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Original Research

Salinity an Environmental "Filter" Selecting for Plant Invasiveness? Evidence from Indigenous *Lepidium alyssoides* on Chihuahuan Desert Shrublands☆

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ABSTRACT

A better understanding of site-specific factors such as soil salinity that regulate plant invasions is needed. We conducted a 3-mo greenhouse study to evaluate the salinity responses of three local maternal sources of *Lepidium alyssoides*, which is an indigenous species shown to aggressively colonize disturbed shrubland sites in the southwestern United States, including those affected by high salinity and sodicity. Results indicated that there were little or no population effects on plant evapotranspiration (ET), growth, and tissue Na and Cl concentrations. Significant reductions in seedling growth and ET were largely independent of various isosmotic saline irrigation solutions that included NaCl, Na_2SO_4, and $CaCl_2$, each at −0.1 MPa and −0.2 MPa, suggesting that ET and growth were controlled by solution osmotic potential. The combined Na and Cl concentrations in leaves were 9–10% of dry weight with no visible sign of injury. However, increasing leaf mortality and abscission as a proportion of total leaf production was observed in the high-salt treatments (−0.2 MPa), with a combined Na and Cl concentration reaching 16% with high NaCl. Under saline conditions, considerable foliage salt loads of this species could deposit high-salt litter to potentially alter a landscape to its own favor and to the detriment of other salt-sensitive species. Results of this study add to a limited quantitative database on site-specific salinity factors governing plant invasions by showing the potential for these populations to behave invasively under saline conditions and, thus, potential for soil salinity assessment to predict incipient populations. However, due to its halophytic traits and indigenous status, *L. alyssoides* may alternatively provide ecosystem services to salinized shrublands of the arid and semiarid southwestern United States.

Introduction

Anthropogenic disturbances promote plant invasions that reduce biodiversity of natural vegetation communities (Hobbs and Huenneke, 1992; Symstad et al., 2003; Sheley et al., 2011). The impacts are especially severe in arid and semiarid regions (D'Antonio and Myerson, 2002), such as southern New Mexico. Many rangelands of the southwestern United States have been degraded by land use intensification to meet the needs of the expanding human populations and industries. Such disturbances include residential development, storm water diversion, road construction, mining operations, excavation, and other landscape changes adjacent to undisturbed lands.

Degradation of the region's rangeland soils and vegetation has important ramifications for the capacity of the land to provide ecosystem services, including those associated with water (Herrick et al., 2010). In recent years, there has been increasing interest in beneficial reuse of nonhazardous water and solid wastes (residuals) on arid and semiarid rangelands of the western United States. Land application of residuals has been recommended as a safe method of disposal to allow the land to process contaminants, increase organic matter and nutrient levels in the soil, and restore disturbed sites (USEPA, 1996; O'Connor et al., 2005). Numerous cases of land application of residuals to arid and semiarid rangeland of the western United States have included treated industrial wastewater, reclaimed municipal wastewater, coproduced water, dairy manure, and municipal biosolids (Levy and Kearney, 1999; Stavast et al., 2005; Sullivan et al., 2006; Bergquist et al., 2007; Brenton et al., 2007; Ganjegunte et al., 2008, 2011; Vance et al., 2008; Cabrera et al., 2009;

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Nemmers et al., 2012; Picchioni et al., 2012a, 2012b). These studies have reported high levels of salinity, sodicity, or both salinity and sodicity in residual materials, and their application to rangeland represents a novel anthropogenic disturbance resulting in secondary salinization to alter quality of the soil water supply and, potentially, the plant species composition. Several of the aforementioned studies have revealed loss in native plant species diversity or encroachment by invasive plant species in response to land application of residuals (Sullivan et al., 2006; Bergquist et al., 2007; Vance et al., 2008; Picchioni et al., 2012b).

Mesa pepperwort (*Lepidium alyssoides* A. Gray var. *alyssoides*) is an herbaceous Brassicaceae perennial that is indigenous to New Mexico and surrounding states (USDA-NRCS, 2015) and has received little study. Two of its herbaceous perennial relatives, perennial pepperweed (*L. latifolium* L.) and whitetop (*L. draba* L.), have attracted considerable attention due to their status as exotic invasive species in the western United States, including rangeland (Francis and Warwick, 2007, 2008). *L. alyssoides* is currently not listed on any state noxious weed list, although it has recently been found to harbor an introduced invasive stink bug (*Bagrada hilaris* Burmeister) along a southern New Mexico highway (Bundy et al., 2012), suggesting that *L. alyssoides* will soon be a plant of concern for land managers in the southwestern United States. In field conditions involving land application of saline-sodic treated industrial effluent to a southern New Mexico shrubland, *L. alyssoides* aggressively colonized the site when shallow-depth soil saturation extract sodium adsorption ratio (SAR) increased from 15 to 35 over a 3-yr period, becoming largely a monotypic stand that replaced six other indigenous herbaceous species in the shrub interspaces (Picchioni et al., 2012a, 2012b). Although indigenous invasive plant species are less common than nonindigenous (introduced) invasive plant species, indigenous plant invasions have been linked to anthropogenic disturbances and loss of biotic integrity (Randall, 1997; Schwartz, 1997). The connection between human land disturbances and indigenous plant species invasiveness represents an understudied yet important component of arid and semiarid shrubland management and biology. A better understanding of these processes may help prevent new indigenous invasions from occurring and thereby aid in the management for indigenous shrubland biodiversity.

Limited data are available for how salinity may regulate plant species invasiveness, although "nonresource" edaphic factors, such as salinity, may play a role in regulating plant species populations on arid and semiarid land (Cox et al., 2006; Miller et al., 2006). Substantial documentation has advocated research for better understanding of site-specific factors, including edaphic factors such as salinity, that lead to proliferation of weedy, invasive plants (Grace, 2001; Byers et al., 2002; D'Antonio and Myerson, 2002; Brooks, 2003; Hobbs et al., 2003; Abella et al., 2009; Andrew and Ustin, 2009; Reynolds and Boyer, 2010; Bertrand et al., 2012). Evidence has supported a role for salinity in driving vegetation distribution patterns, but salinity has received little study in the arid vegetation science literature, particularly in reference to plant invasions (Bui, 2013). Thus, research is needed to identify specific soil salinity characteristics and salinity tolerances of successful invader species in arid and semiarid climates in order to predict incipient populations and their invasive risk.

The aim of our study was to investigate salt tolerance of the indigenous *L. alyssoides*. Improved knowledge of *L.* alyssoides responses to salt stress will clarify the potential role of soil salinity in facilitating *L. alyssoides* invasions previously observed on disturbed Chihuahuan Desert shrubland (Picchioni et al., 2012a, 2012b). Since the growth of some halophytes is known to be stimulated in saline conditions (Flowers and Läuchli, 1983; Subbarao et al., 2003; Flowers and Colmer, 2008), we hypothesized a similar condition for *L. alyssoides*, in that this species possesses halophytic traits that confer salt tolerance. An additional objective was to address potential ecotypic variation in *L. alyssoides* salinity response and further improve the database on the species. For example, a population that is preadapted to high-Na (Picchioni et al., 2012b) may possess higher salt tolerance than nonadapted populations (Epstein and Bloom, 2005). Thus, we studied the growth, water use, and salt partitioning patterns of three local Chihuahuan Desert shrubland populations of this species under various saline irrigation treatments in a greenhouse.

Our study was designed to include isosmotic saline irrigation solutions to address questions on *L. alyssoides*, including: Would Na serve as a beneficial element as for some halophyte species (Subbarao et al., 2003), a plausible hypothesis as suggested by findings from the earlier field study (Picchioni et al., 2012b)? Would either high-Na waters or high-Cl waters impose specific ion toxicity? Would the growth response be indifferent to the ionic composition of irrigation waters and instead, would the osmotic effect predominate? Targeted questions about plant salinity responses address important deficits in the vegetation science literature that have slowed an understanding of factors regulating weed invasions upon arid and semiarid landscapes.

Materials and methods

Seed Collection and Cleaning, as Well as Site Sampling

Seeds of *L. alyssoides* were collected in June 2012, from densely populated stands on disturbed northern Chihuahuan Desert shubland sites near Las Cruces, New Mexico. Three populations of *L. alyssoides*, spanning a land area of approximately 174 km^2, were sampled from the Las Cruces West Mesa (WM, N32°15′9″, W106°54′28″, 1 300-m elevation), the Interstate-10 freeway exit at the town of Mesquite, New Mexico (MQ, N32°10′28″, W106°40′7″, 1 200-m elevation), and the Las Cruces East Mesa (EM, N32°19′46″, W106°43′8″, 1 290-m elevation). The WM seed collection site was adjacent to an industrial park. Since 2002, the WM site has been sprinkler irrigated with saline-sodic, treated industrial effluent from a wastewater treatment plant (WWTP) (Picchioni et al., 2012a, 2012b). The low-lying MQ seed collection site was previously altered by clearing of shrubland vegetation, land grading, road construction, and diverted stormwater incursion. The EM seed collection site was on a raised bank constructed of excavated soil, adjacent to an intermittent discharge stream below a municipal WWTP.

At each site, seeds were collected from three to five well-dispersed positions within an approximate 100-m^2 area and from the upper half of aboveground tissue that included stems, leaves, flowers, and fruit (siliques). Single soil core samples (20 cm in depth and 2.5 cm in width) were taken at each of the seed collection positions and composited for each of the three population sites. The bulked vegetation samples were stored in a laboratory and dried at room temperature for 4 mo. After drying, the vegetation samples were gently abraded with a rubber board to release any seeds remaining in siliques. Seeds were then collected and passed through a 2-mm sieve to screen out large plant debris. A seed blower (757 South Dakota, Seedburo Equipment Co, Des Plaines, IL) was then used to remove any remaining chaff from the seeds. The cleaned seeds of each population were then transferred to sealed watertight glass vials and stored at 4°C to await sowing.

Greenhouse Climate

The study was conducted in a climate-controlled A-frame greenhouse located at the New Mexico State University Fabian Garcia Science Center in Las Cruces, from 18 March to 7 August, 2013. Greenhouse climate data were collected using a Watchdog 2475 Plant Growth Weather Station and analyzed with SpecWare 9 Basic software (Spectrum Technologies, Inc, Aurora, IL). For the duration of saline irrigation (described later), maximum daytime temperature ranged from 25–38°C with a mean of 32°C. Minimum nighttime temperature ranged from 15–23°C with a mean of 20°C. Daily relative humidity ranged from 4% to 93% with a mean of 47%. Maximum photosynthetically active radiation (PAR) was 706 $\mu mol\ m^{-2}\ s^{-1}$, and the mean daily light integral (DLI) was 11 $mol\ m^{-2}\ d^{-1}$. A nylon shade cloth atop the greenhouse

roof was used throughout the study to block approximately 50% of the incoming solar radiation. A photoperiod consisting of 16 hr light and 8 hr dark was maintained throughout the duration of the study by operating high-intensity discharge metal halide lamps from 5:00 to 8:00 AM and from 5:00 to 9:00 PM.

Seedling Establishment

Seeds were sown on 18 March in individual 107-mL grow cells (3.8-cm width x 14-cm height, SC7 Ray Leach "Cone-tainers," Stuewe and Sons, Inc., Tangent, Oregon). Pure, coarse silica sand was used as the growing medium and was acid washed with 0.1 N sulfuric acid and flushed with tap water before sowing. The bottom of each cell was plugged with a cotton ball, and the cells were filled with approximately 110 g of silica sand. A 1- to 2-cm headspace remained at the top of each cell to later allow for overhead saline irrigation that is described later. Seeds were then sown by hand in each cell at a depth of 1 cm. Three seeds were sown in each cell to ensure successful germination but were later thinned at the cotyledon stage to a single plant per cell. A total of 98 cells were seeded per population.

Seedlings were established in the greenhouse under daily subirrigation in tap water with quarter-strength complete Hoagland's nutrient solution 1 (Hoagland and Arnon, 1950). Six wk after sowing, seedlings bore multiple whorls of true leaves, at which time 63 visually uniform plants per population were selected for the experiment.

Saline Irrigation Treatments

Salt treatments were developed to evaluate the specific effects of Na and Cl on the growth of *L. alyssoides*. In addition to NaCl, $CaCl_2$ and Na_2SO_4 were selected to evaluate the effects of Cl and Na, respectively. For each treatment salt, isosmotic concentrations were calculated to provide −0.1 MPa and −0.2 MPa osmotic potentials (Richards, 1954; Weast, 1985). Hereafter in the text, the −0.1 MPa and −0.2 MPa salt treatments are also referred to as low- and high-salt treatments, respectively. The compositions and properties of the seven treatment solutions, including a tap water control, are shown in Table 1. The electrical conductivities (ECs) of the six saline solutions (low and high salt treatments) met or exceeded those of the previous report that demonstrated invasiveness of *L. alyssoides* on a salt-affected Chihuahuan Desert shrubland (Picchioni et al., 2012a, 2012b). All treatments were prepared using tap water (EC of 0.6 dS m^{-1} and pH of 7.8) and the complete Hoagland's nutrient solution at half-strength (1 dS m^{-1}) and stored in 18.9-L sealed buckets at the greenhouse. The tap water included (in meq L^{-1}) Na (2.8), Ca (2.4), Mg (1.0), Cl (0.5), SO_4 (4.0), and HCO_3 (1.8). Iron (for the nutrient solution) was supplied in chelated form as ferric ethylenediamine di-(o-hydroxyphenylacetate; Sprint 138, Becker Underwood, Inc., Ames, IA). All salts for Hoagland's nutrient solution and for salinization were laboratory analytical grade.

Table 1
Composition and properties of the control and saline irrigation solutions used throughout the study.

Treatment	OP (MPa)[1]	Concn. (mM)	EC (dS m^{-1})[2]	EC (dS m^{-1})[3]	SAR[4]
Control	—	—	—	1.6	1.2
NaCl	−0.1	23.8	2.3	3.9	11.7
NaCl	−0.2	47.9	4.6	6.2	22.3
$CaCl_2$	−0.1	16.5	3.4	5.0	0.6
$CaCl_2$	−0.2	33.8	6.1	7.7	0.4
Na_2SO_4	−0.1	17.1	3.3	4.9	16.2
Na_2SO_4	−0.2	36.7	5.8	7.4	33.5

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

On the day of the first irrigation, 10 plants of each population were harvested and dried at 60°C to determine initial dry weight of shoots and roots. The salt treatments were initiated on 6 May, 2013 and applied overhead using a 50-mL syringe. Irrigation was supplied when approximately 50% of the total water in the sand medium had been depleted and in an amount to cause an approximate 50% leaching fraction. Approximately 48-hr stepwise increments (−0.05 MPa) of the salt treatments were applied initially, and for the −0.2 MPa salt treatments, final osmotic potentials were reached 14 May.

Leachate Characteristics, ET, and Leaf Mortality During Growth Period

After the final stepwise increment of the high-salt treatments was reached, leachates were collected on a biweekly basis and volumes were recorded in mL. The leaching fraction (%) was calculated by dividing the leachate volume by the applied irrigation volume and multiplying by 100. The EC of the leachates was recorded in dS m^{-1} using a TechPro II TPH1 sensor (Myron L Co, Carlsbad, CA).

At the start of saline solution irrigation, daily weights of the growing cells were recorded in grams, and the evapotranspiration (ET) was calculated as the difference between the recorded weights on adjacent days. For days following an irrigation, ET was calculated as the difference between the cell capacity weight (0% water depletion following irrigation and 10 min drainage) and the current daily weight. The cell capacity weights were revised throughout the study to account for increases in plant fresh biomass. Weekly cumulative ET was determined by summation of daily ET and plotted on a weekly basis. The total ET over the duration of the experiment was also determined.

In all treatments and populations, some mortality of mature basal leaves was observed at about two-thirds into the study (1 July) and up to the time of termination. All dead and abscised leaves were collected and saved in dried form for dry weight and mineral determinations, as described later.

Termination, Harvest, and Sample Processing and Analysis

The study was terminated 5 August (after a duration of 91 d), and leaves were harvested by blocking order (experimental design described later). Aboveground tissue was cut at the sand level and quickly rinsed in three successive reverse osmosis water baths that were monitored and maintained below 30 μS cm^{-1}. The harvested shoot tissues were then blotted dry and separated into stems and healthy leaves. The dead leaves were not washed and were kept separate from the healthy leaves.

Belowground tissue harvest consisted of true roots and propagating structures that gave rise to clonal shoots. The belowground propagating structures have yet to be described in the literature for *L. alyssoides*. Similar structures have been described in at least two other related species, *L. draba* and *L. latifolium*, although discrepancy seems to exist in the literature as to their proper structural name, whether they are rhizomes (Francis and Warwick, 2007, 2008) or creeping roots (Young et al., 1997; McInnis et al., 2003; Zouhar, 2004; Reynolds and Boyer, 2010; Renz et al., 2012). Regardless, *L. alyssoides* was observed in the present study to possess clonal propagation abilities, similar to those described in *L. draba* and *L. latifolium*. These tissues could not be physically separated due to their tangled and interwoven nature; therefore, all belowground tissues were pooled together and, for simplicity hereafter, are referred to as "roots." The roots were carefully extracted from each cell and separated from the sandy growing medium by hand, followed by rinsing in reverse osmosis water baths as described earlier. In cases where clonal shoots arose from roots, they were harvested and pooled with their appropriate stem and leaf tissues as described earlier.

After harvesting, all fresh tissue samples were taken to complete dryness at 60°C and the dry weights were recorded. The total plant dry weight (TDW) included roots, stems, and healthy leaves. Dry weights were also recorded for the dead leaves, and the total dried

leaf biomass included the weights of dead and healthy leaves. The dried samples were then ground in a Thomas Wiley Mini-Mill (Thomas Scientific, Swedesboro, NJ) to pass a 40-mesh (0.42-mm) screen. Dried vegetation samples from the seed collection sites were also ground as described earlier. All ground samples were stored in air-tight bags at room temperature.

The ground tissues were thoroughly mixed, and 0.25-g subsamples were extracted using a MARS 5 microwave digestion system (CEM Corp, Matthews, NC) using the methods of Jones et al. (1991) for determination of Na (all tissues) and K (leaves only) by inductively coupled plasma atomic emission spectroscopy (Optima 4300V ICP-AES, Perkin Elmer, Shelton, CT). A second, 0.1-g subsample was subjected to 2% acetic acid extraction at room temperature (Jones et al., 1991) for determination of Cl on an auto-analyzer (AAII, Technicon Instruments, Tarrytown, NY). Bulked vegetation samples from the seed collection sites were also ground and analyzed for Na and Cl as described earlier. For the dead leaves, Na and Cl analysis was limited to the MQ population, and to only the control and −0.2 MPa salt treatments.

The composited soil samples from the seed collection sites were first passed through a 2-mm sieve, and a single subsample per site was analyzed for texture, saturation percentage, organic matter, pH, EC, SAR, Cl, NO_3-N, soluble K, and Olsen-P, all by the online methods of the New Mexico State University Soil, Water, and Air Testing Laboratory (NMSU-SWAT, 2016).

Experimental Design and Statistical Analysis

The study was designed as a two-way, randomized complete block (RCB) with three blocks and split plots. Blocking was necessary to account for greenhouse ventilation and temperature patterns, as well as to accommodate management and harvest tasks with the available personnel. The three populations of *L. alyssoides* (WM, MQ, and EM) served as main plots, and the seven irrigation treatments served as subplots. Three plants growing individually in each of three separate cells represented a single experimental unit (EU), replicated three times. At termination of the study, the analysis of variance (ANOVA) was performed for total ET, tissue dry weights, tissue Na and Cl concentrations, and leaf K/Na molar ratios using PROC GLM in SAS (version 9.3, SAS Institute, Inc., Cary, NC). Means within subplots and main plots were separated by Duncan's Multiple Range Test at an alpha of 0.05.

Results

Soil and Vegetation Analysis of Seed Collection Sites

The soils from the three collection sites of *L. alyssoides* (WM, MQ, and EM) were sandy, with saturation percentages ranging from 15 to 18 and organic matter ranging from 0.4% to 1.2% (Table 2). The pH of the soils was basic and ranged from 7.2 to 7.9, with EC ranging from 1.6 to 2.0 dS m^{-1} and Cl from 4 to 12 meq L^{-1}. The soils from the MQ and EM sites were nonsodic, with SAR ranging from 0.6 to 1.7, while the SAR at the WM site (12.5) was at the sodic level (SSSA, 2015). The higher SAR in the WM soil may be attributed to the application of saline-sodic treated wastewater (Picchioni et al., 2012a). At all sites, the soil NO_3-N and Olsen-P concentrations were low, and soluble K was moderate to sufficient on agricultural crop standards (R. Flynn, personal communication).

Bulked aboveground vegetation samples of *L. alyssoides* from each of the three collection sites had Na and Cl concentrations that ranged from 0.01% to 0.13% and 0.56% to 0.94% dry weight, respectively (data not presented). Of these values, the WM population had the highest Na and Cl concentrations.

Leachate Characteristics

Leaching fraction averaged 44.2% ± 6.2 across all treatments and populations throughout the study (data not presented). Leachate ECs were stable and did not increase during the study, varying by < 5% within treatments and across the populations. As expected, leachate EC was lowest for the control plants (2.5 dS m^{-1} ± 0.5). For the −0.1 MPa salts (NaCl, $CaCl_2$, and Na_2SO_4) the average leachate ECs were 8.1 ± 1.4, 9.4 ± 1.6, and 9.3 ± 1.2 dS m^{-1}, respectively. With the same salts at −0.2 MPa, the average leachate ECs were 13.4 ± 1.4, 16.4 ± 1.7, and 15.2 ± 1.5 dS m^{-1}, respectively. Within each osmotic potential, leachate ECs differed slightly depending on the salt. These differences followed the inherent conductance properties of these salts under isosmotic conditions (see Table 1).

Weekly Cumulative ET

The ET steadily increased throughout the study and was similar across all populations (Fig. 1). Salt-induced reductions in weekly cumulative ET became apparent by around the sixth week after initiating treatments, with incremental effects of salinity (−0.1 MPa to −0.2 MPa) appearing at about 7–10 wk, depending on population.

Total Plant ET, Dried Biomass, and Ion Concentrations at Termination

For each of the 15 response variables pertaining to total ET, tissue dry weights, tissue Na and Cl concentrations, and the leaf K/Na molar ratio, the salt treatment effect was highly significant (Table 3). For the majority of response variables, there was neither a population main effect nor a population X treatment interaction ($P > 0.05$; see Table 3). Those data were pooled across populations resulting in nine, three-plant replications per treatment. For three response variables (total leaf dry weight, total plant dry weight, and Cl concentration in healthy leaves), ANOVA showed a significant population main effect (see Table 3); however, multiple comparison tests did not reveal any specific differences between populations, which will be discussed no further.

The total ET (data not shown) reflected weekly cumulative ET in that the control plants had the highest (4.8 kg per three plants), followed by incremental reductions with the −0.1 MPa salts (3.6−3.8 kg per three plants) and −0.2 MPa salts (2.9−3.1 kg per three plants). At −0.1 MPa, a marginally significant difference was detected between NaCl and Na_2SO_4 (3.6 and 3.8 kg per three plants, respectively). However, at −0.2 MPa, no differences between the salts were detected.

At the initiation of salt treatments, average root dry weight per 10 plants ranged from 0.21 to 0.30 gm, and average shoot dry weight (leaves plus stems) per 10 plants ranged from 0.42 to 0.51 gm. The average weights did not differ between populations ($P > 0.05$).

Table 2
Soil characteristics of the seed collection sites of the West Mesa (WM), Mesquite (MQ), and East Mesa (EM) populations of *Lepidium alyssoides*. Saturation percentage (SP), pH, electrical conductivity (EC), sodium adsorption ratio (SAR), and Cl were determined in the soil saturation extract, and NO_3-N, Soluble K, and Olsen-P were determined on a dry weight basis.

Population	Texture	SP (%)	OM (%)	pH	EC (dS m^{-1})	SAR[1]	Cl (meq L^{-1})	NO_3-N (mg kg^{-1})	Soluble K (mg kg^{-1})	Olsen-P (mg kg^{-1})
WM	Sand	18.1	0.4	7.9	1.7	12.5	6.3	3.9	81.0	7.2
MQ	Sand	15.8	1.2	7.2	1.6	1.7	4.1	17.3	76.5	9.4
EM	Sand	15.3	0.4	7.2	2.0	0.6	12.4	4.6	51.8	5.2

OM indicates organic matter.
[1] Calculated as $Na/(Ca+Mg)^{1/2}$, all ions in mM.

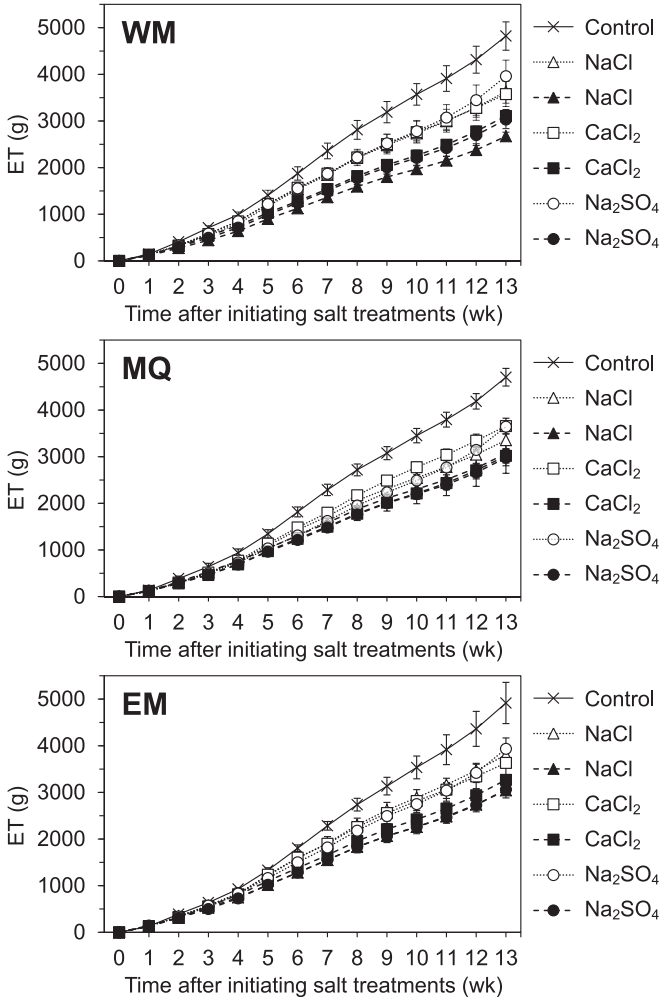

Figure 1. Cumulative evapotranspiration (g per three plants) of the West Mesa (WM), Mesquite (MQ), and East Mesa (EM) *L. alyssoides* populations. Open symbols represent −0.1 MPa salt treatments and closed symbols represent −0.2 MPa salt treatments. Each observation is the mean ± SD of three replications. For treatment composition and properties, see Table 1.

Dry weight of healthy leaves was highest in the control plants and followed incremental reductions from −0.1 MPa to −0.2 MPa salts (Table 4). High Na_2SO_4 produced the lowest healthy leaf dry weight. For all treatments, healthy leaf dry weight comprised 49%–61% of TDW and that proportion did not decline as salinity increased (at $P > 0.05$).

The healthy leaf dry weight did not account for the total leaf biomass production under these conditions, some of which included dead leaves collected during the study. For dead leaf dry weight, there was no indication that the salt treatments caused higher absolute leaf mortality than the control, other than two exceptions of WM and EM at −0.2 MPa $CaCl_2$ (see Table 4). In the control, low $CaCl_2$, and both low and high Na_2SO_4, the MQ population generally experienced less absolute leaf mortality than the WM and EM populations. Adding the contributions of dead leaves to healthy leaves, salt-suppressive effects on total leaf dry weight at −0.1 MPa were not as pronounced as they were against healthy leaves only, and only with high Na_2SO_4 was there an incremental loss in total leaf dry weight from −0.1 MPa to −0.2 MPa for all populations (see Table 4). When expressing dead leaf weight as a percentage of total leaf dry weight, the −0.1 MPa treatment percentages did not differ from that of the control, while the −0.2 MPa treatment percentages were higher than in the control (see Table 4). That is, high salt (−0.2 MPa) caused highest leaf mortality rates as a proportion of the total leaf production.

Table 3
Results from F-tests in analysis of variance for all plant response variables, including total evapotranspiration (ET), dry weight (DW), Na and Cl concentrations, and K/Na molar ratio after 91-d salt treatment to 3 populations of *Lepidium alyssoides*. For each response variable, the numerator and denominator degrees of freedom, respectively, were as follows: Treatment (6, 36); Population (2, 4); and Treatment × Population (12, 36). Significance as follows: ($^{NS, *, **, ***}$: Nonsignificant ($P > 0.05$) or significant at $P < 0.05$, $P < 0.01$, or $P < 0.001$, respectively).[1]

Response variable	Source of variation		
	Treatment (T)	Population (P)	T × P
Total ET	***	NS	NS
Leaf DW			
Healthy	***	NS	NS
Dead	***	*	NS
Total	***	*	NS
Dead (%)[2]	***	NS	NS
Stem DW	***	**	NS
Root DW	***	NS	NS
TDW	***	*	NS
Na concentration (%)			
Healthy leaf	***	NS	NS
Stem	***	NS	NS
Root	***	*	NS
Cl concentration (%)			
Healthy leaf	***	*	NS
Stem	***	NS	NS
Root	***	**	*
Healthy leaf K/Na	***	NS	NS

[1] Response variables based on 3-plant experimental units replicated 3 times.
[2] Dead leaf dry weight expressed as a percentage of total leaf dry weight.

Stem dry weight was highest for all populations in the control treatment but did not follow incremental reductions from −0.1 MPa to −0.2 MPa salts for the WM and EM populations (Table 5). Across the populations, the stem weights of WM were relatively low with −0.2 MPa NaCl and −0.1 MPa $CaCl_2$, and the stem weights of EM were high in −0.2 MPa Na_2SO_4. As a percentage of TDW for all treatments, stem dry weight comprised 7%–16% (WM), 12%–21% (MQ), and 11%–27% (EM), and these proportions generally declined in response to increased salinity ($P < 0.05$).

Root dry weight was highest in the control plants with clear incremental reductions from −0.1 MPa to −0.2 MPa salts (see Table 5). For all treatments, root dry weight comprised 27%–35% of TDW, and that proportion did not differ from the control plants as salinity increased. Fifty-nine percent of all EUs had propagating structures (discussed previously) at various stages, either within the sand medium or rising above the surface of the sand (data not presented). Biomass of the propagating structures was not determined separately, although when examining all of the EUs, there was a trend for fewest sightings of these propagating structures with the −0.2 MPa salts.

The TDW was highest in the control plants with incremental reductions from −0.1 MPa to −0.2 MPa salts (see Table 5). At −0.1 MPa, there were a few differences in TDW between the salts. However, at −0.2 MPa, no differences in TDW were detected between the salt treatments.

Tissue Na concentrations were generally highest in plants receiving NaCl and Na_2SO_4 while tissue Cl was highest in plants receiving NaCl and $CaCl_2$ (Tables 6 and 7). Depending on treatment, healthy leaf Na and Cl concentrations were as low as 0.04% and 0.60%, respectively, and reached as high as 4.20% and 6.63%, respectively. By contrast, stem and root Na and Cl concentration ranges were much narrower and, for all treatments, at or below ≈1%. In healthy leaves, there were incremental increases in Na concentrations from −0.1 MPa to −0.2 MPa NaCl and Na_2SO_4 (see Table 6). However, there were little or no increases in healthy leaf Cl concentrations from −0.1 MPa to −0.2 MPa NaCl and CaCl2 (see Table 7).

For high NaCl and Na_2SO_4, dead leaf Na concentrations of the MQ population (5.7%−6.8%; data not presented) were 1.4–1.8× higher than they were in the healthy leaves pooled across populations and

Table 4
Dry weight (DW) of leaf tissue, including healthy leaf, dead leaf, and the total leaf biomass production (healthy plus dead) in g per 3 plants, and the dry weight percentage of the dead leaf DW to total leaf DW of the 3 populations of *L. alyssoides:* West Mesa (WM), Mesquite (MQ), and East Mesa (EM). Populations were pooled in the absence of population main effect. For treatment composition and properties, see Table 1.[1]

Treatment	Healthy leaf DW (g)	Dead leaf DW (g)			Total leaf DW (g)			Dead leaf DW (% of total)
		WM	MQ	EM	WM	MQ	EM	
Control	6.37 A	2.35 BC a	1.39 AB b	2.00 B a	8.90 A a	7.35 A a	8.61 A a	23.0 B
NaCl (−0.1 MPa)	4.30 CD	1.77 D a	1.88 A a	1.69 B a	5.82 B a	6.10 ABC a	6.31 BC a	29.5 B
NaCl (−0.2 MPa)	3.33 E	2.19 CD a	1.73 AB a	1.86 B a	5.31 B a	4.91 CD a	5.54 BC a	36.7 A
$CaCl_2$ (−0.1 MPa)	5.73 B	2.79 AB a	1.75 AB b	2.59 AB a	8.60 A a	7.23 AB a	8.49 A a	29.2 B
$CaCl_2$ (−0.2 MPa)	3.67 DE	2.89 A a	1.90 A a	2.96 A a	6.16 B a	5.80 BC a	6.80 AB a	40.8 A
Na_2SO_4 (−0.1 MPa)	4.90 C	2.02 CD a	1.10 B b	1.80 B a	6.44 B a	6.22 ABC a	6.96 AB a	25.1 B
Na_2SO_4 (−0.2 MPa)	2.61 F	1.71 D ab	1.55 AB b	1.86 B a	4.21 C a	3.95 D a	4.78 C a	39.7 A

[1] Means followed by different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows.

reported in Table 6. For high NaCl and $CaCl_2$, dead leaf Cl concentrations of this population (9.8%−10.5%; data not shown) were about double those in the healthy leaves (see Table 7). Despite a substantially high combined Na plus Cl concentration of 16% in the dead leaves of −0.2 MPa NaCl, there was no indication that this treatment resulted in a higher dead leaf proportion than the other high salt treatments (see Table 4). For high NaCl and Na_2SO_4, Na masses in the dead leaves were comparable with those in the healthy leaves, as were the leaf Cl masses in dead and healthy leaves for high NaCl and $CaCl_2$ (Fig. 2).

The leaf K/Na molar ratio may distinguish glycophytes (normally high leaf K/Na ratios) from halophytes (normally low leaf K/Na ratios; Flowers and Läuchli, 1983). Examples of foliar K/Na ratios of glycophytes under nonsaline conditions range from 15 to 44, while those of halophytes under saline conditions range from 0.13 to 0.24, calculated from data cited by Flowers and Läuchli (1983). We then determined the healthy leaf K/Na molar ratios in our study (data not presented), and those of the control and $CaCl_2$-treated plants were in the glycophyte range, from 13 to 43. The leaf K/Na ratios in the NaCl and Na_2SO_4 treatments ranged from 0.19 to 0.43, which were in the halophyte range.

Discussion

Interactions between natural landscapes and human disturbance are difficult to clearly measure (Manier et al., 2014), as was the case for one of the *L. alyssoides* populations on the saline-sodic site mentioned previously (Picchioni et al., 2012a, 2012b). Limitations to that field study included mixed vegetation analysis; spatial and temporal variability in water supply and quality; confounding effects of water, nutrients, and salinity on vegetation biomass; and an inability to confirm a cause-and-effect relationship between soil salinity and growth stimulation of *L. alyssoides*, or between salinity and growth suppression of the co-occurring indigenous species. Thus, a controlled greenhouse study was essential to focus specifically on salinity responses of *L. alyssoides*.

Plant populations adapt to local conditions, and evidence is available for edaphic (soil-related) ecotypes of a given plant species (Epstein and Bloom, 2005). *Lepidium perfoliatum* L. germinated at higher rates under saline conditions if seed sources were from saline habitats as compared with seed sources from nonsaline habitats (Choudhuri, 1968). In our study, however, there were little or no population effects on plant ET and growth, and the Na and Cl concentrations of the three populations, within each tissue and salt treatment, were broadly similar. Lack of population effect may be due to the relatively small geographic range of the population sites. Even though the WM site had a sodic soil while the soils at the EM and MQ sites were nonsodic, there was no evidence to suggest that the WM population was adapted to perform best in NaCl and Na_2SO_4 treatments, which had high Na proportions. Rather, the present findings on site soil characteristics, ET, and growth suggest that *L. alyssoides* is an adaptive and resilient species with respect to soil sodicity, which is consistent with the concept that plant acclimation to a broad range of environmental conditions may be conducive for invasiveness (Higgins and Richardson, 2014). Irrespective of saline conditions, indigenous ruderal species may act like nonindigenous weeds and become invasive in response to human disturbance (Schwartz, 1997), and Brassicaceae members such as *Lepidium* spp. are largely ruderal in nature (Chapin, 1980). Two of the disturbed seed collection sites were nonsaline and nonsodic, and disturbance is known to increase competitiveness of ruderal over desirable native plant species (St. John, 1987).

Comparisons between isosmotic saline irrigation solutions may reveal the relative importance of adverse water relations (osmotic effects) and toxic effects of ion excess, particularly Na and Cl (Greenway and Munns, 1980). Our data on *L. alyssoides* suggest that plant ET and growth were largely controlled by the osmotic potential of the salt treatments. Comparing the −0.2 MPa NaCl treatment with the −0.2 MPa $CaCl_2$ and Na_2SO_4 treatments, there were no additional ET or growth suppressions with healthy leaf Na plus Cl concentrations (additive plant stresses in −0.2 MPa NaCl) reaching 9%–10% of dry weight. We were unable to detect an increase in dead leaf proportion or any decline in total ET, healthy leaf dry weight, root dry weight, or TDW with high

Table 5
Dry weight (DW) of stem and root tissue and total plant dry weight (TDW, healthy leaf from Table 6 plus stem and root) in g per 3 plants of the 3 populations of *L. alyssoides:* West Mesa (WM), Mesquite (MQ), and East Mesa (EM). Populations were pooled in the absence of population main effect. For treatment composition and properties, see Table 1.[1]

Treatment	Stem DW (g)			Root DW (g)	TDW (g)		
	WM	MQ	EM		WM	MQ	EM
Control	2.06 A a	2.56 A a	3.64 A a	3.98 A	13.15 A a	12.50 A a	13.66 A a
NaCl (−0.1 MPa)	0.99 B a	1.19 BC a	1.36 B a	2.73 B	7.58 C a	7.87 C a	9.18 B a
NaCl (−0.2 MPa)	0.49 B b	0.76 C ab	0.94 B a	1.90 C	5.22 D a	6.01 D a	6.65 C a
$CaCl_2$ (−0.1 MPa)	0.65 B b	1.46 B a	1.11 B a	2.85 B	9.79 B a	9.19 BC a	9.97 B a
$CaCl_2$ (−0.2 MPa)	0.64 B a	0.76 C a	0.77 B a	1.63 C	5.37 D a	6.35 D a	6.34 C a
Na_2SO_4 (−0.1 MPa)	1.03 B a	1.53 B a	1.92 B a	3.02 B	8.91 BC a	9.55 B a	9.78 B a
Na_2SO_4 (−0.2 MPa)	0.78 B b	0.76 C b	1.03 B a	1.85 C	4.95 D a	5.04 D a	5.96 C a

[1] Means followed by different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows.

Table 6
Sodium concentrations (percent of dry weight) in healthy leaves, stems, and roots of 3 populations of *Lepidium alyssoides:* West Mesa (WM), Mesquite (MQ), and East Mesa (EM). Populations were pooled in the absence of population main effect. For treatment composition and properties, see Table 1.[1]

Treatment	Na concentration (% of dry wt.)				
	Healthy leaves	Stems	Roots		
			WM	MQ	EM
Control	0.12 C	0.18 D	0.23 C a	0.28 BCD a	0.17 D a
NaCl (−0.1 MPa)	3.01 B	0.82 C	0.72 B a	0.68 AB a	0.55 BC a
NaCl (−0.2 MPa)	4.20 A	1.02 AB	0.80 AB a	0.87 A a	0.73 AB a
$CaCl_2$ (−0.1 MPa)	0.14 C	0.17 D	0.21 C a	0.19 CD a	0.24 CD a
$CaCl_2$ (−0.2 MPa)	0.04 C	0.15 D	0.22 C a	0.15 D b	0.15 D b
Na_2SO_4 (−0.1 MPa)	2.66 B	0.90 BC	0.71 B a	0.59 ABC a	0.93 A a
Na_2SO_4 (−0.2 MPa)	3.84 A	1.09 A	0.97 A a	0.97 A a	0.86 AB a

[1] Means followed by different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows.

NaCl than with high $CaCl_2$ and Na_2SO_4, the latter of which did not result in such high combined leaf Na and Cl concentrations as 9%–10%. The high salt accumulation indicates a leaf tissue tolerance to salinity by these populations and an ability to manage leaf Na and Cl through cellular compartmentation processes, while using the electrolytes beneficially to maintain water uptake.

In greenhouse potting substrates, leachate ("PourThru") EC is about 30% higher than the EC from a corresponding substrate saturation extract (SSE; Cox, 2005) that has long been the standard soil salinity metric for assessing crop salt tolerance (Maas and Hoffman, 1977). Given this relationship, leachate EC of the high-salt-treated plants in the present study (≈13–16 dS m^{-1}) would correspond to SSE salinities of ≈10–13 dS m^{-1}, at which numerous crops would have no yield potential (Ayers and Westcot, 1985). Nonetheless, vegetative growth (as TDW) of these *L. alyssoides* populations was suppressed by ≈50–60% at −0.2 MPa (high salt) relative to that of the control. The reductions in total ET can be attributed to salt-induced osmotic stress that hinders a plant's ability to absorb water, thereby leading to growth suppression (Munns and Tester, 2008). Further study is needed to determine salt effects on *L. alyssoides* belowground vegetative propagule production.

Regardless of the reductions in ET and dry matter production, continued growth, water use, and minimal symptoms of salt stress were observed in plants exposed to salinity throughout the duration of the 13-wk study, indicating tolerance to salinity. The healthy leaf Na concentrations in the NaCl and Na_2SO_4 treatments (2.7–4.2%) and the healthy leaf Cl concentrations in the NaCl and $CaCl_2$ treatments (4.4–6.6%) were exceptionally high compared with agricultural standards in that many crop species would express severe leaf necrosis at even much lower leaf Na and Cl concentrations (Ayers and Westcot, 1985). This was not the case with *L. alyssoides*, even with the high Na and Cl concentrations in healthy leaves. The combined Na and Cl concentration in healthy leaves of high NaCl of 9%–10% of leaf dry weight is on the order of halophyte concentrations (Glenn et al., 1994; Miyamoto et al., 1996). In addition, the low leaf K/Na ratios in the NaCl and Na_2SO_4 treatments may be regarded as a halophyte trait. Most halophytes are ion "includers" and store Na and Cl in leaf vacuoles as energy-efficient osmolytes for maintaining turgor pressure and water uptake in high-salt conditions (Flowers et al., 1977, 2015; Greenway and Munns, 1980; Munns and Tester, 2008).

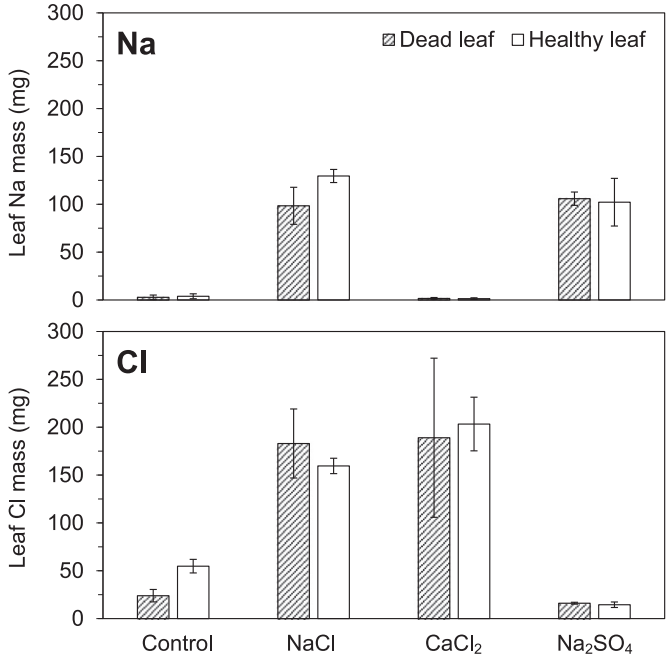

Figure 2. Masses of Na and Cl in dead and healthy leaves of the Mesquite (MQ) population of *L. alyssoides* (mg per three plants) under the high salt conditions (−0.2 MPa). For treatment composition and properties, see Table 1. Each observation is the mean ± standard deviation of three replications.

The findings implicate salinity and sodicity as facilitating factors for the invasive behavior of *L. alyssoides*. Grace (2001) stated that salinity may be an important "nonresource" factor regulating species pools. *L. alyssoides* may be able to exploit this growth-limiting factor as a vacant niche due to its tolerance, namely by using high leaf Na and Cl concentrations in ways that other species cannot. We propose that high salinity acts as an environmental "filter" by providing a competitive advantage for *L. alyssoides* over co-occurring, salt-sensitive plant species.

Despite the salt "inclusion" trait of these *L. alyssoides* populations, there may be an upper tolerance limit to Na and Cl accumulation in the leaves, beyond which leads to premature leaf senescence. There

Table 7
Chloride concentrations (percent of dry weight) in healthy leaves, stems, and roots of 3 populations of *Lepidium alyssoides:* West Mesa (WM), Mesquite (MQ), and East Mesa (EM). Populations were pooled in the absence of population main effect. For treatment composition and properties, see Table 1.[1]

Treatment	Cl concentration (% of dry wt.)						
	Healthy leaves			Stems	Roots		
	WM	MQ	EM		WM	MQ	EM
Control	0.98 B a	0.92 B a	0.90 D a	0.17 C	0.19 C a	0.20 C a	0.14 C a
NaCl (−0.1 MPa)	5.56 A a	4.65 A a	4.37 C a	0.60 A	0.74 A a	0.52 B ab	0.42 B b
NaCl (−0.2 MPa)	5.56 A a	5.02 A a	5.12 B a	0.68 A	0.77 A a	0.82 A a	0.60 A a
$CaCl_2$ (−0.1 MPa)	6.63 A a	4.93 A a	6.15 A a	0.46 B	0.58 B a	0.53 B a	0.48 AB a
$CaCl_2$ (−0.2 MPa)	6.44 A a	5.22 A a	5.03 BC a	0.61 A	0.73 A a	0.48 B b	0.48 AB b
Na_2SO_4 (−0.1 MPa)	0.63 B a	0.57 B a	0.60 D a	0.09 C	0.14 C a	0.13 C a	0.16 C a
Na_2SO_4 (−0.2 MPa)	0.75 B a	0.61 B a	0.59 D a	0.13 C	0.15 C a	0.14 C a	0.13 C a

[1] Means followed by different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows.

were sizeable salt masses in dead leaves of the MQ population, in light of their high dry weight proportions (up to ≈40% of total leaf dry weight) and high Na and Cl concentrations. For that population, both dead and abscised leaves, as well as healthy leaves, contained comparably high Na and Cl masses. Thus, in high-saline field conditions, considerable amounts of salt deposition from leaf litter could occur during the growing season and at the time of annual leaf shedding in autumn to winter months. Francis and Warwick (2007) concluded that Na-containing aboveground litter deposition by the related exotic invasive, *L. latifolium,* may offer a competitive advantage to that species over nonhalophytic plants. Their review referred to Blank and Young (2002), which reported much lower aboveground Na concentrations in that species (≈0.1–0.5% of dry weight) as compared with the potential that we report for these populations of *L. alyssoides*. Under saline-sodic soil conditions, *L. alyssoides* could recycle large amounts of Na and Cl back onto the landscape, thereby altering the ecosystem by governing the species pool to its own favor.

Dichotomously, this study supports the possibility that *L. alyssoides* can provide ecological value in the restoration of salinized landscapes, particularly when considering its indigenous heritage and tolerance to saline and sodic soils. For example, sustainable management of rangeland applications of saline residuals needs improved methods for halophyte community establishment (Flores et al., 2015) because halophytes have a competitive advantage to provide ecosystem services in saline conditions. On the basis of current findings, *L. alyssoides* may be a candidate to provide such services.

In conclusion, our study characterizes three southern New Mexico populations of *L. alyssoides* with a dual-role potential, in that 1) they can dominate salt-affected landscapes and perpetuate soil salinity through leaf litter deposition at the expense of other native species, and 2) they may provide beneficial ecosystem services to salinized landscapes due to their indigenous heritage and ability to tolerate saline-sodic soils. We hope that our report on *L. alyssoides* will raise awareness for research need on the effects of soil salinity and sodicity on rangeland ecosystems.

Implications

There is little understanding of specific soil salinity characteristics and salinity tolerances of invasive plants on arid and semiarid rangelands. The present study addresses this scientific deficit, particularly in reference to secondary salinization, and the attendant needs to predict plant invasions or exploit halophyte productivity on salt-affected landscapes, including those receiving nonhazardous saline residuals. We have identified three Chihuahuan Desert shrubland populations of the indigenous *L. alyssoides* possessing halophytic characteristics that, in turn, may facilitate their invasiveness on saline and sodic Chihuahuan Desert shrubland soils. Our findings contribute to a scarcity of quantitative data that reveal how salt-tolerant, salt-"including" plant species can exploit a saline environment and become invasive.

If osmotic effects control the salt responses of *L. alyssoides*, as indicated in the present study, then predicting vulnerability of landscapes to its dominance over salt-sensitive species can be assessed by soil osmotic potential or by the related colligative property of soil solution EC. Soil salinity appraisal by EC is a much simpler task than determination of specific ion concentrations. A broader implication of our study, limited to a single species, is that this straightforward procedure should be applicable to any invasive weedy species with demonstrable salt tolerance. While more study on additional *L. alyssoides* populations is needed, implications of the present findings to land managers are twofold. If the objective of the land manager is to maintain native plant species diversity on disturbed shrublands, then this species and other salt-tolerant species could be the target of a prevention strategy that is focused on scouting disturbed areas affected by salinity. A simple EC test of the soil or water can be a practical and cost-effective assessment tool to help predict their invasions. If the objective of the land manager is to exploit the halophyte trait, then *L. alyssoides* and salt-tolerant counterparts may have ecological value. In particular, such species may be suitable candidates for the management scenario of halophyte community establishment on saline-sodic rangelands. Our model of *L. alyssoides* may have unique roles in that it may be targeted as an invasive species on salinized landscapes while, alternatively, it may serve beneficially to restore and maintain viability of salt-affected landscapes due to its halophyte characteristics and indigenous status.

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