

*Halophyte ion regulation traits support saline adaptation of *Lepidium latifolium*, *L. draba*, and *L. alyssoides**

**Geno A. Picchioni, Triston N. Hooks,
Brian J. Schutte, Manoj K. Shukla &
David L. Daniel**

Plant Ecology
An International Journal

ISSN 1385-0237
Volume 221
Number 4

Plant Ecol (2020) 221:295-308
DOI 10.1007/s11258-020-01012-5

Your article is protected by copyright and all rights are held exclusively by Springer Nature B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Halophyte ion regulation traits support saline adaptation of *Lepidium latifolium*, *L. draba*, and *L. alyssoides*

Geno A. Picchioni · Triston N. Hooks · Brian J. Schutte · Manoj K. Shukla · David L. Daniel

Received: 27 September 2019 / Accepted: 11 February 2020 / Published online: 19 February 2020
© Springer Nature B.V. 2020

Abstract Identification of saline resistance traits of invasive plants has received little study and could reveal how some plant species utilize salt to encroach upon salinized landscapes. We conducted a 3-mo greenhouse study to identify saline resistance mechanisms of three North American invasive Brassicaceae species, *Lepidium latifolium*, *L. draba*, and *L. alyssoides*, in response to increasing salinity. Seedlings of central and southern New Mexico, USA populations were exposed to NaCl irrigation solutions at 0, – 0.1, and – 0.2 MPa (0, 24, and 48 mM, respectively). Saline resistance of these populations was attributable to salt *tolerance* behavior commonly observed as signature traits of halophytes, including a combined Na and Cl accumulation in leaves of up to

13% of dry weight with no injury, dominance of leaves as the salt accumulation site, leaf tissue water Na and Cl at \approx 300–400 mM, leaf K:Na molar ratio of less than 1, and the development of leaf succulence. In saline environments, high salt loads in shoots may increase soil salinity through annual litter fall and potentially alter vegetation community structure. A broader implication of this study is in the need to detect salt resistant traits of additional plant species to broaden the narrow understanding of how salinity affects vegetation communities.

Keywords Invasive plants · Brassicaceae · Sodium chloride · Succulence · Litter · Propagule pressure

Communicated by Daniel L. Potts.

G. A. Picchioni (✉) · T. N. Hooks · M. K. Shukla
Department of Plant and Environmental Sciences, New Mexico State University, MSC 3Q,
Box 30003, Las Cruces, NM 88003, USA
e-mail: gpicchio@nmsu.edu

B. J. Schutte
Department of Entomology, Plant Pathology, and Weed Science, New Mexico State University, MSC 3BE,
Box 30003, Las Cruces, NM 88003, USA

D. L. Daniel
Department of Economics, Applied Statistics, and International Business, New Mexico State University, MSC 5280, Box 30001, Las Cruces, NM 88003, USA

Introduction

Salinity is a driving factor in plant community assembly (Bui 2013) because on salinized sites, species compositions shift towards dominance by saline resistant plants (Walker and Smith 1997; Vance et al. 2008). In the western USA, salinity can be a “non-resource” factor determining plant species diversity and composition (Cox et al. 2006; Vance et al. 2008; Picchioni et al. 2012a; Sagers et al. 2017). Environmental “filtering” by abiotic stress including salinity restricts species migration and survival as a result of functional trait convergence (Gong et al. 2019). Thus, high selection pressure on functional

traits that confer resistance to salt toxicity (Li et al. 2017) may play an important role in regulating community composition due to differential plant saline resistance (Munns and Tester 2008).

Unlike the established crop salinity database (Ayers and Westcot 1985), there has been limited quantitative study on salt uptake and transport characteristics of non-cultivated, invasive plant species. Improved knowledge of saline resistance mechanisms of invasive plant species is needed for further development of management tactics that aim to prevent and mitigate plant invasions in the western USA, a region where non-native plant species occupy about half of the total land area (Herrick et al. 2010). One general mechanism by which invasive plants might tolerate salinity is sequestration of salt in aboveground, herbaceous tissues. This salinity tolerance mechanism is sometimes referred to as shoot salt “inclusion” and is a prominent trait expressed by many halophytes (Flowers et al. 2015). Shoot salt inclusion in invasive plant species could result in high salt deposition to the ground through annual shoot litter fall, thereby increasing soil salinity and displacing salt intolerant native species (Vivrette and Muller 1977; Sagers et al. 2017). Shoot salt “exclusion” is a characteristic of salt-sensitive glycophytes (Munns and Tester 2008). In invasive plant species, shoot salt exclusion could sequester salt in perennial underground tissues (Picchioni et al. 1990) and potentially reduce soil salinity.

Lepidium latifolium L. (perennial pepperweed) and *L. draba* L. (whitetop) are herbaceous Brassicaceae perennials that are valued in their indigenous Eurasian countries for genetic resources (Singh et al. 2016; Sinha et al. 2014; Grover et al. 2014), site restoration and phytoremediation (Francis and Warwick 2008; Suchkova et al. 2014; Hajiboland et al. 2018), and nutraceuticals (Boestfleisch et al. 2014; Francis and Warwick 2008; Kaur et al. 2013). In the western USA, however, the alien *L. latifolium* and *L. draba* are considered noxious and highly invasive (Andrew and Ustin 2009; Renz et al. 2012; Cripps et al. 2009). Salt responses of these species have not been adequately explained because claims of adaptability to soil salinity and alkalinity were based on habitat occurrences and not on quantitative data related to plant growth and ion uptake (Hooks et al. 2018a and references cited therein).

Lepidium alyssoides A. Gray var. *alyssoides* (mesa pepperwort), another Brassicaceae herbaceous

perennial species, is indigenous to the southwestern USA and has received sparse attention in the vegetation science literature. We reported the invasive behavior of *L. alyssoides* that coincided with a seven-fold loss in species richness on a salinizing Chihuahuan Desert shrubland (Picchioni et al. 2012a, b). Under greenhouse conditions, leaf Na and Cl accumulation of NaCl-treated *L. alyssoides* reached a halophytic proportion of 10% of leaf dry weight with no leaf injury (Hooks et al. 2018b). The question arises as to whether the two exotic and invasive relatives, *L. latifolium* and *L. draba*, exhibit a similar halophyte salt regulation pattern.

Disclosing functional traits that confer high competitiveness in saline ecosystems is needed to explain how salt resistant species can exploit salinity to become dominant and adversely affect ecosystems. Understanding how invasive plants respond to increasing salinity may help improve ability to identify vulnerable habitats, predict invasions, and preserve biodiversity (Grewell et al. 2016). Due to the highly competitive nature of *L. latifolium* and difficulty in controlling its infestations, Leininger and Foin (2009) suggested that the best strategy is to prevent colonization and to consider soil salinity as a useful metric for assessing invasibility of the environment—a key factor determining ecological success of invasive species (Dyderski and Jagodziński 2018; You et al. 2016)—and thus for prioritizing control and eradication efforts.

Hooks et al. (2018a) confirmed the saline resistance of *L. latifolium*, *L. draba*, and *L. alyssoides* by comparing their water use and total dry matter production to that of the salt tolerant standard, cotton (*Gossypium hirsutum* L.) (Ayers and Westcot 1985), under the same greenhouse experimental conditions. In that study, despite 30% to 40% reductions in total plant dry matter accumulation by -0.2 MPa NaCl in the irrigation solution, water use and dry matter production of the *Lepidium* spp. met or exceeded that of cotton as the saturation extract of the root substrate reached an estimated 10 dS m^{-1} , a lethal salinity level for numerous agricultural crops (Ayers and Westcot 1985). Hooks et al. (2018a) did not disclose the physiological basis of the salt resistance, or whether the species behave as shoot salt “includers” or shoot salt “excluders” in common experimental conditions. We hypothesized that the three *Lepidium* spp. in question express traits of *saline tolerance*, namely

high Na and Cl uptake and transport to leaves, and low leaf K/Na ratio when exposed to high salinity. The objective of the present study was to clarify the physiological basis of saline resistance of New Mexico, USA populations of *L. latifolium*, *L. draba*, and *L. alyssoides*, particularly to verify if these species possess halophytic traits by evaluating their ion uptake and transport characteristics when exposed to increasing salinity. A broader intent was to use these data as a case for further testing, the quantification of salt resistance, uptake, and transport characteristics for the wider array of invasive plants on arid and semiarid lands.

Materials and methods

Seed sources, greenhouse environment, and seedling establishment

Seeds of all species were collected from heavy infestations at rural sites in New Mexico (1200 to 1481 m elevation) that were altered by grading, paving, excavation, surface water diversion, or vegetation clearing (Hooks et al. 2018a). *Lepidium alyssoides* seeds were collected near the town of Mesquite (southern New Mexico; 106° 41' W, 32° 10' N). Seeds of *L. latifolium* and *L. draba* were obtained near Los Lunas (central New Mexico; 106° 40' W, 34° 49' N and 106° 43' W, 34° 43' N, respectively). Further details on seed collection and handling are in Hooks et al. (2018a).

The study was completed in a greenhouse at the New Mexico State University (NMSU) Fabian Garcia Agricultural Science Center in Las Cruces, located about 1.5 km from the NMSU campus. In the greenhouse, the average maximum and minimum temperatures were 27 °C and 18 °C, respectively, maximum photosynthetic photon flux was 717 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the daily light integral averaged 13 $\text{mol m}^{-2} \text{day}^{-1}$, and a constant photoperiod of 16 h was maintained by daylength extension with supplemental lighting (Hooks et al. 2018a). Seeds of each species were sown at a depth of 1 cm in coarse acid-washed silica sand that filled 107-mL conical plant grow tubes measuring 3.8 cm wide by 14 cm tall (SC7 Ray Leach Cone-tainers, Stuewe and Sons Inc., Tangent, Oregon, USA). Three seeds were sown per tube. Small volumes of tap water were added to the sand surface until

emergence (\approx 1 week after sowing), at which time the tubes were thinned to a single seedling. The seedlings were established for a period of 11 weeks after sowing by subirrigation with tap water that was supplemented with complete Hoagland nutrient solution #1 (Hoagland and Arnon 1950) at half-strength (1.6 dS m^{-1} ; pH 5.8). The tap water (0.6 dS m^{-1} ; pH 7.8) included an extra 6 meq L^{-1} of both cations (combined Ca, Na, and Mg) and anions (combined Cl, SO_4 , and HCO_3). At 12 weeks after sowing, seedlings had produced multiple whorls of true leaves.

Saline irrigation, leaf growth, and plant ion analysis

Saline irrigation began 12 weeks (87 days) after sowing using the three solutions shown in Table 1. For the two NaCl solution treatments, 2 days stepwise increments of -0.05 MPa (\approx 12 mM) NaCl were initially applied to prevent osmotic shock. The final osmotic potential of the -0.2 MPa solution was reached 8 d after initiation of treatment. Irrigation was supplied to the sand surface when approximately 50% of the total water storage in the sand (measured gravimetrically) had been depleted, and in an amount to cause an average $42 \pm 6\%$ leaching fraction [(leachate volume/irrigation volume) \times 100].

After 13 weeks (89 days) of saline irrigation, the shoot tissues were cut at the sand surface, rinsed three times in deionized water, blotted dry, and separated into leaves and stems. Underground tissues (combined roots and rhizomes) were washed free of sand and rinsed as described for shoots. Total leaf area was measured using a LI-3100C area meter (LI-COR Biosciences, Lincoln, Nebraska, USA). Total leaf fresh weight, total number of leaves, and the average area per leaf were also determined. All tissues were dried for 48 h at 60 °C in a forced draft oven, weighed, and the leaf fresh weight:dry weight ratio (FW:DW) was determined. Dried tissues were ground in a wiley mill to pass a 40-mesh (0.42 mm) screen. The ground tissues were thoroughly mixed, and 0.25-g subsamples were subjected to microwave extraction with a MARS 5 microwave digestion system (CEM Corp., Matthews, North Carolina, USA) using the methods of Jones et al. (1991). Analyses of Na in all plant organs (leaves, stems, and underground tissues) and K (leaves only) were made on an inductively coupled plasma atomic emission spectrometer (Optima 4300 V ICP-

Table 1 Composition and properties of the irrigation solutions used in the experiment

Treatment	NaCl addition (mM)	EC (dS m ⁻¹) ^a	EC (dS m ⁻¹) ^b	SAR ^c
Control	0	–	1.6	1.2
NaCl (– 0.1 MPa)	24	2.3	3.9	11.7
NaCl (– 0.2 MPa)	48	4.6	6.2	22.3

^aElectrical conductivity due to NaCl addition only and corresponding to osmotic potential

^bElectrical conductivity of irrigation solutions, including NaCl, half-strength Hoagland's complete nutrient solution, and tap water

^cSodium adsorption ratio of irrigation solutions calculated as $\text{Na}/(\text{Ca} + \text{Mg})^{1/2}$, all ions in mM, and including ion contributions from NaCl, half-strength Hoagland's solution, and the tap water

AES, Perkin Elmer, Shelton, Connecticut, USA). Additional 0.1-g subsamples of the leaves, stems, and underground tissues were digested in 2% acetic acid at room temperature (Jones et al. 1991) for determination of Cl on an auto-analyzer (AA II, Technicon Instruments, Tarrytown, New York, USA). The Na and Cl concentrations were expressed on the basis of percentage of dry weight. The masses (milligrams) of Na and Cl per plant organ were determined as the product of ion concentration by organ dry weight. Plant distributions of Na and Cl were calculated as ion mass per organ divided by total plant ion mass, times 100. For leaves only, Na and Cl concentrations were expressed on a tissue water basis (mmol L⁻¹) and the K:Na ratio was expressed on a mol mol⁻¹ basis.

Experimental design and statistical analysis

The study was arranged as a randomized complete block with three replications and split plots. Saline solution treatment was the main plot and species was the subplot. Three plants, each in their separate grow tubes, represented one replication. For all leaf growth and plant ion response variables, the analysis of variance was performed using PROC GLM in SAS (version 9.3, SAS Institute, Cary, North Carolina, USA). Significance ($P \leq 0.05$) of saline treatment and species main effects, as well as the treatment \times species interaction, were determined by *F*-tests. Where appropriate, main plot (saline solution) treatment means for a given subplot (species) and subplot means within main plots were separated by Duncan's multiple range test at an alpha of 0.05.

Results

Leaf growth

Only the species affected the total number of leaves ($P < 0.0001$; data not shown). On average, *L. latifolium* produced the fewest leaves (102 leaves per three plants), while *L. draba* and *L. alyssooides* produced the most (378 and 397 leaves per three plants, respectively). The average area per leaf was affected by saline treatment, species, and the treatment \times species interaction ($P < 0.0110$; data not shown). Across all treatments, *L. latifolium* had the largest area per leaf (7.2 to 10.8 cm²) followed by *L. draba* (3.3 to 4.7 cm²) and by *L. alyssooides* (1.1 to 2.0 cm²). Increasing salinity did not affect area per leaf of *L. alyssooides*. However, the – 0.1 MPa NaCl solution caused 25–30% reductions in area per leaf of *L. draba* and *L. latifolium*, with no further reductions at – 0.2 MPa NaCl.

The main effects of species and saline treatment on total leaf fresh weight and on the leaf FW:DW ratio were significant ($P < 0.0200$), but there were no salinity \times species interactions. The highest leaf fresh weights were noted for *L. draba* (Table 2). High NaCl at – 0.2 MPa reduced the *L. draba* leaf weight by 14% below the control, whereas the leaf weights of *L. alyssooides* and *L. latifolium* were unaffected by increasing salinity. In general, *L. draba* had the highest leaf FW:DW across the treatments (Table 2). Unlike *L. alyssooides*, *L. draba* maintained high leaf FW:DW when exposed to both – 0.1 MPa and – 0.2 MPa NaCl salinity, and *L. latifolium* expressed incremental increases in leaf FW:DW with each increase in NaCl salinity.

Table 2 Total leaf fresh weight, leaf fresh weight:dry weight ratio (FW:DW), and total leaf area of *L. alyssoides*, *L. draba*, and *L. latifolium*

Treatment	Species		
	<i>L. alyssoides</i>	<i>L. draba</i>	<i>L. latifolium</i>
Total leaf fresh weight (g per three plants)			
Control	53.22 AB b ^z	77.21 A a	54.51 A b
NaCl (– 0.1 MPa)	57.74 A b	74.41 A a	55.66 A b
NaCl (– 0.2 MPa)	46.95 B b	66.04 B a	52.52 A b
Leaf FW:DW			
Control	4.32 A b	5.48 B a	4.72 C b
NaCl (– 0.1 MPa)	5.01 A b	6.73 A a	5.31 B b
NaCl (– 0.2 MPa)	4.95 A b	6.61 AB a	5.79 A ab
Total leaf area (cm ² per three plants)			
Control	514.37 A c	1707.11 A a	955.95 A b
NaCl (– 0.1 MPa)	565.89 A c	1449.60 B a	870.05 B b
NaCl (– 0.2 MPa)	443.57 A c	1168.32 C a	721.52 C b

For treatment composition and properties, see Table 1

^zWithin response variables, means with different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows

Treatment, species, and the treatment × species interaction affected total leaf area ($P < 0.0020$). For all treatments, *L. draba* had the highest total leaf area, *L. alyssoides* the lowest, with *L. latifolium* intermediate (Table 2). Progressive declines in total leaf area of *L. draba* and *L. latifolium* were observed with each addition of NaCl. By contrast, leaf area of *L. alyssoides* did not decline significantly with increasing salinity.

Plant Na and Cl concentrations in the dry matter

Apart from lack of a species main effect on stem Na concentrations ($P = 0.1593$), both treatment and species main effects on plant Na and Cl concentrations were significant for all plant organs ($P < 0.0052$). There were no treatment × species interactions on plant Na or Cl concentrations ($P > 0.1054$), except for leaf Na ($P = 0.0237$) and stem Cl ($P = 0.0180$). The latter interactions arose from the relatively large increases in leaf Na and stem Cl in *L. draba* between the control and – 0.1 MPa NaCl solution treatments, as compared with the smaller increases in leaf Na and stem Cl in *L. alyssoides* and *L. latifolium* at – 0.1 MPa NaCl (Tables 3, 4).

The increases in plant Na and Cl concentrations with increasing salinity were not consistently additive across the treatment levels (Tables 3, 4). At – 0.1 MPa and – 0.2 MPa NaCl, Na and Cl concentrations in leaves were markedly higher than in stems and underground tissues. In those treatments, *L. draba*

Table 3 Sodium (Na) concentrations as percent of dry weight in leaf, stem, and underground tissue of *L. alyssoides*, *L. draba*, and *L. latifolium*

Treatment	Species		
	<i>L. alyssoides</i>	<i>L. draba</i>	<i>L. latifolium</i>
Leaf Na (%)			
Control	0.13 B c ^z	0.50 B b	0.66 C a
NaCl (– 0.1 MPa)	2.06 A b	3.95 A a	3.12 B a
NaCl (– 0.2 MPa)	2.63 A b	5.52 A a	4.45 A ab
Stem Na (%)			
Control	0.16 B	0.10 B	0.10 B
NaCl (– 0.1 MPa)	0.63 A	1.08 AB	0.77 A
NaCl (– 0.2 MPa)	1.03 A	1.57 A	1.04 A
Underground tissue Na (%)			
Control	0.23 B a	0.22 B a	0.13 C a
NaCl (– 0.1 MPa)	0.54 A a	0.60 A a	0.30 B b
NaCl (– 0.2 MPa)	0.65 A a	0.66 A a	0.42 A a

For treatment composition and properties, see Table 1

^zWithin response variables, means with different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows

and *L. latifolium* registered generally higher leaf Na than did *L. alyssoides*, reaching up to 4.5–5.5% (Table 3). Leaf Cl of *L. draba* was highest among all species at – 0.1 MPa NaCl, although its high leaf Cl at – 0.2 MPa NaCl (7.4%) did not differ significantly ($P \leq 0.05$) from that of the other species (Table 4). Regardless of the high combined leaf Na

Table 4 Chloride (Cl) concentrations as percent of dry weight in leaf, stem, and underground tissue of *L. alyssoides*, *L. draba*, and *L. latifolium*

Treatment	Species		
	<i>L. alyssoides</i>	<i>L. draba</i>	<i>L. latifolium</i>
Leaf Cl (%)			
Control	1.10 B c ^z	1.63 B a	1.42 C b
NaCl (– 0.1 MPa)	3.85 A b	5.84 A a	3.56 B b
NaCl (– 0.2 MPa)	4.52 A a	7.38 A a	4.99 A a
Stem Cl (%)			
Control	0.11 C c	0.45 B b	0.66 B a
NaCl (– 0.1 MPa)	0.40 B c	1.94 A a	1.35 A b
NaCl (– 0.2 MPa)	0.68 A b	2.83 A a	1.65 A ab
Underground tissue Cl (%)			
Control	0.13 C c	0.23 B b	0.44 C a
NaCl (– 0.1 MPa)	0.43 B b	0.71 A a	0.57 B ab
NaCl (– 0.2 MPa)	0.72 A a	0.96 A a	0.81 A a

For treatment composition and properties, see Table 1

^zWithin response variables, means with different letters indicate a significant difference according to Duncan's Multiple Range Test ($P < 0.05$); uppercase within columns, lowercase within rows

and Cl at – 0.2 MPa NaCl (7% to 13% of dry weight), none of the species expressed leaf necrosis or abscission.

With increasing salinity, stem Na concentrations in all species increased in magnitude more noticeably than in the underground tissues and rose to 1–1.6% at – 0.2 MPa NaCl. A similar pattern was observed for stem Cl in *L. draba* and *L. latifolium* vis-à-vis underground tissue Cl, with the stem Cl increasing to 1.7–2.8%. This pattern was not expressed by *L. alyssoides* which had relatively low stem Cl concentrations in all treatments.

Leaf K:Na ratio

Both treatment and species affected the leaf K:Na molar ratio ($P < 0.0009$), as did the treatment \times species interaction ($P < 0.0001$). The K:Na ratio of the control treatment ranged from 4 to 15 depending on species, whereas the K:Na ratio of the NaCl-treated plants ranged from only 0.16 to 0.56 (Fig. 1). In the controls, the leaf K:Na ratio of *L. alyssoides* was variable (cv = 29%) but more than 2–4 times higher than the K:Na ratios of *L. draba* and *L.*

latifolium. However, all species shared equally low ratios in the NaCl treatments.

Leaf Na and Cl masses

The Na and Cl distribution patterns in plants irrigated with – 0.1 MPa and – 0.2 MPa NaCl showed that $\geq 70\%$ of the amount of Na and Cl was in leaves. We focused on the leaf ion masses in light of their dominance throughout the plant. Both treatment and species affected leaf Na and Cl masses ($P < 0.0001$). The treatment \times species interaction affected leaf Na mass ($P = 0.0006$) but not leaf Cl mass ($P = 0.0541$). The leaf Na and Cl masses were smallest in the controls, as expected (Fig. 2). Unlike for *L. alyssoides* leaves, there were additional increments in leaf Na mass of *L. draba* and *L. latifolium* as NaCl was increased from – 0.1 to – 0.2 MPa NaCl, although only *L. latifolium* leaves experienced a second increase in leaf Cl at – 0.2 MPa NaCl. In the NaCl treatments, *L. draba* leaves contained the highest amounts of Na and Cl among all species. Added together, the combined Na and Cl masses in leaves at high salinity (– 0.2 MPa NaCl) per three-seedling experimental unit averaged 673 mg for *L. alyssoides*, 856 mg for *L. latifolium*, and 1270 mg for *L. draba*.

Leaf Na and Cl concentrations in the tissue water

Leaf Na and Cl concentrations expressed on a tissue water basis were significantly affected by salt treatment ($P < 0.0001$) and by species ($P < 0.0001$ and $P < 0.0400$ for Na and Cl, respectively), but not by the treatment \times species interaction ($P > 0.0569$). Leaf Na in the tissue water of all species increased with each increase in NaCl salinity, although for leaf Cl in the tissue water, this pattern was observed only for *L. latifolium* (Fig. 3). The species trends for Na and Cl in the leaf tissue water of plants treated with – 0.1 MPa and – 0.2 MPa NaCl were broadly consistent with those previously reported in the dry matter. That is, there were generally lower Na concentrations in the leaf tissue water of *L. alyssoides* than there were in *L. draba* and *L. latifolium*, and the Cl concentrations in the leaf tissue water of *L. draba* tended to be the highest of all species. At – 0.2 MPa NaCl, leaf Na increased to 287–425 mM and leaf Cl to 294–367 mM depending on species.

Fig. 1 Potassium:sodium (K:Na) molar ratio in leaf tissue of *L. alyssoides*, *L. draba*, and *L. latifolium*. Each value is the mean \pm SD of three replications. Means with different letters indicate significant differences according to Duncan's Multiple Range Test ($P \leq 0.05$); uppercase within species across treatments, lowercase within treatments across species. For treatment composition and properties, see Table 1

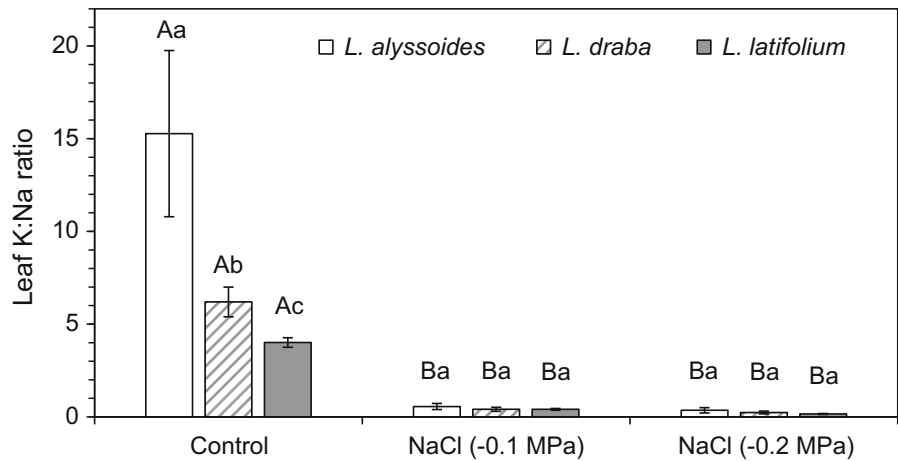
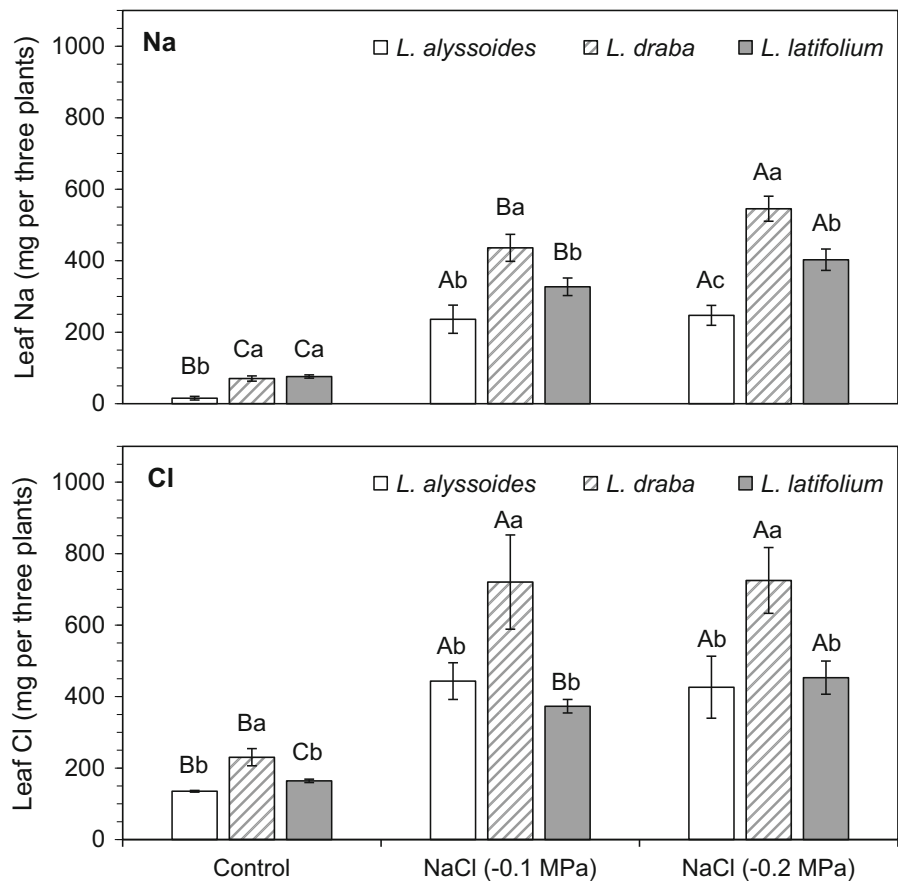


Fig. 2 Total Na and Cl masses in leaf tissue of *L. alyssoides*, *L. draba*, and *L. latifolium*. Each value is the mean \pm SD of three replications. Means with different letters indicate significant differences according to Duncan's Multiple Range Test ($P \leq 0.05$); uppercase within species across treatments, lowercase within treatments across species. For treatment composition and properties, see Table 1



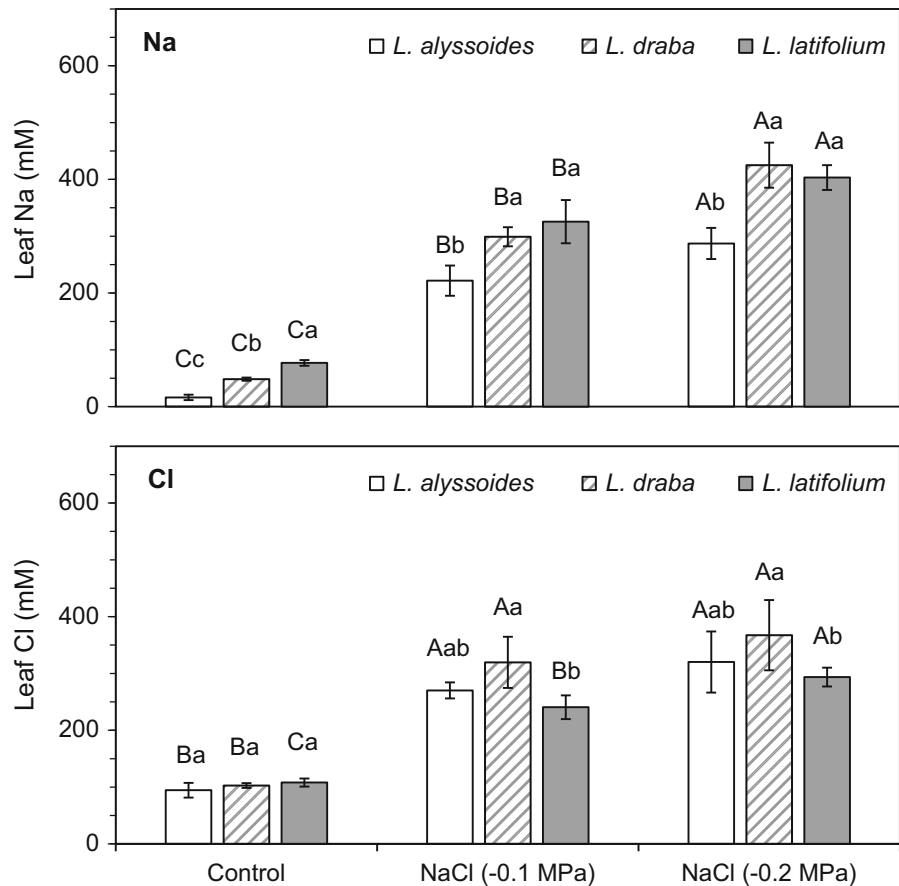
Discussion

Salt tolerance traits

Adaptability of *L. latifolium* and *L. draba* to saline soils has been recounted anecdotally for several

decades (see review in Hooks et al. 2018a). The present study on alien invasive New Mexico populations of *L. latifolium* and *L. draba* validates the earlier reports by defining saline resistance and adaptability as a tolerance to high leaf Na and Cl concentrations. *Lepidium alyssoides* expressed the same halophytic

Fig. 3 Leaf Na and Cl concentrations on a tissue water basis (mmol L^{-1}) of *L. alyssoides*, *L. draba*, and *L. latifolium*. Each value is the mean \pm SD of three replications. Means with different letters indicate significant differences according to Duncan's Multiple Range Test ($P \leq 0.05$); uppercase within species across treatments, lowercase within treatments across species. For treatment composition and properties, see Table 1



traits as the exotic relatives that facilitate its colonization of salinized shrubland, and that add to an emerging concern over “native-invasive” plant species (Al Hassan et al. 2016; Hooks et al. 2018b).

Underpinning the salt tolerance of both exotic *L. latifolium* and *L. draba*, and indigenous *L. alyssoides* are the concentrations of leaf Na (2.6–5.5% of dry weight) and leaf Cl (4.5–7.4% of dry weight) that failed to cause salt toxicity symptoms, and that are exceptionally high on agricultural standards (Ayers and Westcot 1985). Even in the control treatment, leaf Cl ranged from 1.1 to 1.6% when the irrigation solution Cl was only 0.5 meq L^{-1} . Up to now, leaf Na of *Lepidium* spp. as high as that shown in Table 3 has not been reported. Suchkova et al. (2014) reported a Na concentration in *L. draba* (tissue unspecified) of 0.2% of dry weight as “quite high.” In the review by Francis and Warwick (2007), the authors concluded that *L. latifolium* tolerates “high” Na levels by referring to Blank and Young (2002), who reported a

shoot Na concentration of less than 0.4% of dry weight.

Halophytes are characterized by their ability to tolerate high concentrations of Na and Cl in leaves that would be lethal to non-halophytes (Flowers et al. 2015). For example, excessive leaf necrosis of many agricultural crops occurs when leaves accumulate less than 1% Cl and less than 0.5% Na on a dry weight basis (Ayers and Westcot 1985). By contrast, categorically high leaf Na and Cl reported in our study—combined concentration of 7% to 13% of dry weight and with no signs of leaf necrosis—is characteristic of halophytes (Glenn et al. 1994; Miyamoto et al. 1996), and consistent with the necessity of halophytes to deposit substantial amounts of salt in shoots in order to maintain a gradient of free energy from substrate to leaf (Flowers 1972). Salt “includers” store Na and Cl in leaf vacuoles and “out of harm’s way” as inexpensive beneficial osmotica to sustain turgor and water uptake in high salt conditions (Flowers et al.

1977, 2015; Greenway and Munns 1980; Munns and Tester 2008; Subbarao et al. 2003). Since subcellular localization of Na and Cl was beyond the scope of the present study, further research is needed to confirm that the high leaf Na and Cl accumulation in the *Lepidium* spp. was confined to the vacuole. Leaf K:Na molar ratios of glycophytes in non-saline conditions range from ≈ 14 to 44, while those of halophytes under saline conditions vary between ≈ 0.1 to 0.3 (calculated from data presented in Flowers and Läuchli 1983). The present study shows not only that the *Lepidium* spp. tolerated low leaf K:Na ratios (< 1) in the NaCl treatments, but also that the species maintained relatively low leaf K:Na ratios in the non-saline control treatment (< 15).

Tissue water Na and Cl concentrations largely reflect vacuolar concentrations that may reach or exceed 500 mM in halophytes and rarely surpass 100 mM in glycophytes (Flowers et al. 2015). The tissue water Na and Cl concentrations of ≈ 300 –400 mM (Fig. 3) more closely resemble those of halophytes than those of glycophytes. High leaf tissue water Na and Cl parallels tissue tolerance that is, in part, facilitated by increasing succulence through vacuolar expansion and development (Jennings 1976; Wyn Jones 1981). Data in Table 2 suggest that *L. draba* and *L. latifolium* possess leaf succulence traits under saline conditions. We note here the salinity-induced reductions in total leaf area due to smaller leaves with no salt effect on total leaf fresh weight up to -0.1 MPa NaCl (*L. draba*) or to -0.2 MPa (*L. latifolium*). Further indication of leaf succulence is the increase in leaf FW:DW of *L. draba* at -0.1 MPa NaCl, and in the progressive increase in leaf FW:DW of *L. latifolium* up to -0.2 MPa NaCl. These responses may be explained by increased leaf thickness and hydration due to promotion of leaf succulence within the tissue to maintain turgor and lessen toxic effects of stored salt.

Salt plasticity

Species adapted to a broad range of environmental conditions are more likely to be invasive than species with limited adaptability (Higgins and Richardson 2014). For example, northern California *L. latifolium* populations occupy both fresh water and brackish marsh habitats (Leininger and Foin 2009). Common at the *L. latifolium*, *L. draba*, and *L. alyssoides* seed

collection sites were soil disturbances that are known to encourage proliferation of these species regardless of soil salinity and sodicity (Renz et al. 2012; Larson and Kiemnec 2005; Hinz et al. 2012; Francis and Warwick 2008; Hooks et al. 2018b). At the collection sites, the soils were neither saline nor sodic (Hooks et al. 2018a), and the combined Na and Cl concentrations in composited samples of the bulk shoot dry matter were no higher than 0.7% (Picchioni et al. 2015), 10–19 times lower than in leaves of the high-NaCl greenhouse treatment. When irrigated with high-Na waters in a greenhouse, an *L. alyssoides* population from a sodic site showed no greater fitness advantage to high Na than did two other *L. alyssoides* populations from non-sodic sites (Hooks et al. 2018b). These observations suggest that plasticity in salt tolerance enables these species to colonize both saline and non-saline sites.

Plant invasive success is positively associated with genotypic and phenotypic diversity of colonizing populations (Forsman 2014). Phenotypic plasticity, the ability of a plant to alter its morphology and physiology in response to temporal and spatial environmental variability (Schlichting 1986; Valladares et al. 2007), is thought to play an important role in invasions by enabling the expression of adaptive phenotypes over a broad range of environments (Richards et al. 2006). In the salt marsh plant, *Borrichia frutescens* (L.) DC, selection may favor plasticity in leaf succulence and leaf Na concentration across experimental salt treatments (Richards et al. 2010). When exposed to salinity, development of leaf succulence may be adaptive for the *Lepidium* spp. since they lack salt glands and bladder cells to excrete or sequester salt, and they store most of the Na and Cl in leaves (Richards et al. 2010). Phenotypic plasticity in leaf Na and Cl concentration and the leaf K:Na ratio may facilitate adaptation of the *Lepidium* spp. to different levels of salinity.

We found no mention in the literature of *L. draba* and *L. alyssoides* as halophytes, and designation of *L. latifolium* as a halophyte is inconsistent. Francis and Warwick (2007) stated that *L. latifolium* is usually not identified as a halophyte, whereas Boestfleisch et al. (2014) and Ahmed and Khan (2010) later recognized *L. latifolium* as a halophyte with little explanation. The conflicting information, or lack therein, is symptomatic of the absence of quantitative salt tolerance data on this taxon. The present study has demonstrated

characteristic halophytic traits of *Lepidium draba*, *L. latifolium*, and *L. alyssoides*, most notably the high leaf Na and Cl concentrations along with low leaf K/Na ratios. Flowers et al. (2015) stated that the limits to salt tolerance in halophytes are poorly defined in either natural conditions or controlled environments, thus they “arbitrarily” defined halophytes as plants that are capable of completing their life cycle at a NaCl concentration of ≥ 200 mM in their natural environment (Flowers et al. 2015; Flowers and Colmer 2008). Their original definition included NaCl concentrations in excess of 100 to 200 mM (Flowers et al. 1986), which correspond to electrical conductivities (ECs) of ≈ 9 to 18 dS m⁻¹. While our results in a controlled environment may not be directly applicable to the latter criteria that are based on natural environments, the estimated EC of the root substrate saturation extract in our study noted previously (≈ 10 dS m⁻¹) is at the low halophyte salinity range originally reported in Flowers et al. (1986). Unlike obligatory halophytes that require high salinity for their subsistence, facultative halophytes have the ability to grow in either saline or non-saline environments (Parida and Das 2005; Mishra and Tanna 2017). Considering the findings in the present study along with the seed collection site histories, facultative halophyte may be an appropriate classification for these *Lepidium* spp., as has been applied to another exotic *Lepidium* spp. in the USA, *Lepidium ruderale* L. (Grigore and Toma 2017). The saline plasticity of facultative halophytes is adaptive for the fluctuating stress conditions between the field and greenhouse environments of this study (Bradshaw and Hardwick 1989).

Influential roles of shoot litter and rhizomes

A conspicuous feature of *L. latifolium* is its tall canopy cover that produces deep and persistent litter layers in a wide variety of habitats (Renz and Blank 2004). In California wetlands, Wigginton et al. (2014) reported that the canopy biomass and seasonal senescence of *L. latifolium* allow the species to “engineer” an ecosystem by changing both plant and invertebrate communities, and by impacting higher order consumers. The latter study cited the importance of both living and senescent (litter) vegetation on the outcomes of invasions. In New Mexico, both *L. latifolium* and *L. alyssoides* have been found providing microhabitats for the exotic invasive stink bug, *Bagrada hilaris*

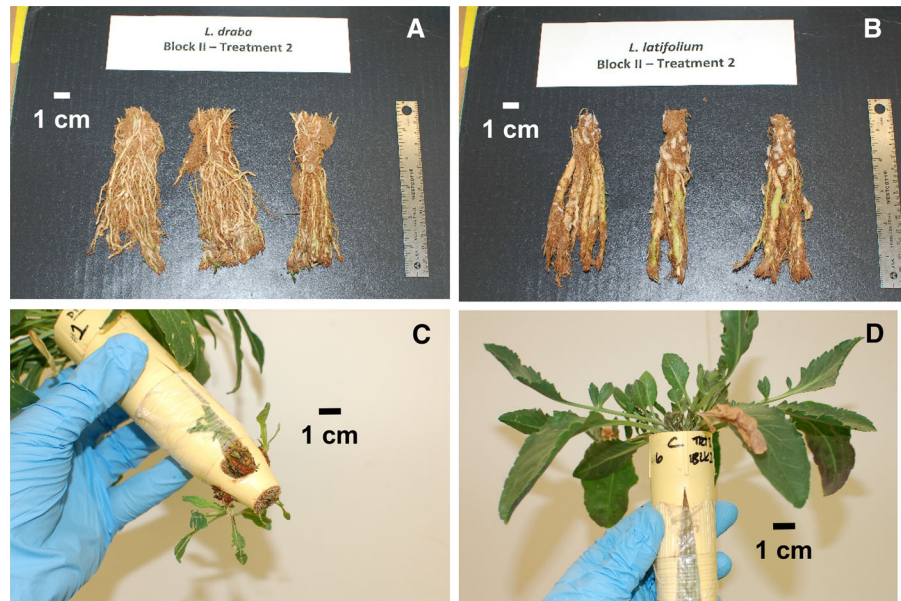
(Burmeister), a recently introduced insect pest of Brassicaceae crops (Taylor et al. 2015; Bundy et al. 2012). It follows that salinity’s role in the dominance of *Lepidium* spp. might amplify these shoot-related effects on ecosystems.

In saline habitats, Na and Cl in the abscising leaves and stems of *L. latifolium*, *L. draba*, and *L. alyssoides* would be released by leaching with the first rains in the autumn, further increasing soil salinity and preventing growth of non-tolerant species (Vivrette and Muller 1977). Despite the admission of saline litter fall by *L. latifolium* (Blank and Young 2002; Francis and Warwick 2007), there are virtually no quantitative data to reveal the true potential for salt deposition by *Lepidium* spp. To our knowledge, we are the first to quantitatively demonstrate the saline potency of their shoot tissues under greenhouse conditions that, in field environments, would likely alter the soil to induce and perpetuate the invasive cycle. Stem Na and Cl masses were excluded from Fig. 2 since they represented no more than 8% of the total plant Na and Cl in the NaCl treatments. However, stem contributions to litter salt loads in field conditions should not be discounted due to relatively high stem Na plus Cl concentrations that we observed (1.7–4.4% of dry weight; Tables 3, 4).

For leaves, the dominant salt accumulation site, combined Na and Cl masses at -0.2 MPa NaCl noted previously were estimated above the approximate greenhouse area of a three-seedling experimental unit (≈ 0.04 to 0.07 m²). These masses could represent ≈ 15 to 35 g Na plus Cl per m², or ≈ 20 to 50 mM NaCl in a 1 cm depth of water on 1 m². Such minimal estimates would increase considerably for field infestations of mature *L. draba* and *L. latifolium* reaching respective heights of 0.6 to 2.4 m (Zouhar 2004a, b), as compared with our final greenhouse heights of about 7 cm in root-confined growing conditions. Unintended experimental consequences of the root confinement provided a visual analogy for propagule “pressure” exerted by the rhizomatous expansion of *L. draba* and *L. latifolium* irrigated with -0.1 MPa NaCl (Fig. 4).

Quantitative studies on the cycling of salt in *Lepidium*-dominant landscapes, and on the interaction between salt tolerance and invasiveness of *L. draba*, *L. latifolium*, and *L. alyssoides* in natural conditions, are lacking. Nevertheless, our observations advance how these species may engineer a saline habitat by forceful expansion and tunneling of underground clonal

Fig. 4 Rhizomes of *L. draba* (a) and *L. latifolium* (b) irrigated with -0.1 MPa NaCl; propagule “pressure” by rhizomatous expansion resulting in longitudinal fracturing to grow cells of *L. draba* (c) and *L. latifolium* (d) irrigated with -0.1 MPa NaCl. Scale line is approximately 1 cm



structures, mining and pumping of salt, modifying trophic levels, and “setting the rules” over community structure (Wigginton et al. 2014; Vivrett and Muller 1977; D’Antonio and Myerson 2002). Salinized sites may be vulnerable to the propagule pressure of these species that could set the scene for their predominance and displacement of other species, much like we observed for *L. alyssoides* on a Chihuahuan Desert shrubland (Picchioni et al. 2012a, b, 2014).

Conclusion

This study sets an example for future studies on other species because it broadens the narrow understanding of why certain plants monopolize salinized habitats, and thus how salinity affects vegetation communities. The findings support salinity as a factor contributing to the invasiveness of *L. latifolium*, *L. draba*, and *L. alyssoides*, and reveal five prominent halophytic traits to explain this behavior: exceptionally high Na and Cl concentrations in the leaf dry matter with no characteristic signs of salt toxicity; very low leaf K:Na ratios; a conspicuous Na and Cl “inclusion” pattern rendering leaves as the dominant salt accumulation center; high leaf Na and Cl concentrations in the tissue water inferring vacuolar expansion and tissue tolerance; and development of leaf succulence. An intriguing possibility from the outcome of this study relates to the role

that salinity plays in governing plant community structure, a relatively unexplored subject. Salinity’s role may not simply be as a “non-resource stress” influence as commonly accepted (Grace 2001; Smit et al. 2009; Tang et al. 2018). As suggested in the study, its probable role as a beneficial resource can give advantages to tolerant species.

Our study was limited to single populations for each *Lepidium* spp. and represents a first step toward quantitative assessment of salt uptake and transport properties of an invasive plant taxon. Additional research on intraspecific variation in salt tolerance of these species is needed. For example, study of variation in plasticity to salinity between introduced populations of *L. latifolium* and *L. draba*, and between native populations of *L. alyssoides*, could disclose whether salt tolerance is an inherent attribute of these species, or if it is based on differentiation of genotypes adapted to given habitats. Our previous efforts showed no differences in *L. alyssoides* populations from southern New Mexico (Hooks et al. 2018b), but more data are needed for its broader indigenous range, and especially for different introduced populations of *L. latifolium* and *L. draba* in North America. A broader implication for land management practice and ecology is to increase habitat salinity assessments and the quantitative study on more weedy invasive species to improve the ability for predicting future outbreaks on saline arid and semiarid lands.

Acknowledgements We express thanks to Hae-Na Chung, NMSU undergraduate research assistant; Barbara Hunter, Senior Research Assistant in the NMSU Department of Plant and Environmental Sciences; Jim Wanstall, State Noxious Weed Coordinator in the New Mexico Department of Agriculture; Nina Klypin (deceased), Agricultural Research Scientist in the NMSU Department of Entomology, Plant Pathology, and Weed Science; and Sharon Martinez, NMSU undergraduate research assistant.

Funding Funding was provided by the New Mexico Water Resources Research Institute Faculty Water Research Grants Program, New Mexico State University, and by the New Mexico Agricultural Experiment Station Rangeland Ecosystems Program.

References

- Ahmed MZ, Khan MA (2010) Tolerance and recovery responses of playa halophytes to light, salinity, and temperature stresses during seed germination. *Flora* 205:764–771
- Al Hassan M, Chaura J, Lopez-Gresa MP, Borsari O, Daniso E, Donat-Torres MP, Mayora IO, Vicente O, Boscaiu M (2016) Native-invasive plants vs. halophytes in Mediterranean salt marshes: Stress tolerance mechanisms in two related species. *Front Plant Sci* 7:473. <https://doi.org/10.3389/fpls.2016.00473>
- Andrew ME, Ustin SL (2009) Habitat suitability modeling of an invasive plant with advanced remote sensing data. *Divers Distrib* 15:627–640
- Ayers RS, Westcot DW (1985) Water quality for agriculture. Food and Agriculture Organization of the United Nations. <https://www.fao.org/DOCREP/003/T0234e/T0234e00.htm>. Accessed 27 Aug 2019
- Blank RR, Young JA (2002) Influence of the exotic invasive crucifer, *Lepidium latifolium*, on soil properties and elemental cycling. *Soil Sci* 167:821–829
- Boestfleisch C, Wagenseil NB, Buhmann AK, Seal CE, Wade EM, Muscolo A, Papenbrock J (2014) Manipulating the antioxidant capacity of halophytes to increase their cultural and economic value through saline cultivation. *Aob Plants* 6:plu046. <https://doi.org/10.1093/aobpla/plu046>
- Bradshaw AD, Hardwick J (1989) Evolution and stress–genotypic and phenotypic components. *Biol J Linn Soc* 37:137–155
- Bui EN (2013) Soil salinity: a neglected factor in plant ecology and biogeography. *J Arid Environ* 92:14–25
- Bundy CS, Grasswitz TR, Sutherland C (2012) First report of the invasive stink bug *Bagrada hilaris* (Burmeister) (Heteroptera: Pentatomidae) from New Mexico, with notes on its biology. *Southwestern Entomol* 37:411–414
- Cox SB, Bloch CP, Stevens RD, Huenneke LF (2006) Productivity and species richness in an arid ecosystem: a long-term perspective. *Plant Ecol* 186:1–12
- Cripps MG, Hinz HL, McKenney JL, Price WJ, Schwarzländer M (2009) No evidence for an ‘evolution of increased competitive ability’ for the invasive *Lepidium draba*. *Basic Appl Ecol* 10:103–112
- D’Antonio C, Myerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor Ecol* 10:703–713
- Dyderski MK, Jagodziński AM (2018) Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. *Plant Ecol* 219:1369–1380
- Flowers TJ (1972) The effect of sodium chloride on enzyme activities from four halophyte species of Chenopodiaceae. *Phytochemistry* 11:1881–1886
- Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. *New Phytol* 179:945–963
- Flowers TJ, Läuchli A (1983) Sodium versus potassium: substitution and compartmentation. In: Läuchli A, Bielecki RC (eds) *Encyclopedia of plant physiology. Inorganic plant nutrition*, vol 15B. Springer, New York, pp 651–681
- Flowers TJ, Troke PF, Yeo AR (1977) The mechanism of salt tolerance in halophytes. *Annu Rev Plant Physiol* 28:89–121
- Flowers TJ, Hajibagheri MA, Clipson NJW (1986) Halophytes. *Quart Rev Biol* 61:313–337
- Flowers TJ, Munns R, Colmer TD (2015) Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. *Ann Bot* 115:419–431
- Forsman A (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. *PNAS* 111:302–307
- Francis A, Warwick SI (2007) The biology of invasive alien plants in Canada. 8. *Lepidium latifolium* L. *Can J Plant Sci* 87:639–658
- Francis A, Warwick SI (2008) The biology of Canadian weeds. 3. *Lepidium draba* L., *L. chalepense* L., *L. appelianum* Al-Shehbaz (updated). *Can J Plant Sci* 88:379–401
- Glenn EP, Swingle RS, Riley JJ, Mota CU, Watson MC, Squires VR (1994) North American halophytes: potential use in animal husbandry. In: Squires VR, Ayoub AT (eds) *Halophytes as a resource for livestock and for rehabilitation of degraded lands*. Kluwer Academic, Dordrecht, pp 165–174
- Gong Y, Ling H, Lv G, Chen Y, Guo Z, Cao J (2019) Disentangling the influence of aridity and salinity on community functional and phylogenetic diversity in local dryland vegetation. *Sci Total Environ* 653:409–422
- Grace JB (2001) The roles of community biomass and species pools in the regulation of plant diversity. *Oikos* 92:193–207
- Greenway H, Munns R (1980) Mechanisms of salt tolerance in non-halophytes. *Annu Rev Plant Physiol* 31:149–190
- Grewell BJ, Castillo JM, Thomason MJS, Drenovsky RE (2016) Phenotypic plasticity and population differentiation in response to salinity in the invasive cordgrass, *Spartina densiflora*. *Biol Invasions* 18:2175–2187
- Grigore MN, Toma L (2017) *Anatomical adaptations of halophytes*. Springer, New York
- Grover A, Singh S, Pandey P, Patade VY, Gupta SM, Nasim M (2014) Overexpression of NAC gene from *Lepidium latifolium* L. enhances biomass, shortens life cycle and induces cold stress tolerance in tobacco: potential for engineering fourth generation biofuel crops. *Mol Biol Rep* 41:7479–7489
- Hajiboland R, Bahrami-Rad S, Akhiani H, Poschenrieder C (2018) Salt tolerance mechanisms in three Irano-Turanian

- Brassicaceae halophytes relatives of *Arabidopsis thaliana*. J Plant Res 131:1029–1046
- Herrick JE, Lessard VC, Spaeth KE, Shaver PL, Dayton RS, Pyke DA, Jolley L, Goebel JJ (2010) National ecosystem assessments supported by scientific and local knowledge. Front Ecol Environ 8:403–408
- Higgins SI, Richardson DM (2014) Invasive plants have broader physiological niches. PNAS 111:10610–10614
- Hinz HL, Schwarzländer M, McKenney JL, Cripps MG, Harmon B, Price WJ (2012) Biogeographical comparison of the invasive *Lepidium draba* in its native, expanded and introduced ranges. Biol Invasions 14:1999–2016
- Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil. California Agricultural Experiment Station Circular 347. College of Agriculture, University of California, Berkeley
- Hooks TN, Picchioni GA, Schutte BJ, Shukla MK, Daniel DL (2018a) 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. Rangeland Ecol Manage 71:433–442
- Hooks TN, Picchioni GA, Schutte BJ, Shukla MK, Daniel DL, Ashigh J (2018b) Salinity an environmental “filter” selecting for plant invasiveness? Evidence from indigenous *Lepidium alyssoides* on Chihuahuan Desert shrublands. Rangeland Ecol Manage 71:106–114
- Jennings DH (1976) The effects of sodium chloride on higher plants. Biol Rev 51:453–486
- Jones JB, Wolf B, Mills HA (1991) Plant analysis handbook: a practical sampling, preparation, analysis, and interpretation guide. Micro-Macro, Athens, GA, USA
- Kaur T, Hussain K, Koul S, Vishwakarma R, Vyas D (2013) Evaluation of nutritional and antioxidant status of *Lepidium latifolium* Linn: A novel phytofood from Ladakh. PLoS ONE 8(8):e69112. <https://doi.org/10.1371/journal.pone.0069112>
- Larson L, Kiemnec G (2005) Germination of two noxious range weeds under water and salt stresses with variable light regimes. Weed Technol 19:197–200
- Leininger SP, Foin TC (2009) *Lepidium latifolium* reproductive potential and seed dispersal along salinity and moisture gradients. Biol Invasions 11:2351–2365
- Li J, Liu H, Yan M, Du L (2017) No evidence for local adaptation to salt stress in the existing populations of invasive *Solidago canadensis* in China. PLoS ONE 12(4):e0175252. <https://doi.org/10.1371/journal.pone.0175252>
- Mishra A, Tanna B (2017) Halophytes: Potential resources for salt stress tolerance genes and promoters. Front Plant Sci 8:829. <https://doi.org/10.3389/fpls.2017.00829>
- Miyamoto S, Glenn EP, Olsen MW (1996) Growth, water use, and salt uptake of four halophytes irrigated with highly saline water. J Arid Environ 32:141–159
- Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681
- Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60:324–349
- Picchioni GA, Miyamoto S, Storey JB (1990) Salt effects on growth and ion uptake of pistachio rootstocks. J Am Soc Hort Sci 115:647–653
- Picchioni GA, Mexal JG, Shukla MK, Ruiz A, Babcock M, Daniel DL, Rodriguez DS (2012a) Land application of treated industrial wastewater on a Chihuahuan desert shrubland: impacts on the natural vegetation. Arid Land Res Manage 26:312–327
- Picchioni GA, Shukla MK, Mexal JG, Babcock M, Ruiz A, Sammis TW, Rodriguez DS (2012b) Land application of treated industrial wastewater on a Chihuahuan Desert shrubland: implications for water quality and mineral deposition. Arid Land Res Manage 26:211–226
- Picchioni GA, Mexal JG, Shukla MK (2014) Land application of treated industrial wastewater on a Chihuahuan Desert shrubland: Water quality assessment, mineral deposition and recovery, and effects on the vegetation. New Mexico Agricultural Experiment Station Bulletin 807 (44 p.). New Mexico State University, Las Cruces. <https://aces.nmsu.edu/pubs/research/water/BL807.pdf>. Accessed 28 Aug 2019
- Picchioni GA, Hooks TN, Schutte BJ, Daniel DL (2015) Drought, salinity, and invasive plants: A new model for sustainable water management. New Mexico Water Resources Research Institute Technical Report 368. <https://nmwri.nmsu.edu/tr-368>. Accessed 27 Aug 2019
- Renz MJ, Blank RR (2004) Influence of perennial pepperweed (*Lepidium latifolium*) biology and plant–soil relationships on management and restoration. Weed Technol 18:1359–1363
- Renz MJ, Steinmaus SJ, Gilmer DS, DiTomaso JM (2012) Spread dynamics of perennial pepperweed (*Lepidium latifolium*) in two seasonal wetland areas. Invasive Plant Sci Manage 5:57–68
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol Lett 9:981–993
- Richards CL, White SN, McGuire MA, Franks SJ, Donovan LA, Mauricio R (2010) Plasticity, not adaptation to salt level, explains variation along a salinity gradient in a salt marsh perennial. Estuaries Coasts 33:840–852
- Sagers JK, Waldron BL, Creech JE, Mott IW, Bugbee B (2017) Salinity tolerance of three competing rangeland plant species: Studies in hydroponic culture. Ecol Evol 7:10916–10929
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. Annu Rev Ecol Syst 17:667–693
- Singh S, Grover A, Nasim M (2016) Biofuel potential of plants transformed genetically with NAC family genes. Front Plant Sci 7:22. <https://doi.org/10.3389/fpls.2016.00022>
- Sinha VB, Grover A, Aslam M, Pande V, Ahmed Z (2014) Isolation and characterization of Ras-related GTP-binding protein (Ran) from *Lepidium latifolium* L. reveals its potential role in regulating abiotic stress tolerance. Acta Physiologica Plant 36:2353–2360
- Smit C, Rietkerk M, Wassen MJ (2009) Influence of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. J Ecol 97:1215–1219
- Subbarao GV, Ito O, Berry WL, Wheeler RM (2003) Sodium—a functional plant nutrient. Crit Rev Plant Sci 22:391–416
- Suchkova N, Tsiripidis I, Alifragkis D, Ganoulis J, Darakas E, Sawidis Th (2014) Assessment of phytoremediation

- potential of native plants during the reclamation of an area affected by sewage sludge. *Ecol Eng* 69:160–169
- Tang L, Wolf AA, Yang G, Wang C (2018) Photosynthetic tolerance to non-resource stress influences competition importance and intensity in an invaded estuary. *Ecology* 99:1327–1337
- Taylor ME, Bundy CS, McPherson JE (2015) Life history and laboratory rearing of *Bagrada hilaris* (Hemiptera: Heteroptera: Pentatomidae) with descriptions of immature stages. *Ann Entomol Soc Am* 108:536–551
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763
- Vance GF, King LA, Ganjgunte GK (2008) Soil and plant responses from land application of saline–sodic waters: implications of management. *J Environ Qual* 37:S-139–S-148
- Vivrette NJ, Muller CH (1977) Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecol Monogr* 47:301–308
- Walker LR, Smith SD (1997) Impacts of invasive plants on community and ecosystem properties. In: Luken JO, Thieret JW (eds) *Assessment and management of plant invasions*. Springer, New York, pp 69–86
- Wigginton RD, Pearson J, Whitcraft CR (2014) Invasive plant ecosystem engineer facilitates community and trophic level alteration for brackish marsh invertebrates. *Ecosphere* 5(4):40. <https://doi.org/10.1890/ES13-00307.1>
- Wyn Jones RG (1981) Salt tolerance. In: Johnson CB (ed) *Physiological processes limiting plant productivity*. Butterworth Press, London, pp 271–292
- You W-H, Han C-M, Fang L-X, Du D-L (2016) Propagule pressure, habitat conditions and clonal integration influence the establishment and growth of an invasive clonal plant, *Alternanthera philoxeroides*. *Front Plant Sci* 7:568. <https://doi.org/10.3389/fpls.2016.00568>
- Zouhar K (2004a) *Cardaria* spp. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <https://www.fs.fed.us/database/feis/plants/forb/carspp3/all.html>. Accessed 28 Aug 2019
- Zouhar K (2004b) *Lepidium latifolium*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <https://www.fs.fed.us/database/feis/plants/forb/leplat/all.html>. Accessed 28 Aug 2019

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.