotton, 2.2 ± 0.1, 8.1 ± 0.4, and 16.4 ± 0.3 dS m⁻¹, respectively. There was some fluctuation in leachate EC across the measurement dates, as expected, but no observable trends of increasing or decreasing salinity over time. The average leaching fraction for bean at -0.2 MPa was relatively high (54%), which in turn, produced the leachate EC that averaged 20% lower than the *Lepidium* spp. average in that treatment. Conversely, the average leaching fraction for cotton at -0.2 MPa was relatively low (40%), which corresponded to the leachate EC that was 24% higher than the *Lepidium* spp. average in that treatment. Thus, we advise that the reader exercise caution for the ET and TDW comparisons between *Lepidium* spp. and cotton at -0.2 MPa, namely that cotton saline resistance may be underestimated when compared with *Lepidium* spp. for this high saline solution treatment. Nonetheless, ET and TDW comparisons between all species at low salinity (-0.1 MPa) may be made with

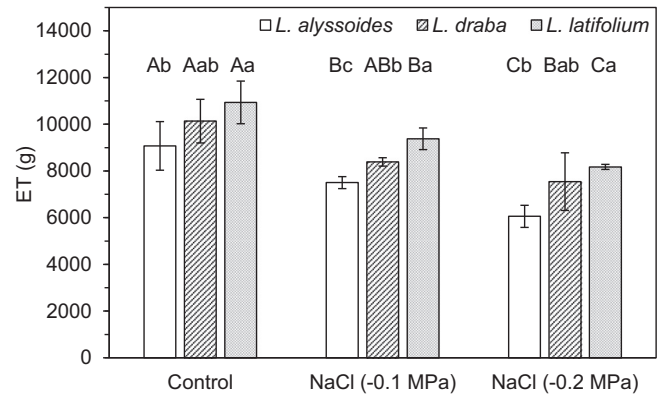


Figure 3. Total evapotranspiration (ET; grams per three plants) of *L. alyssoides*, *L. draba*, and *L. latifolium* throughout the 89-d experimental duration. Each observation is the mean ± SD of three replications. Means followed by different letters indicate significant difference according to Duncan's multiple range test ($P < 0.05$); upper case within species and across treatments, lower case within treatment and across species. For treatment composition and properties, see Table 1.

confidence considering the nearly identical average leachate ECs noted earlier; that is, within 4% of each other.

Evapotranspiration

Weekly cumulative ET of the *Lepidium* spp. increased steadily during the study (Fig. 2). The control plants had the highest cumulative ET, with incrementally suppressive effects of salinity (-0.1 MPa and -0.2 MPa) appearing at about 6–8 wk. For the final total ET (Fig. 3), there was no interaction between species and treatment ($P = 0.9123$) but there were treatment and species main effects ($P = 0.0200$ and $P < 0.0001$, respectively). In general, *L. latifolium* had the highest total ET in all

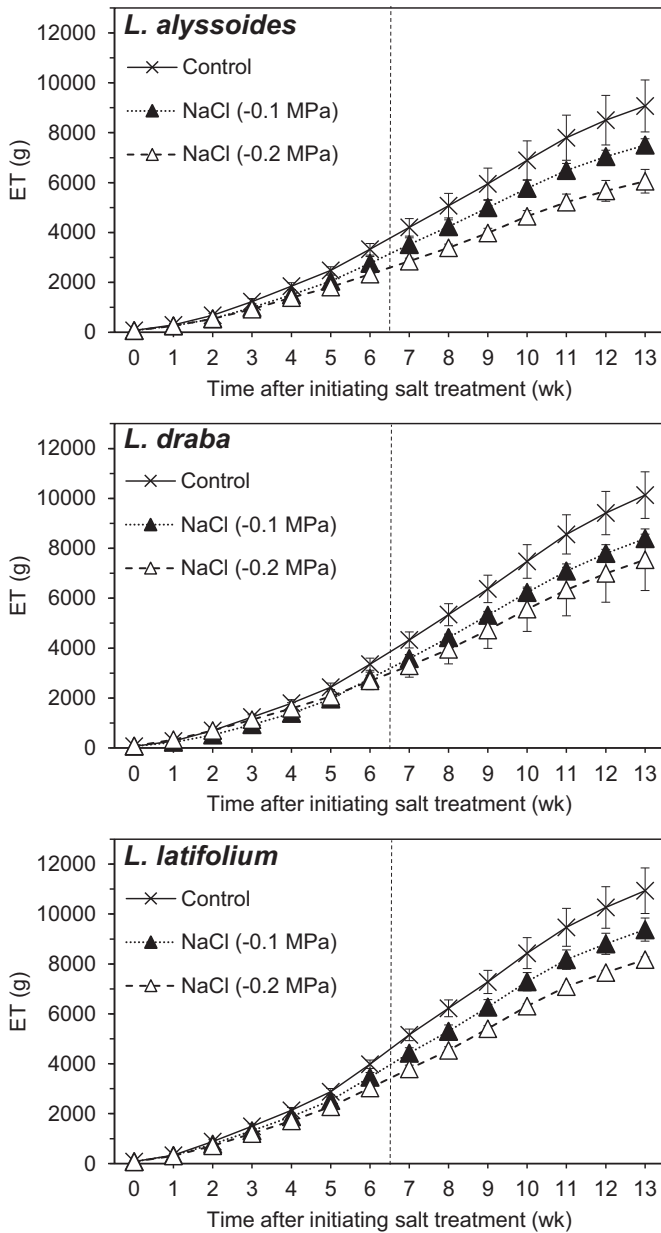


Figure 2. Cumulative evapotranspiration (ET; grams per three plants) of *L. alyssoides*, *L. draba*, and *L. latifolium*. Each observation is the mean ± SD of three replications; for some means, the SD is not visible. The vertical dashed line represents the time at which approximately 500 GDD accumulated, for comparisons to bean and cotton. For treatment composition and properties, see Table 1.

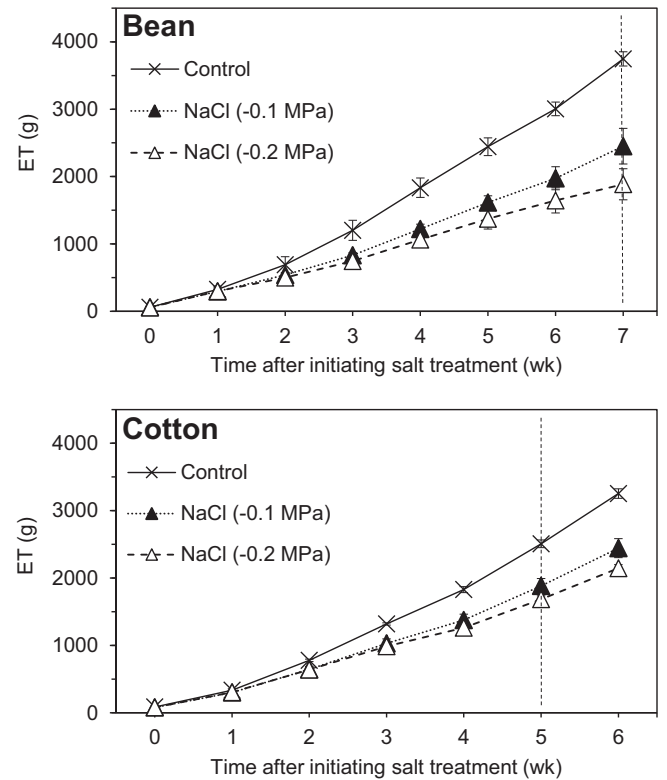


Figure 4. Cumulative evapotranspiration (ET; grams per three plants) of bean and cotton. Each observation is the mean ± SD of three replications; for some means, the SD is not visible. The vertical dashed line represents the time at which approximately 500 GDD accumulated, for comparisons to *Lepidium* spp. For treatment composition and properties, see Table 1.

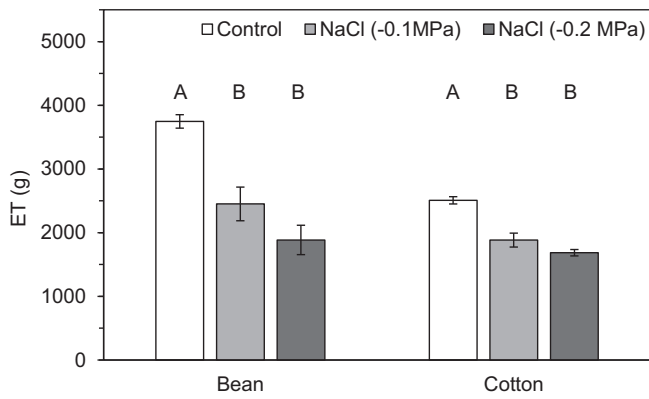


Figure 5. Total evapotranspiration (ET; grams per three plants) of bean and cotton at approximately 500 GDD. Each observation is the mean \pm SD of three replications. Data are from independent experiments, with means (within crop species) followed by different letters indicating significant difference according to Duncan's multiple range test ($P < 0.05$). For treatment composition and properties, see Table 1.

three treatments and *L. alyssooides* had the lowest, with *L. draba* intermediate. As with weekly cumulative ET, incremental effects of salinity (-0.1 MPa and -0.2 MPa) were also observed in the total ET, although for *L. draba*, only between the control and -0.2 MPa NaCl treatments.

Weekly cumulative ET of bean and cotton (Fig. 4) followed a similar pattern as with the *Lepidium* spp. After 2–3 wk, ET reductions by -0.1 MPa and -0.2 MPa NaCl became apparent and intensified thereafter. The irrigation treatment affected total ET of bean and cotton at 500 GDD ($P = 0.0022$ and 0.0007 , respectively), which was highest in the controls (Fig. 5). Total ET in the -0.1 MPa and -0.2 MPa treatments did not differ in either the bean or cotton studies, which reflected the relatively small

incremental suppressions in ET between -0.1 MPa and -0.2 MPa for most of the experimental durations (see Fig. 4).

Considering the ET at 500 GDD for all species and experiments together (*Lepidium* spp., bean, and cotton), we expressed their averages in the low and high salt treatments as percentages of their control treatment averages from the data in Figures 2 and 4. As expected, bean ranked the lowest in both -0.1 MPa and -0.2 MPa solutions (65% and 50% of the control, respectively). Cotton ranked in the middle (75% and 67% of the control, respectively), and the three *Lepidium* spp. ranked the highest (84–86% and 70%–79% of their controls, respectively).

Plant Dry Weights

At the initiation of saline irrigation to the *Lepidium* spp., underground tissue dry weights ranged from 0.21 to 0.51 g per three plants, and the shoot dry weights (leaves plus stems) ranged from 0.36 to 0.43 g per three plants. At termination of the study, there were significant main effects of treatment and species on leaf dry weight, underground tissue dry weight, and TDW ($P < 0.0228$). However, only the species main effect was significant for stem dry weight ($P < 0.0001$). Species interacted with the treatment on stem and underground tissue dry weight and on TDW ($P < 0.0421$), but not on leaf dry weight ($P = 0.6514$ and 0.0753 , respectively).

Leaf dry weight of all *Lepidium* spp. was highest in the control treatment (Fig. 6A) and comprised 26%–58% of TDW, depending on treatment and species. There was no decline in leaf dry weight of *L. alyssooides* or *L. draba* from -0.1 MPa to -0.2 MPa as there was for *L. latifolium*. Although leaf dry weight among the species did not show statistically significant differences within the latter treatments, *L. draba* tended to have the highest leaf dry weight in the control treatment.

Across the treatments, *Lepidium* stems comprised only 3–10% of TDW, depending on species (Fig. 6B). Regardless of the treatment,

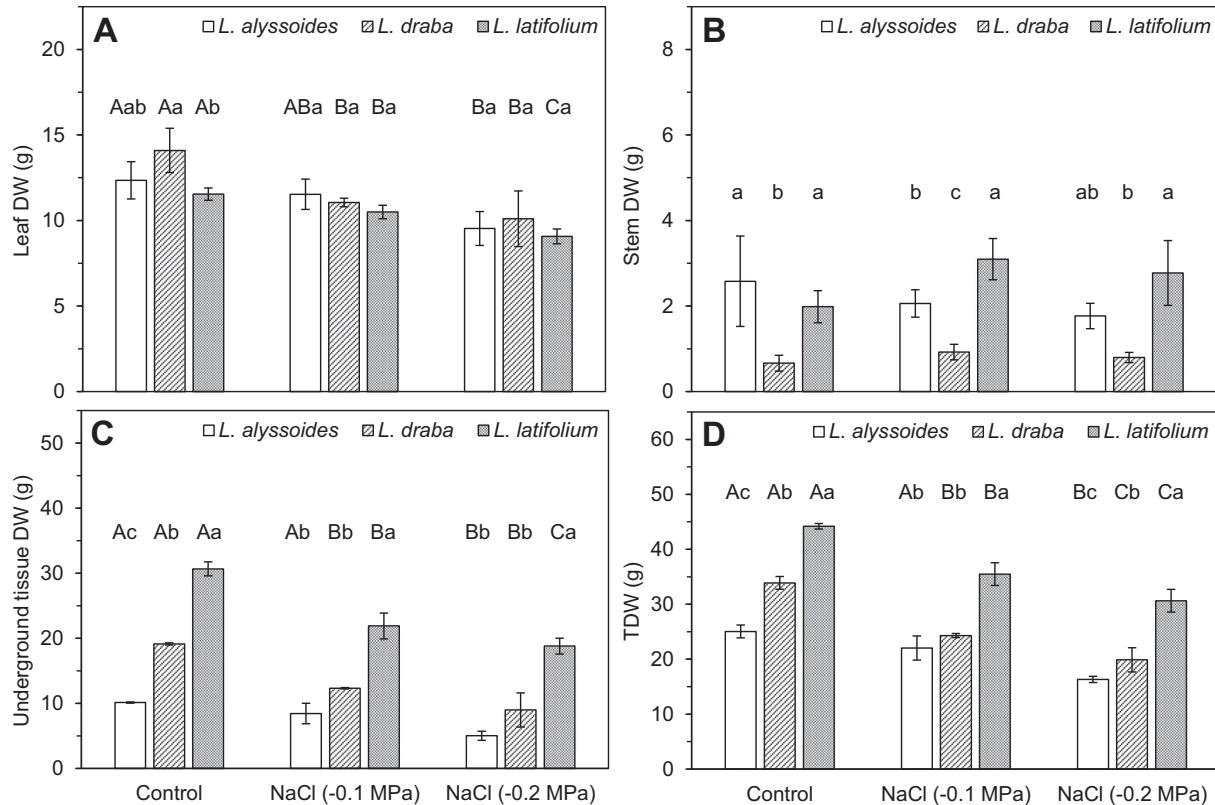


Figure 6. Leaf (A), stem (B), and underground tissue (C) dry weight (DW), and total dry weight (D;TDW) in grams per three plants of *L. alyssooides*, *L. draba*, and *L. latifolium*. Each observation is the mean \pm SD of three replications. The underground tissues consisted of both clonal vegetative propagating structures and true roots. Within (A), (B), (C), or (D), means followed by different letters indicate significant difference according to Duncan's multiple range test ($P < 0.05$); upper case within species and across treatments, lower case within treatment and across species. For treatment composition and properties, see Table 1.

L. draba had the lowest stem dry weight of all species. The treatment × species interaction on stem dry weight mentioned previously resulted from differential species responses between the control and −0.1 MPa treatments.

For all treatments, underground tissue dry weight comprised 66%, 50%, and 38% of TDW of *L. latifolium*, *L. draba*, and *L. alyssoides*, respectively. All *Lepidium* spp. produced underground propagating structures of various numbers and at various stages of budding within the sand medium or rising above the sand surface. The underground propagating structures of *L. latifolium* were substantially thickened, and this was reflected in the highest underground tissue dry weight of all the species (Fig. 6C). Underground tissue dry weight of *L. draba* and *L. latifolium* declined at −0.1 MPa salinity, whereas that of *L. alyssoides* declined only at −0.2 MPa salinity, leading to the treatment × species interaction noted earlier. At −0.2 MPa, there was an additional decline in *L. latifolium* underground tissue dry weight but not in *L. draba* underground tissue dry weight, which also contributed to the interaction.

Increasing salinity caused incremental declines in TDW of the *Lepidium* spp. that were lacking only at −0.1 MPa for *L. alyssoides* (Fig. 6D), leading to the treatment × species interaction reported previously. For all treatments, *L. latifolium* had the highest TDW, while *L. alyssoides* had the lowest TDW except at −0.1 MPa salinity, for which its TDW did not differ from that of *L. draba*.

Before saline irrigation to bean, the initial root dry weight averaged 0.54 g per three plants and the total shoot dry weight (leaves plus stems) averaged 0.55 g per three plants. At the end of the study, there was a treatment effect of salinity on leaf, stem, and root dry weight and on TDW ($P < 0.0119$; Fig. 7A). However, treatment did not affect fruit dry weight ($P = 0.2523$), which was highly variable in the control and −0.1 MPa treatments. Discounting the fruit, individual organ weights and TDW were highest in the control treatment with

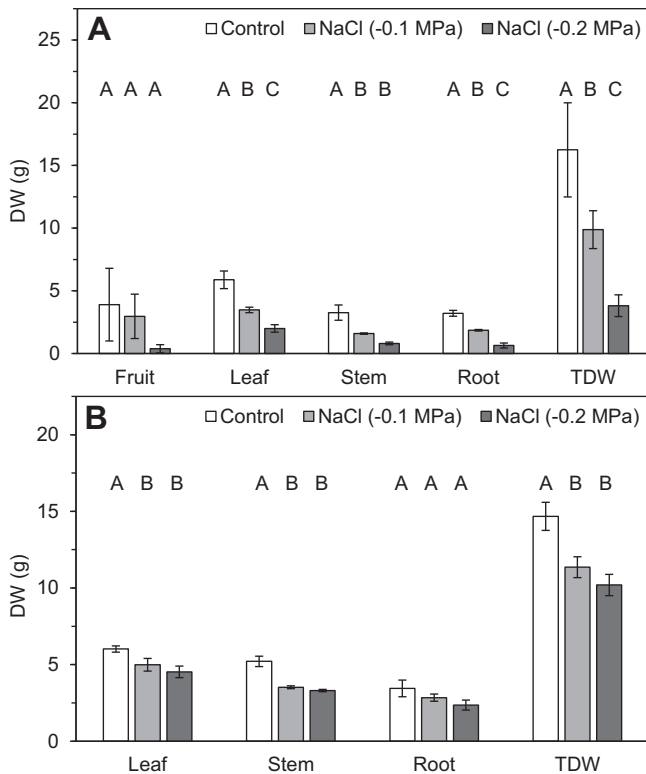


Figure 7. Fruit, leaf, stem, root, and total dry weight (DW) in grams per three plants of bean (A) and cotton (B). Cotton plants produced no fruit. Each observation is the mean ± SD of three replications. Within crop species and tissue type, means followed by different letters indicate significant difference according to Duncan's multiple range test ($P < 0.05$). For treatment composition and properties, see Table 1.

Table 3

Total dry weight (TDW) expressed as percent of control for *L. alyssoides*, *L. draba*, *L. latifolium*, bean, and cotton. The percentage values were calculated from the data in Fig. 6D and Figs. 7A–B, and represent the mean ± SD of three replications. *Lepidium* spp., bean, and cotton were independent experiments. For treatment composition and properties, see Table 1

Treatment	TDW (% of control)				
	<i>L. alyssoides</i>	<i>L. draba</i>	<i>L. latifolium</i>	Bean	Cotton
NaCl (-0.1 MPa)	88.3 ± 12.6	71.8 ± 3.5	80.3 ± 4.4	63.9 ± 21.3	77.8 ± 9.4
NaCl (-0.2 MPa)	65.2 ± 2.7	58.8 ± 8.2	69.4 ± 5.3	25.4 ± 12.4	69.8 ± 9.2

incremental reductions at −0.1 MPa and −0.2 MPa, except for stem dry weight that declined only at −0.2 MPa.

In the cotton study, initial root dry weight averaged 0.39 g per three plants with shoot dry weight (leaves plus stems) averaging 1.0 g per three plants. Following saline irrigation, there were treatment effects on leaf and stem dry weight and on TDW ($P < 0.0110$), but not on root dry weight ($P = 0.0889$; Fig. 7B). Aside from the roots, the organ dry weight and TDW means were highest in the controls, declined at −0.1 MPa, but declined no further with high salinity at −0.2 MPa.

The relative TDW (as percentage of the control treatment) was calculated for each of the plant growth studies (Table 3), using the data from Figure 6D and Figure 7A–B. The foregoing discussion is only broadly based on the numerical averages (± standard deviation) in three independent experiments under common growing conditions. In the −0.1 MPa saline irrigation treatment, the relative TDW was lowest in salt-sensitive bean and considerably higher in salt-resistant cotton, as expected. Considering all of the *Lepidium* spp. at −0.1 MPa, their relative TDW values were more similar to that of cotton than they were to bean, and in the cases of *L. alyssoides* and *L. latifolium*, somewhat higher than that of cotton. At high salinity (−0.2 MPa), a similar trend was observed in that relative TDW declined substantially in bean but was only slightly reduced in cotton, consistent with the differential salt resistance of those crop species. For all three *Lepidium* spp., relative TDW at −0.2 MPa had a decline similar to that of cotton. Of the three *Lepidium* spp., *L. draba* had the lowest relative TDW at both −0.1 MPa and −0.2 MPa, although its values were higher than those of bean in both of the latter treatments.

Discussion

Seed germination is a key factor in determining a species ability to establish in saline conditions (Ungar, 1995). Others have reported on optimized temperature and light regimes for germination of *L. latifolium* (Miller et al., 1986; Larson and Kiemnec, 2005) and *L. draba* (Kiemnec and Larson, 1991). To our knowledge, we are the first to report on germination of *L. alyssoides* (present study and Flores et al., 2015) and to study germination of all three of these *Lepidium* spp. together. We needed to develop a temperature and photoperiod regime that would be suitable for the germination of all three of these species. For the plant growth study, *L. alyssoides*, *L. draba*, and *L. latifolium* germinated readily under the greenhouse temperature and photoperiod conditions during late January to early February. Subsequently, the latter conditions served as the basis for the seed germination chamber diurnal temperature and photoperiod regime.

High germinability of *L. alyssoides*, *L. draba*, and *L. latifolium* in our laboratory saline-sodic solutions suggest that these species are capable of establishing in natural environments under similar saline-sodic conditions in the semiarid southwest. The importance of seeds in regeneration of *L. latifolium* and *L. draba* is well recognized (Francis and Warwick, 2007, 2008; Leininger and Foin, 2009), and our field observations show that *L. alyssoides* is also a prolific seed producer. Germination of *L. alyssoides* was more sensitive to our high saline conditions (−0.2 MPa) than was that of *L. draba* and *L. latifolium*. Earlier, we found no salt-induced suppression in *L. alyssoides* germination up to ECs of 4–8 dS m^{−1} under the same laboratory conditions as in the

present study (Flores et al., 2015), except that the earlier study involved mixed saline solutions with much lower Na and Cl proportions than in the present investigation. In both studies, however, we recorded nearly identical percentages of nongerminated, viable seed of *L. alyssoides* in nonsaline control conditions (7–8%). This pattern may indicate the presence of dormant *L. alyssoides* seeds for seed bank establishment favoring a long-term survival strategy and playing a role in invasiveness. On the basis of the findings in Figure 1A, such a strategy may be absent for *L. draba* and *L. latifolium*. More research is needed to investigate these possibilities.

The lack of a high salinity effect on germination of *L. draba* matches laboratory findings by Kiemnec and Larson (1991). By contrast, the high germinability of *L. latifolium* (> 99%), irrespective of salinity, was not consistent with laboratory findings by Larson and Kiemnec (2005), who reported that germination of a *L. latifolium* population from Oregon declined as salinity was increased under constant light and 12-hr light/dark cycles at 20°C. This inconsistency may be due to either a seed source (population) effect, or a temperature effect, since temperature interacts with salinity in controlling seed germination (Ungar, 1995). Larson and Kiemnec (2005) concluded that *L. latifolium* is suited to germinate in sodic field conditions. While their study did show that *L. latifolium* is capable of germinating under saline conditions (EC up to 16 dS m⁻¹), nonsodic solutions (SAR of 2) were used in their study. Our findings assert that *L. latifolium*, *L. draba*, and *L. alyssoides* can germinate unhindered in highly sodic conditions (SARs in Table 1 are minimal sodicity estimates due to only trace levels of Ca and Mg in the deionized water used for germination). Whether more pronounced salinity effects on germination would apply under field conditions with other stress factors warrants further study. However, in the context of our laboratory conditions, an MT delay of 1 d or less with the low and high salinity treatments on *L. draba* and *L. latifolium* would not likely preclude infestations in light of the absence of salt effect on their germinability.

We observed aggressive vegetative budding through underground clonal propagating structures on all three of these *Lepidium* spp., particularly on *L. latifolium*. By termination of the plant growth study, numerous plastic grow cells of *L. latifolium* had begun to fracture longitudinally, which provided a visual analogy of its intensive vegetative propagule pressure (photos available from authors). Propagule pressure is a major factor leading to invasive plant establishment (Von Holle and Simberloff, 2005), as might be the case for the *Lepidium* spp. under study considering their vegetative reproductive structures. Further research is needed to characterize underground tissue biomass partitioning of these *Lepidium* spp. and to determine salt effects on growth of the underground shoot structures. Nevertheless, *L. latifolium* maintained the highest underground tissue dry weight across all solution treatments, which may be inherently related to its highly thickened and abundant underground stems.

In the *Lepidium* spp. plant growth study, our leaching fractions varied by <5% and leachate ECs varied by <0.3 dS m⁻¹ from those values we recently reported using the same irrigation methods and salinities (Hooks et al., 2018). In the latter study, identical effects of NaCl salinity were observed on *L. alyssoides* ET and dry matter production as in the present study. This indicates good reproducibility of our saline culture system resulting from use of the homogeneous coarse sandy substrate and from constant leaching fractions of ≈50% to maintain a steady-state salt balance. Given the relationship between leachate EC and soil saturation extract (SSE) EC in greenhouse substrates (Cox, 2005), the average leachate EC of the -0.1 MPa and -0.2 MPa saline irrigation treatments would correspond to SSE salinities of ≈6–10 dS m⁻¹. Yield and survival of many salt-sensitive crop species are severely limited at this level of salinity (Ayers and Westcot, 1985).

Aside from the extensive crop salt tolerance database, our study contributes to a limited database on salinity responses of noncultivated, invasive plant species on natural landscapes. We relied on the crop salt tolerance database by including two species with contrasting levels of salt resistance (bean and cotton) in order to provide realistic

assessments of relative salt resistance of the *Lepidium* spp., all under common greenhouse conditions. Under the greenhouse conditions, we were able to detect a significant growth suppression of salt-resistant cotton at an average leachate EC of 8.1 dS m⁻¹ corresponding to an SSE EC of about 6.2 dS m⁻¹, which was somewhat lower than the cotton SSE salinity threshold of 7.7 dS m⁻¹ in Maas and Hoffman (1977). In view of the established cotton salt resistance as a known standard and the common experimental conditions wherein the growth (dry matter production) and ET of the *Lepidium* spp. met or exceeded the growth and ET of cotton, the *Lepidium* spp. should indeed be classified as salt resistant. This finding strengthens a narrow database that has not provided sufficient quantitative data to substantiate the claims of *Lepidium* spp. salt tolerance. On the basis of our findings on seed germination and plant growth, saline-sodic sites of the semiarid southwest may be particularly susceptible to emergent and expanding *Lepidium* infestations. For example, on a previously undisturbed southern New Mexico Chihuahuan Desert shrubland, a sparse population of *L. alyssoides* became invasive and dominant only following salinization and increased sodicity of the site (Picchioni et al., 2012a, 2012b).

None of the soils at our three *Lepidium* seed collection sites were saline or sodic; thus, the parents were not preconditioned to high salinity and sodicity. Rather, the sites were affected by land disturbances that included grading, road construction, farming, surface water diversion, and clearing of vegetation. *Lepidium draba* and *L. latifolium* are reported to occupy disturbed and degraded sites (Larson and Kiemnec, 2005; Francis and Warwick, 2008; Renz et al., 2012), and on the basis of our observations, site disturbances may encourage proliferation of *L. draba*, *L. latifolium*, and *L. alyssoides* irrespective of soil salinity and sodicity. Nonetheless, salinity—a “nonresource” factor—may regulate the composition of plant species pools (Grace, 2001). Due to their salt resistance, we hypothesize that these *Lepidium* spp. are able to use salt-affected, vacant niches in ways that other species cannot (Hooks et al., 2018) and thus intensify their invasiveness and dominance over other co-occurring members of a species pool.

Andrew and Ustin (2009) stated a need for improved understanding of *L. latifolium* habitat requirements in order to identify landscapes that are vulnerable to future invasions. Accounting for edaphic factors that depict soil toxicity for plants (i.e., salinity) could increase accuracy in predicting plant species distributions (Bertrand et al., 2012) and, in particular, could help predict how lands that support *L. latifolium* will respond to saline intrusion (Wigginton et al., 2014). Our study supports these needs for invasive *Lepidium* spp. Growth and ET of three *L. alyssoides* populations were largely indifferent to various isosmotic saline irrigation solutions (Hooks et al., 2018). While more data pertaining to isosmotic salt effects on *L. draba* and *L. latifolium* are needed, measuring the soil EC (total salinity) is a quick and reliable method that could have particular value for water and land managers in assessing the risk of *Lepidium* invasions.

An important physiological basis for saline resistance of *L. latifolium*, *L. draba*, and *L. alyssoides*, to be published elsewhere, is a tolerance to high salt accumulation in leaves. Under our saline greenhouse culture conditions, their combined leaf Na and Cl concentrations reach halophytic proportions (7–13% of dry weight) and with no characteristic symptoms of salt toxicity (Picchioni et al., 2015).

Implications

Lepidium latifolium, *L. draba*, and *L. alyssoides* are capable of germinating and growing proficiently under saline conditions. There was no growth stimulation of these species in response to salinity, as is the case with some halophytes. However, comparative observations of growth and ET with salt-resistant cotton under common experimental conditions indicate that these *Lepidium* spp. are, in themselves, salt resistant. *Lepidium latifolium* and *L. draba* have earned their reputations as exotic invasive species throughout much of the western United States, although their level of salt resistance is somewhat speculative

due to lack of quantitative data. By contrast, comparatively little information has been published on *L. alyssoides*. Taken together, the present study supports the possibility that these three *Lepidium* spp. could become invasive under saline conditions. We acknowledge a limitation in this study due to the use of single seed sources for each species, and thus we recommend further studies to include multiple populations and locations to better understand the connection between salt resistance and invasive potential of these species.

This study addresses the need to overcome knowledge gaps in quantifying salt resistance of invasive plant species. In particular, the findings increase an understanding of how salinization can threaten biodiversity of semiarid landscapes. Expanded research could equip land managers with cost-effective ways to predict and prevent invasions of salt-resistant weedy species on salt-affected lands.

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