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Salinity Reduces the Forage Quality of Forage Kochia: A Halophytic *Chenopodiaceae* Shrub[☆]

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ABSTRACT

Forage kochia (*Bassia prostrata* [L.] A.J. Scott) is a perennial, halophytic *Chenopodiaceae* shrub adapted to semiarid rangelands and steppes. It is noted for its ability to produce edible forage in saline environments, but the effect of salinity on its nutritive value has not been determined. Therefore, this study evaluated the dose–response of increasing salinity on the forage quality of forage kochia and Gardner's saltbush (*Atriplex gardneri* [Moq.] D. Dietr., a chenopod forage shrub indigenous to the United States). Individual plants were evaluated in hydroponics for 28 days at 0, 150, 300, and 600 mM NaCl. Salt from accumulated ions, minerals, and forage nutritive value were determined using ground shoot samples. Analysis of forage nutritive value is problematic in plants with high salt concentrations, so neutral detergent fiber (NDF) and in vitro true digestibility (IVTD) were also predicted on an ash-corrected dry matter (DM) basis (NDF_{corrected} and IVTD_{corrected}). Forage kochia exhibited a dose–response for salt concentration, IVTD_{corrected}, and crude protein (CP) as salinity increased. Salt concentrations increased to 19% of DM at 600 mM NaCl, which may reduce voluntary intake by ruminants grazing forage kochia. Results indicated that uncorrected IVTD estimates were inflated as forage kochia IVTD_{corrected} decreased from 65% to 56% with the major change between 300 and 600 mM NaCl. Crude protein did not differ between two forage kochia cultivars but decreased from 26% to 15% between 0 and 600 mM NaCl, whereas Gardner's saltbush CP decreased by only five percentage points as salinity increased. Nonetheless, despite the greater CP sensitivity to salinity level, forage kochia salt concentration was less and digestibility and metabolizable energy (ME) were greater than Gardner's saltbush. Overall, salinity reduced the forage quality of forage kochia, though not as dramatically as for Gardner's saltbush, thus supporting use of forage kochia to improve the forage base of saline rangelands.

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Introduction

Approximately 6% of the earth's land, and 20% of agricultural lands, are affected by salt (Munns and Tester 2008), and the highest proportion of saline lands are found in the arid and semiarid environments of the world (Masters et al. 2007). Ben Salem and Smith (2008) reported that shrubs adapted to harsh, semiarid environments may provide needed solutions to the lack of available forage for ruminants on such rangelands. As such, the halophytic *Chenopodiaceae* shrubs, including the *Atriplex* species (saltbush), that are

well adapted to saline, semiarid rangelands have been evaluated for their potential for livestock grazing (Masters et al. 2007; Ben Salem et al. 2010; Masters et al. 2010; Pearce et al. 2010). However, Norman et al. (2013) indicated that determining the grazing potential of halophytic shrubs was not straightforward, with varying reports of salt tolerance, complications due to spatial heterogeneity of salinity, and the confounding effects of aridity and associated abiotic stresses. They further found that most literature on salt-tolerant forages reported physiological mechanisms and biomass growth, with few papers on the effect of saline environments on their forage quality (e.g., composed of both voluntary intake and nutritive value of the ingested biomass) (Norman et al. 2013).

Available reports indicate that high salinity greatly reduces the digestibility and overall nutritive value of halophytic *Atriplex* shrubs (Masters et al. 2010). Likewise, Norman et al. (2013) also reported that halophytic chenopod shrubs often have high soluble ash and salt concentrations when grown in saline environments, which

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affect not only the forage nutritive value but also the dry matter intake (DMI) by grazing livestock. Moreover, past reports probably have overestimated the nutritive value of halophytic chenopods, as the large soluble ash component (i.e., primarily consisting of accumulated salt ions) would have appeared to be digested but in reality had no energy content (Masters et al. 2007; Norman et al. 2013). Thus, it is clear from the literature that a shrub's forage mass and survival do not by themselves adequately describe its grazing potential on saline rangelands and that additional evaluations of the effect of salinity on halophyte's forage quality are needed. Plant response to salinity is frequently evaluated in hydroponic culture, in part, to reduce spatial heterogeneity at the root zone, confounding of osmotic stress due to drought versus salinity, and other associated abiotic stresses that can occur in soil-based media, including limited nutrients (Flowers and Colmer 2008; Munns and Tester 2008). These hydroponic data are primarily useful for relative comparisons among plant species and salinity levels; however, hydroponic salinity levels can be extrapolated to gross approximations of soil salinity (Norman et al. 2013) for limited and cautious comparison to rangeland/field conditions.

In forage quality analyses of halophytic chenopods, 63% to 81% of the ash is composed of Na^+ , K^+ , and Cl^- (Norman et al. 2013), and the amount of potential NaCl and KCl (g/kg dry matter [DM]) in a ruminant's diet coming from these chenopods has been predicted using soluble ash (Norman et al. 2010). The amount of NaCl and KCl can also be estimated if the amounts of Na^+ , K^+ , and Cl^- accumulated in the plant tissues are known (Norman et al. 2010). However, in human nutrition, the amount of NaCl and KCl ingested is predicted without knowing Cl^- levels by equating Na^+ and K^+ concentrations to the ionic compound using the appropriate molar mass for each ion and assuming a 1:1 ratio with Cl^- (Anon 2019a, 2019b). In contrast, halophytic plants are known to accumulate significant but lesser concentrations of Cl^- than Na^+ and K^+ in their shoots, with $\text{Na}^+ + \text{K}^+ / \text{Cl}^-$ ratios of 1.35 and ~2 for chenopod and grass species, respectively (Flowers and Colmer 2008). Thus, potential NaCl and KCl dietary levels from ingesting halophytic forages can be predicted by knowing the Na^+ and K^+ content in the biomass and using these $\text{Na}^+ + \text{K}^+ / \text{Cl}^-$ ratios. This predicted NaCl + KCl in the biomass resulting from plant accumulated Na^+ , K^+ , and Cl^- is frequently referred to as "salt content," "salt accumulation," and potential "salt intake" in halophytic forage/ruminant nutrition papers (Norman et al. 2004; Masters et al. 2005b; Masters et al. 2007; Masters et al. 2010; Norman et al. 2010; Norman et al. 2013; Norman et al. 2019).

Gardner's saltbush (*Atriplex gardneri*) is perennial chenopod shrub indigenous to the salt desert shrub ecosystems of the western United States, where it is a valuable source of browse for sheep and wildlife (Smith et al. 2016). Recently, Gardner's saltbush has been shown to be extremely vulnerable to invasion from halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.) (Smith et al. 2016). Halogeton is a fleshy annual weed, native to Eurasia, which was discovered in the United States in 1935, and now has spread throughout many semiarid, saline western US rangelands (Dayton 1951; Young 2002). This species is of concern since it develops oxalates, which are toxic to livestock, resulting in frequent sheep deaths in the western United States (Cronin and Williams 1966). Forage kochia (*Bassia prostrata* [L.] A.J. Scott; = syn. *Kochia prostrata* L.) is also a perennial chenopod shrub, indigenous to Eurasia, where it is used as forage by sheep, goats, cattle, camels, and horses (Waldron et al. 2010b). Waldron et al. (2011) recommended the use of forage kochia in the western United States, as it is well adapted to these semiarid and arid rangelands and increases nutritional value, carrying capacity, and livestock performance, especially for fall/winter grazing. Furthermore, forage kochia can be used to rehabilitate disturbed rangeland areas where frequent wildfires occur and/or invasive annuals such as halogeton have displaced native perennials,

including Gardner's saltbush (Monaco et al. 2003; Newhall et al. 2004; Bailey et al. 2010; Smith et al. 2016).

Given these attributes, forage kochia is being evaluated throughout the world to determine its potential for small ruminant production, especially in dry, saline regions, where there are efforts to increase or provide more stable and nutritious forage production (Bailey et al. 2010). Waldron et al. (2010b) reviewed many aspects of the forage value of forage kochia and recommended this shrub for grazing on saline rangelands, but they did not address the effect of salinity and salt accumulation on the forage quality of this species. This lack of information may be particularly important inasmuch as forage kochia, as well as Gardner's saltbush, have recently been classified as halophytes, and similar to other chenopod shrubs accumulate Na^+ , K^+ , and Cl^- , resulting in high concentrations of ash (20–40%) in shoot tissues as salinity increases (Karimi et al. 2005; Wang et al. 2015; Sagers et al. 2017). Thus, past reports may have overestimated forage kochia's and Gardner's saltbush nutritive value. Therefore, the objective of this study was to determine the effect of increasing salinity on the forage quality of forage kochia and Gardner's saltbush. Macrominerals and microminerals and potential salt from ingesting the biomass, as well as the forage nutritive value, were examined. To account for accumulation of salt ions, forage nutritive values were corrected for ash and evaluated using dose-response curves across a range of hydroponic salinity levels.

Materials and Methods

Organic Matter, Minerals, and Salt Concentration

The responses of forage kochia, Gardner's saltbush, and check plants to increasing salinity were evaluated in a hydroponic setting. Plant entries included the two US commercial cultivars of forage kochia (cv 'Snowstorm', gray-type forage kochia, subsp. *grisea*) [Waldron et al. 2013] and cv 'Immigrant', green-type forage kochia, subsp. *virescens* [Stevens et al. 1985]; Gardner's saltbush (commercial source variety not stated); halogeton (wildland collection); tall wheatgrass (*Thinopyrum ponticum* [Podp.] Z.-W. Liu & R.-C. Wang, a salt-tolerant cool-season grass, USDA experimental population originated from accession PI2555149); and alfalfa (*Medicago sativa* L. subsp. *falcata* [L.] Arcang., USDA experimental population 'HS-B' selected for salt tolerance). The study design, growth response, and ion accumulation were previously reported by Sagers et al. (2017). In brief, 12-wk-old greenhouse-started seedlings of these species were transplanted to hydroponic solutions and solution salinity was increased using NaCl in 10% daily increments over a period of 10 d to the targeted salinity levels of 0, 150, 300, and 600 mmol/L (electrical conductivity [EC] of 2, 15, 30, and 60 dS m^{-1}). Once final solution molarity was reached, the plants were grown an additional 28 d in the hydroponic solutions.

All hydroponic growth occurred within a greenhouse. The temperature was 25/20°C day/night, with a relative humidity of 40% day and 70% night. Uniformity of temperature and humidity among replicates was maintained by internal circulation fans. Supplemental lighting was provided by 1 000-W high-pressure sodium fixtures to provide a daily light integral (DLI) of 12 to 30 moles m^{-2}/d . The hydroponic solution included 1 g L^{-1} Peters Professional 5-11-26 Hydro-Sol water-soluble fertilizer (The Scotts Company, Marysville, OH), 0.6 g L^{-1} of calcium nitrate, and 0.15 g L^{-1} calcium chloride (dehydrate). The Peters Professional Hydro-Sol fertilizer is designed specifically for hydroponics and provides P, K, Mg, S, B, Cu, Fe, Mn, Mo, and Zn, whereas calcium nitrate was the main source of N (Table S1; available online at <https://doi.org/10.1016/j.rama.2019.12.005>). After 28 d of hydroponic growth, plant shoots were harvested, dried at 65°C for 72 h, and weighed to determine mass. Sagers et al. (2017) repeated the experiment three

independent times (runs), and each run consisted of three replicates of a single plant (i.e., experimental unit) of all plant entries at all salinity levels; however, only the two runs with start dates of 30 September 2015 and 9 March 2016 were used to measure forage quality in this study (i.e., $N = 6$). In addition, shoot mass of tall wheatgrass and alfalfa at the 600-mM salinity level was insufficient for forage nutritive analyses.

As reported by Sagers et al. (2017), the dried shoot samples were ground to 1 mm and ion content in the shoots was analyzed using a Thermo electron iCAP inductively coupled plasma spectrophotometer by a commercial laboratory (Utah State University Analytical Laboratory, Logan, UT). The concentration of 23 ions was determined and included microminerals Zn, Mn, Fe, Cu, Mo, and B and macrominerals Na, K, Mg, Ca, P, and S, but Cl was not included in the analysis. Ground shoot samples were also ashed at 500°C to determine the percent organic matter (OM) in samples (i.e., $OM = 100 - \% \text{ ash}$). Sagers et al. (2017) published the change in shoot mass and Na, K, Ca, Mg, and P concentrations as salinity increased but did not report microminerals nor the potential impact of NaCl and KCl. Therefore, for this study we examined both the macrominerals and microminerals and potential NaCl and KCl concentrations in the biomass in relation to forage quality. Salt concentration, as NaCl + KCl, was predicted by equating the shoot Na^+ and K^+ concentrations to the ionic compound using the following equations:

Chenopods:

$$NaCl + KCl \text{ g kg}^{-1} \text{ DM} \\ = ([Na^+ / 1.35] \cdot 2.54) + ([K^+ / 1.35] \cdot 1.91) \quad [\text{Eq. 1}]$$

Alfalfa and tall wheatgrass:

$$NaCl + KCl \text{ g kg}^{-1} \text{ DM} \\ = ([Na^+ / 2.0] \cdot 2.54) + ([K^+ / 2.0] \cdot 1.91) \quad [\text{Eq. 2}]$$

where 1.35 and 2.0 equal the ratio of $Na^+ + K^+$ to Cl^- in chenopods and nonchenopods, respectively (Flowers and Colmer 2008), and 2.54 and 1.91 equal the molar mass conversion to the compound form of NaCl and KCl, respectively (i.e., $2.54 = 58.5 \text{ g mole}^{-1} \text{ NaCl} / 22.99 \text{ g mole}^{-1} \text{ Na}$, and $1.91 = 74.55 \text{ g mole}^{-1} \text{ KCl} / 39.10 \text{ g mole}^{-1} \text{ K}$). The estimated concentration of NaCl + KCl from the measured plant accumulated Na^+ and K^+ is interchangeably referred to as "salt" herein.

Forage Nutritive Value Analysis

Dried shoot samples were ground to pass through a 1-mm screen using a Thomas Wiley Laboratory Model 4 mill (Arthur H. Thomas Co, Swedesboro, NJ) and were scanned with a Foss XDS near-infrared reflectance spectroscopy instrument (Foss, Eden Prairie, MN) to determine forage nutritive value. NIRSystem software was used to calibrate forage nutritive value equations that were appropriate for the species in this study. Random samples were selected from each run, salinity level, and species and were used for a calibration data set for wet laboratory analysis. Validation of the new equation was determined from a different set of random samples for crude protein (CP; $N \times 6.25$), neutral detergent fiber (NDF), in vitro true digestibility (IVTD), ether extract (EE), organic matter (OM), and insoluble ash in NDF and IVTD residues. Samples used for calibration were analyzed for N using a LECO CHN-2000 and a FP-628 Elemental Analyzer (LECO Corp., St. Joseph, MI). Concentrations of NDF and IVTD were determined as described in the ANKOM procedures (Anon 2005a, 2005b). Analyses for NDF were made using the ANKOM-200 Fiber Analyzer (ANKOM Technology, Macedon, NY). The first stage of the IVTD analysis consisted

of a 48-h in vitro fermentation in the ANKOM Daisy II incubator (ANKOM Technology), and the second stage was performed with the NDF procedure mentioned earlier. Insoluble ash in the residue was determined by ashing the NDF and IVTD residues and sample bag, at 550°C for 120 min using a microwave ashing oven (Milestone Pyro). Ether extract (EE) analysis was performed after the AOAC 2003.05 official method by a commercial laboratory (Dairy One, Ithaca, NY).

Forage nutritive value analysis is known to be problematic in plants that have high salt ion accumulation, and values are often inflated for digestibility, fiber content, and metabolizable energy (Norman et al. 2010). Therefore, in addition to the described in vitro wet chemistry, NDF and IVTD were predicted on an OM basis (NDF_{om} and IVTD_{om}) and ash-corrected DM basis (NDF_{corrected} and IVTD_{corrected}) by following the methodology of Norman et al. (2004) as follows:

$$NDF_{om} \text{ and } IVTD_{om} = (OM \text{ in sample} - OM \text{ in residue}) \\ / OM \text{ in sample};$$

$$NDF_{corrected} \text{ and } IVTD_{corrected} = (OM \text{ in sample} - OM \text{ in residue}) / \text{sample DM};$$

where *OM in samples* was determined by multiplying sample dry weights by percent OM, and *OM in residue* was determined by subtracting the insoluble ash in residual dry matter (remaining after digestion and ashing) from the residual dry matter (remaining after digestion). The resulting NIR standard error of prediction (SEPC) and R^2 values for validation computed across runs were 2.85 and 0.90 for OM, 1.62 and 0.77 for CP, 4.27 and 0.39 for NDF, 4.18 and 0.30 for NDF_{om}, 4.01 and 0.52 for NDF_{corrected}, 2.86 and 0.72 for IVTD, 3.38 and 0.59 for IVTD_{om}, 2.69 and 0.73 for IVTD_{corrected}, 0.85 and 0.36 for insoluble ash in IVTD residue, 0.23 and 0.48 for insoluble ash in NDF residue, and 0.39 and 0.17 for EE, respectively. Lower than desired R^2 values were noted; however, the predicted values were used inasmuch as the low R^2 values were mostly due to a limited range of observed values and all SEPC values were acceptable to predict within the limited range. Total digestible nutrients (TDN) on a DM basis were then calculated using the appropriate values in the following formula:

$$TDN = (NFC \times 0.98) + (CP \times 0.87) + (FA \times 0.97 \times 2.25) \\ + [NDFn \times (NDFDp \div 100)] - 10;$$

where nonfibrous carbohydrates (NFC) = $100 - (NDFn + CP + EE + \text{ash})$, fatty acids (FA) = $EE - 1$, nitrogen free NDF (NDFn) = $NDF_{corrected} \times 0.93$, NDF digestibility (NDFD) = 48-h in vitro NDF digestibility on an OM basis, and NDFDp = $22.7 + 0.664 \times NDFD$ (Saha et al. 2013). Metabolizable energy (ME) was calculated on a DM basis as $TDN \times 0.04409 \times 0.82$ (National Research Council 2000).

Statistical Analysis

All data were analyzed with the MIXED procedure of SAS (SAS Institute Inc., Version 9.3, Cary, NC) across runs to test main effects and get estimates of the entry \times salinity level means and standard errors. Entry and salinity level were considered fixed effects, whereas run and replication were random variables. Dose response curves across salinity levels were then fit using SIGMAPLOT (Systat Software Inc., Version 13, San Jose, CA). Salt concentration and forage nutritive values were fit to standard dose-response curves using nonlinear three-parameter sigmoidal logistic (Equation 3) or sigmoid (Equation 4) models as shown:

Table 1
Pearson's correlations between nutritive traits¹ ($N = 107$) of plants grown in increasingly saline hydroponic solution. Correlation values (r) are shown in the lower diagonal, and significant levels (P) are listed in the upper diagonal.

	SALT	OM	CP	IVTD	IVTD _{om}	IVTD _{corrected}	NDF	NDF _{om}	NDF _{corrected}	NDFD	ME
SALT		0.0001	0.0001	0.0001	0.0142	0.0001	0.0001	0.0001	0.0001	0.0033	0.0001
OM	-0.82		0.0483	0.0001	0.0063	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
CP	-0.52	0.19		0.8458	0.0071	0.0001	0.1422	0.3140	0.1668	0.0567	0.0155
IVTD	0.55	-0.60	-0.02		0.0001	0.0002	0.0002	0.0042	0.0001	0.0001	0.0001
IVTD _{om}	0.24	-0.26	0.26	0.88		0.3659	0.9432	0.6872	0.8762	0.0001	0.7967
IVTD _{corrected}	-0.82	0.91	0.45	-0.35	0.09		0.0001	0.0001	0.0001	0.0001	0.0001
NDF	-0.69	0.84	0.14	-0.36	-0.01	0.85		0.0001	0.0001	0.0001	0.0001
NDF _{om}	-0.65	0.76	0.10	-0.27	0.04	0.79	0.98		0.0001	0.0001	0.0001
NDF _{corrected}	-0.69	0.84	0.13	-0.37	-0.02	0.86	0.99	0.98		0.0001	0.0001
NDFD	-0.29	0.37	0.18	0.39	0.69	0.61	0.67	0.72	0.67		0.0001
ME	-0.78	0.97	0.23	-0.40	-0.03	0.95	0.84	0.77	0.84	0.53	

¹ OM indicates organic matter; CP, crude protein; IVTD, in-vitro true digestibility; IVTD_{om}, IVTD of the organic matter; IVTD_{corrected}, IVTD corrected for ash; NDF, neutral detergent fiber; NDF_{om}, NDF of the organic matter; NDF_{corrected}, NDF corrected for ash; NDFD, NDF digestibility; ME, metabolizable energy.

$$Y = a / \left(1 + \left(\frac{x}{x_0} \right)^b \right) \quad [\text{Eq. 3}]$$

$$Y = a / \left(1 + e^{\left(\frac{x-x_0}{b} \right)} \right) \quad [\text{Eq. 4}]$$

where a indicates the upper limit, x_0 represents the solution salinity levels at which 50% of maximum salt accumulation in tissues occurred (i.e., MAX₅₀), or where nutritive value was reduced 50% (i.e., NVR₅₀), and b is the slope of the line around the MAX₅₀ and NVR₅₀ values. The resulting MAX₅₀ or NVR₅₀ values provide an objective comparison among the plant species of the effect of salinity on forage nutritional value. When sigmoidal models did not fit the data or were not significant, the nutritional value response across salinity levels was fit to polynomial (linear or quadratic) models also using SIGMAPLOT. The most appropriate and simplest models were plotted, as determined by R^2 and significance of parameters. When the dose responses were not significant, individual points were plotted and the trend was shown by a dotted line.

Because of the large discrepancy between the IVTD and IVTD_{corrected} values, the relationship between these traits in forage kochia and Gardner's saltbush was further studied by regressing and plotting them against each other using SIGMAPLOT. Furthermore, correction functions for forage kochia and Gardner's saltbush digestibility were derived using the REG procedure of SAS by regressing the reduction in apparent digestibility due to salts (i.e., IVTD_{corrected} - IVTD) with the corresponding OM (%).

Results

Salt and Minerals

The predicted concentration of salt (as NaCl + KCl) in the biomass was highly correlated with OM (Table 1), and increasingly greater salinity had a significant effect on salt concentration in all species (Fig. 1A). Gardner's saltbush and halogeton "actively" accumulated salt ions in plant tissues, resulting in the greatest ($P < 0.05$) salt concentrations at all salinity levels with an average of 269 g salt kg⁻¹ DM at the 600 mM salinity level (see Fig. 1A). Regression analysis indicated that 50% of maximum salt concentration (MAX₅₀) occurred at 38 and ~0 mM NaCl, for Gardner's saltbush and halogeton, respectively (Table S2; available online at <https://doi.org/10.1016/j.rama.2019.12.005>). In comparison, salt concentrations in Immigrant and Snowstorm forage kochia were less, with average maximum salt of 190 g kg⁻¹ DM at 600 mM NaCl (see Fig. 1A). As reported by Sagers et al. (2017), the 600 mM NaCl

solution level severely stunted growth of tall wheatgrass and alfalfa such that there were insufficient samples of these plants to evaluate their salt concentrations or other forage quality characteristics above the 300 mM salinity level. Nevertheless, up to the 300 mM NaCl level, salt concentration for these species was less ($P < 0.05$) than the chenopod species, with the maximum salt of 75 g kg⁻¹ DM for tall wheatgrass being greater ($P < 0.05$) than the 44 g kg⁻¹ DM in the alfalfa (see Fig. 1A). Furthermore, as expected for the non-halophyte check, alfalfa salt concentration was much less responsive to increasing solution salinity compared with the other species, with no increase ($P > 0.05$) in NaCl + KCl between the 0 and 300 mM salinity levels (see Fig. 1A).

In general, increases in salinity resulted in increased ($P < 0.05$) Na accumulation, which corresponded with decreases in K, Mg, and Ca content (Table 2). The other macromineral, P, was primarily affected ($P < 0.05$) by salinity in Gardner's saltbush (only at the highest salinity level) and halogeton (beginning at the 150-mM salinity level) (see Table 2). For the most part, macromineral concentrations in the halophyte species (e.g., all entries except alfalfa) exceeded maximum tolerable levels to beef cattle, with the exceptions that sodium and potassium levels were acceptable in the control treatment (i.e., 0 mM salinity) and at all salinity levels greater than the control treatment, respectively (see Table 2). Increasing salinity had a varying effect on micromineral accumulation, with increased Fe and Cu only in the nonchenopod species, increased Mn only in Gardner's saltbush and halogeton, and increased Zn in all entries except Snowstorm and tall wheatgrass (see Table 2). Even so, no potentially toxic levels were observed for any micromineral among all entries and salinity levels (see Table 2).

Forage Nutritive Value

Crude protein was affected by increasing doses of salinity in all species except halogeton and alfalfa (see Fig. 1B). Crude protein declined in all three forage shrubs (see Fig. 1B) as salinity increased, but much more so for the forage kochia entries compared with Gardner's saltbush as evidenced by NVR₅₀ values of 831, 845, and 1 596 mM NaCl for Immigrant, Snowstorm, and Gardner's saltbush, respectively (see Table S2). In contrast, tall wheatgrass exhibited a much different response than these shrubs, with a sharp decrease in CP between 150 mM and 300 mM salinity (see Fig. 1B).

Lesser NDF is associated with improved livestock intake and greater dietary energy of forages. In this study NDF and ash-corrected NDF (i.e., NDF_{corrected}) were highly correlated ($r = 0.99$, $P < 0.0001$, see Table 1) and had similar values ranging from 12.9% to 24.6% and 12.0% to 23.7% DM, respectively. Overall, entry, salinity level, and entry \times salinity level interaction were highly significant

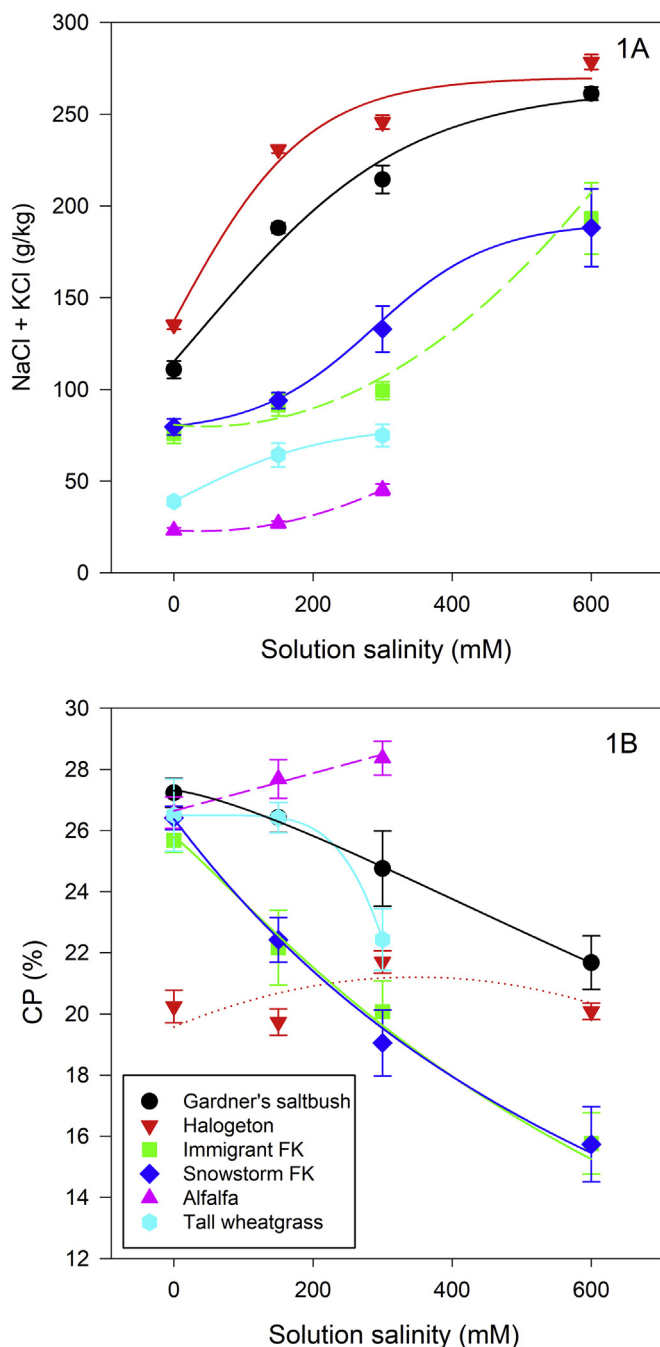


Figure 1. Salt concentrations (NaCl + KCl) from accumulated ions (A) and crude protein (CP) (as % of dry matter) (B) of plants grown in hydroponics with increasing amounts of NaCl. Best-fit dose-response lines were drawn using parameter estimates (Table S2; available online at <https://doi.org/10.1016/j.rama.2019.12.005>). Values represent mean \pm SE ($n = 6$). Solid lines represent a significant sigmoid response, whereas dashed lines are a significant polynomial response and dots indicate a nonsignificant response.

($P < 0.0001$) for $\text{NDF}_{\text{corrected}}$ as evidenced by large differences among entries in total amounts and the patterns of $\text{NDF}_{\text{corrected}}$ response to increased salinity levels (Fig. 2A). Gardner's saltbush had the least ($P < 0.05$) $\text{NDF}_{\text{corrected}}$ of all entries, forage kochia was intermediate ($P < 0.05$), and the nonchenopod forages (i.e., tall wheatgrass and alfalfa) exhibited the greatest ($P < 0.05$) $\text{NDF}_{\text{corrected}}$ (see Fig. 2A). Increasing salinity did not influence ($P > 0.05$) $\text{NDF}_{\text{corrected}}$ in forage kochia and only had a minor effect on tall wheatgrass and alfalfa ($P < 0.05$ but $R^2 \leq 0.41$) (see Table S2).

However, $\text{NDF}_{\text{corrected}}$ did decrease in Gardner's saltbush and halogeton as salinity increased (see Fig. 2A).

In contrast to $\text{NDF}_{\text{corrected}}$, all three chenopod shrubs exhibited similar NDFD values, but these concentrations were much less ($P < 0.05$) than the NDFD of tall wheatgrass and alfalfa (see Fig. 2B). Halogeton exhibited intermediate levels of NDFD, which decreased ($P = 0.007$) between 300 mM NaCl and 600 mM NaCl (see Fig. 2B). A sigmoidal dose response did not fit the NDFD data for any of the three chenopod shrubs (see Fig. 2B). However, salinity had a polynomial effect on forage kochia NDFD ($P = 0.0009$ and 0.0008 , for Immigrant and Snowstorm, respectively) and approached significance in Gardner's saltbush ($P = 0.0746$) with greater (more favorable) NDFD at the 600 mM NaCl level (see Fig. 2B and Table S2).

Three groups were evident for overall forage digestibility with tall wheatgrass and alfalfa having greater ($P < 0.05$) $\text{IVTD}_{\text{corrected}}$ than forage kochia, which in turn was greater ($P < 0.05$) than Gardner's saltbush and halogeton (Fig. 3A). Overall, $\text{IVTD}_{\text{corrected}}$ concentrations responded negatively to increasing salinity in all entries, but responses varied as indicated by the range of NVR_{50} values (see Table S2). Decreases in $\text{IVTD}_{\text{corrected}}$ in response to salinity were similar between Snowstorm forage kochia and Gardner's saltbush (NVR_{50} values of 1 962 mM and 1 911 mM, respectively). Immigrant forage kochia exhibited overall greater $\text{IVTD}_{\text{corrected}}$ than Snowstorm at 300 mM NaCl ($P = 0.0228$) and 600 mM NaCl ($P = 0.0011$) but had a lesser NVR_{50} value of 1 394 mM, indicating that Immigrant was predicted to be more negatively affected by extremely high salinity compared with Snowstorm (see Table S2).

Alfalfa, tall wheatgrass, and forage kochia had greater ($P < 0.05$) overall ME than Gardner's saltbush and halogeton, and except for Snowstorm forage kochia, ME in these entries did not respond to increasing salinity levels (see Fig. 3B). Gardner's saltbush and halogeton ME concentrations decreased with increasing salinity (see Fig. 3B). Metabolizable energy was positively correlated with NDFD ($r = 0.53$, $P = 0.0001$), $\text{NDF}_{\text{corrected}}$ ($r = 0.77$, $P = 0.0001$), and $\text{IVTD}_{\text{corrected}}$ ($r = 0.95$, $P = 0.0001$) but was not correlated with IVTD_{Dom} ($r = -0.03$, $P = 0.7967$) and negatively correlated with uncorrected IVTD ($r = -0.40$, $P = 0.0001$) (see Table 1).

Relationship Between IVTD and $\text{IVTD}_{\text{corrected}}$

Overall, IVTD not corrected for ash was positively correlated with IVTD_{Dom} ($r = 0.88$, $P = 0.0001$) but negatively correlated to $\text{IVTD}_{\text{corrected}}$ ($r = -0.36$, $P = 0.0002$) (see Table 1). Figure 4 shows uncorrected IVTD values regressed against $\text{IVTD}_{\text{corrected}}$ for all six entries and is indicative of the issues associated with standard forage digestibility analysis on plants that accumulate salt ions. There was no relationship between IVTD and $\text{IVTD}_{\text{corrected}}$ in alfalfa, whereas for all other entries, these two measures of digestibility were negatively associated ($r = -0.54$ to -0.76). Ash and/or organic matter are frequently reported with forage nutritive value; therefore, correction functions for forage kochia and Gardner's saltbush digestibility were derived by regressing the OM (% of DM) on the difference between $\text{IVTD}_{\text{corrected}}$ and IVTD . In both species, polynomial models were highly significant and fit the reduction in digestibility very well, explaining a high percentage of the variation. The resulting equations were:

$$\text{Reduction to forage kochia digestibility} \\ = \text{IVDT}_{\text{FK,REDUCED}} = -131.48 + 1.37x \quad [\text{Eq. 5}]$$

where $x = \text{OM}$, $P = 0.0001$, and $R^2 = 0.90$

Table 2
Macromineral and micromineral concentration in shrub biomass as a response to increasing salinity levels in a hydroponic study.

Entry ¹	Salinity (mM)	Macrominerals					Microminerals												
		Na	K	Mg	Ca	P	Fe	Cu	Mn	Zn									
		g kg ⁻¹ DM					mg kg ⁻¹ DM												
Alfalfa	0	0.1	j	24.2	fgh	2.0	lm	14.4	a	5.2	e	47.0	de	4.4	j	88.6	ijk	13.5	j
	150	4.5	j	22.0	ghijk	1.5	m	10.8	b	5.7	de	66.3	bcd	12.9	bcd	62.3	k	37.8	fghij
	300	23.4	ghi	15.7	ijkl	1.6	lm	7.3	cd	8.5	cde	73.6	bc	10.3	defg	66.9	jk	67.3	efgh
Gardner's SB	0	9.0	ij	65.9	b	11.6	a	15.1	a	7.5	cde	65.2	bcd	8.0	efghi	72.6	jk	53.6	fghi
	150	81.8	d	24.0	fgh	6.4	cd	4.5	fgh	7.8	cde	48.0	de	10.7	de	59.4	k	128.9	abc
	300	101.1	b	16.7	ijkl	6.4	cd	4.1	fgh	8.4	cde	62.5	bcde	10.7	cdef	144.6	fgh	143.1	a
Halogeton	0	12.5	hij	79.6	a	4.0	fgh	6.7	cde	11.7	bcd	39.4	e	5.2	ij	69.2	jk	32.5	hij
	150	100.2	bc	30.4	ef	2.7	ijklm	1.4	ij	38.5	a	61.5	bcde	8.0	efghi	123.9	ghij	74.3	def
	300	108.4	b	30.2	ef	2.3	klm	1.1	j	32.2	a	69.4	bcd	8.0	efghi	144.1	fgh	75.7	def
Immigrant FK	0	129.5	a	24.0	fghi	3.5	ghijk	2.4	hij	36.1	a	38.6	e	7.3	ghi	173.0	defg	100.3	bcde
	150	0.2	j	54.5	c	6.5	cd	13.7	a	6.1	de	50.4	cde	7.0	hi	163.0	efg	22.0	ij
	300	28.0	g	28.7	efg	3.7	fghi	7.9	c	6.7	de	64.1	bcd	8.7	efgh	235.9	bc	31.2	hij
Snowstorm FK	0	41.0	f	16.2	kl	2.7	jkl	5.3	defg	4.8	e	48.7	de	7.2	ghi	193.8	cdef	35.3	hij
	150	86.5	cd	21.4	hijk	2.8	hijkl	3.9	fgh	13.5	bc	55.6	cde	8.0	efghi	184.3	def	69.6	efg
	300	0.2	j	56.3	c	8.6	b	11.5	b	6.9	de	47.2	de	8.4	efgh	100.1	hijk	19.8	ij
Tall wheatgrass	0	26.2	g	32.4	e	5.6	de	8.6	c	8.7	cde	53.1	cde	10.6	de	130.7	ghi	37.2	ghij
	150	60.2	e	17.3	ijkl	4.7	ef	5.7	def	4.6	e	64.0	bcd	7.3	ghi	115.4	hij	35.0	hij
	300	84.6	d	20.1	hijk	4.6	efg	4.8	efg	9.6	cde	58.8	bcde	6.2	hij	124.8	ghij	48.4	fghij
Beef cattle dietary values ²	0	0.2	j	40.6	d	2.7	ijklm	3.8	gh	7.1	de	57.9	bcde	17.8	a	242.2	b	107.4	bcd
	150	25.5	gh	33.0	e	2.8	hijkl	2.5	hij	6.8	de	79.2	b	13.8	bc	220.9	bcd	96.5	cde
	300	41.9	f	23.4	fghij	3.6	ghij	3.4	ghi	5.9	de	107.3	a	14.4	b	327.5	a	136.5	ab
Requirement		0.6 to 1.0		5.0 to 7.0		0.15-0.3		0.5 to 1.0		0.2 to 0.8		50 to 100		4 to 20		20 to 40		30	
Max. tolerable		17.9		30.0		0.6		1.5		1.0		500		40		2000		500	

¹ Values within a column followed by a different letter indicate that the values are significantly different than each other at the 0.05 level of probability.

² Source of beef cattle dietary requirements and maximum tolerable levels was National Research Council (2005).

Reduction to Gardner's saltbush digestibility

$$= \text{IVTD}_{\text{GSB,REDUCED}} = -251.55 + 5.80x + -0.038x^2 \quad [\text{Eq. 6}]$$

where $x = \text{OM}$; $P = 0.0001$, and $R^2 = 0.95$

Discussion

Effect of Salinity on Mineral and Salt Concentrations in Forage Kochia

Norman et al. (2019) recently hypothesized that some halophytic shrubs would contain micromineral concentrations that exceed requirements needed by grazing ruminants and thereby could be a good source of antioxidants. In our study, both Gardner's saltbush and forage kochia did at least meet approximate ruminant requirements for Fe, Cu, Mn, and Zn but regardless of salinity level did not supply excess Fe or Cu (see Table 2). In contrast, increasing salinity resulted in forage kochia Mn concentrations and Gardner's saltbush Zn concentrations that were threefold to fivefold of that required by ruminants (see Table 2). In comparison, Norman et al. (2019) found that most halophytic shrubs they evaluated contained at least twofold the required Mn, whereas 60% contained fourfold the required Mn level. However, they found that Zn was much more affected by environment with far fewer shrubs exhibiting excess levels of Zn (Norman et al. 2019). Overall, our results indicate that in saline environments both forage kochia and Gardner's saltbush could be an important source of antioxidants, especially during the periods of heat-induced oxidative stress that would be common for grazing ruminants on semiarid saline rangelands.

Sagers et al. (2017) classified forage kochia as a halophyte with passive uptake of Na⁺ in saline conditions and, thus, not surprisingly in this study exhibited a significant salt concentration dose response to increasing hydroponic solution salinity

(see Fig. 1A). Average salt concentration in forage kochia was 9.4%, 11.9%, and 19.0% of DM for the 150 mM, 300 mM, and 600 mM salinity levels, respectively, and the two cultivars differed ($P = 0.0004$) only at the 300 mM salinity level. Forage kochia is generally considered highly saline tolerant, largely based on its ability to establish and produce edible forage in dry, saline environments where many other species either fail to establish or do not persist (Balyan 1972; Durikov 1986; Gintzburger et al. 2003; Monaco et al. 2003; Newhall et al. 2004). Francois (1976) attempted to quantify forage kochia's salt tolerance and reported that forage kochia produced abundant forage when grown in soils with electrical conductivity of the saturation extract (EC_e) ranging up to 17 dS/m. Equating his reported tissue Na⁺ and K⁺ levels to NaCl + KCl, as per the methods of this manuscript, he found that salt concentrations in the shoots of Immigrant forage kochia (i.e., PI314929) were 6.9%, 7.4%, and 7.9% of DM at soil EC_e levels of 7 dS/m, 11 dS/m, and 17 dS/m, respectively (Francois 1976). For comparison purposes, our hydroponic salinity levels can be converted to approximate moist soil EC_e values of 7.5 dS/m, 15 dS/m, and 30 dS/m, respectively (conversion between NaCl [mM] and EC_e [dS/m] is based on $\text{EC}_{\text{soil solution}}$ at field capacity is $\sim 2 \times$ the EC_e , and NaCl [in mM] is $\sim 10 \times$ the EC [in dS/m] (Bennett et al. 2009; Norman et al. 2013), indicating that our forage kochia salt accumulation at comparable EC_e was greater than Francois (1976). Nevertheless, the overall change in salt concentrations as salinity increases supports the conclusion that forage kochia accumulates salts when growing in a saline environment.

High salt concentrations, in and of themselves, can depress ruminant DMI and thus reduce the forage quality of a plant, perhaps even more significantly than the inherent low digestibility of many chenopod shrubs (Norman et al. 2013). Masters et al. (2005a) found that NaCl concentrations > 5% of forage mass reduced sheep DMI, and liveweight gains were reduced by up to 57% as the salt concentration in the diet increased from 0% to 20%. In comparison, the National Research Council (2005) reported that sheep and cattle could tolerate 7–10% salt in diet before feed intake

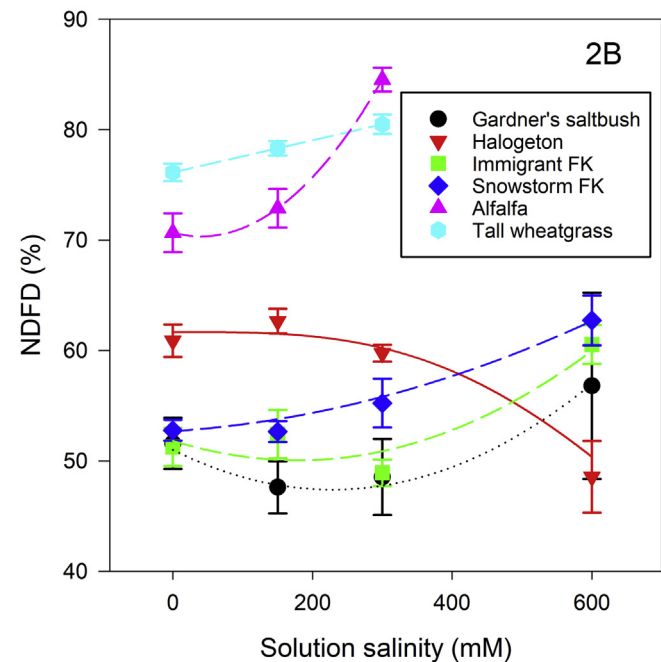
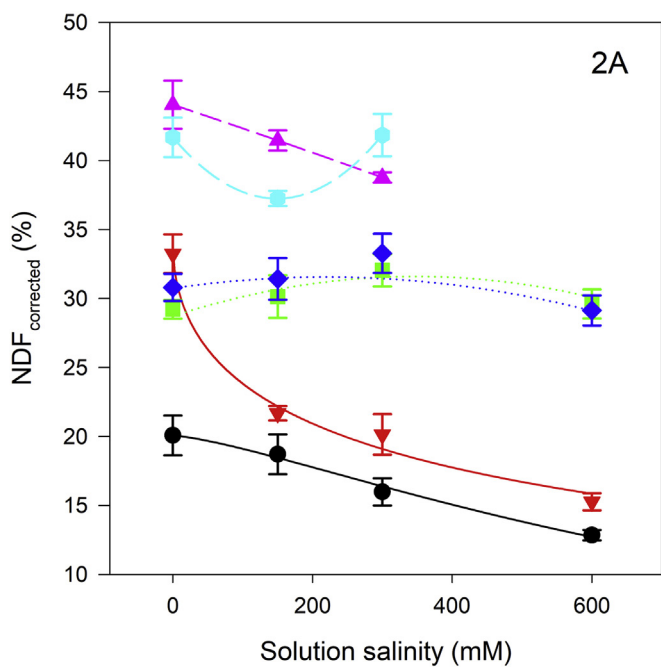


Figure 2. Neutral detergent fiber corrected for ash ($NDF_{corrected}$) (as % of dry matter) (A) and neutral detergent fiber digestibility (NDFD) (as % of $NDF_{corrected}$) (B) of plants grown in hydroponics with increasing amounts of NaCl. Best-fit dose-response lines were drawn using parameter estimates (Table S2; available online at <https://doi.org/10.1016/j.rama.2019.12.005>). Values represent mean \pm SE ($n = 6$). Solid lines represent a significant sigmoid response, whereas dashed lines are a significant polynomial response and dots indicate a nonsignificant response.

is depressed. Our results of 11.9% salt at 300 mM solution ($\sim EC_e$ of 15 dS/m) suggest that accumulated salt could affect the forage quality of forage kochia when growing on saline soils approaching or $> EC_e$ of 15 dS/m. It should be noted that dietary salt concentration of ruminants on rangelands is likely less than individual plant salt concentration due to mixed grazing of grass and forage kochia and selective grazing of seeds and leaves of forage kochia. Evidence of this grazing behavior includes reports that cattle spend more time grazing crested wheatgrass as compared with forage

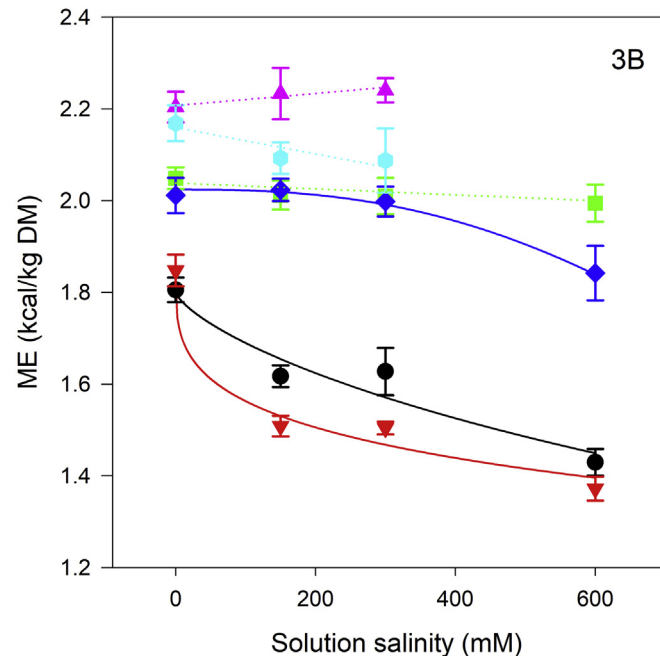
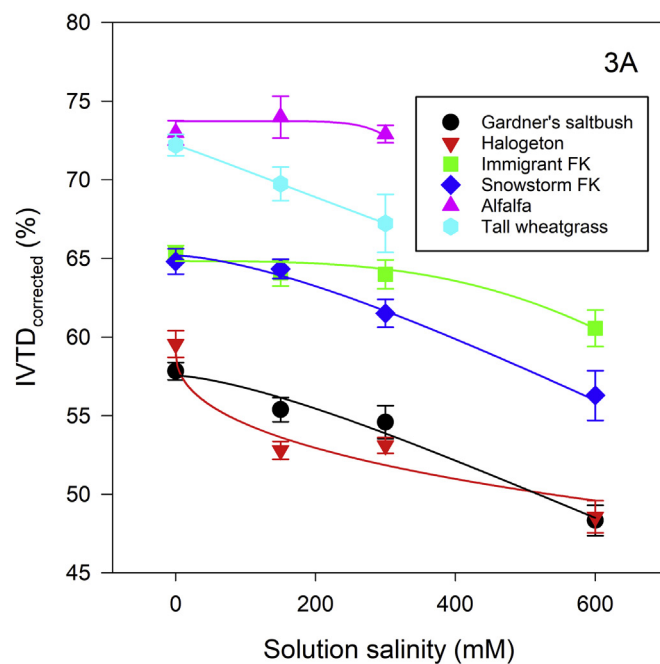


Figure 3. In-vitro true digestibility corrected for ash ($IVTD_{corrected}$) (as % of dry matter) (A) and metabolizable energy (ME) (B) of plants grown in hydroponics with increasing amounts of NaCl. Best-fit dose-response lines were drawn using parameter estimates (Table S2; available online at <https://doi.org/10.1016/j.rama.2019.12.005>). Values represent mean \pm SE ($n = 6$). Solid lines represent a significant sigmoid response, whereas dashed lines are a significant polynomial response and dots indicate a nonsignificant response.

kochia (Waldron et al. 2010a) and greater dietary CP in the rumen than whole-plant CP when grazing forage kochia (Waldron et al. 2006).

Effect of Increasing Salinity on Crude Protein and Neutral Detergent Fiber in Forage Kochia

Several papers have discussed the effect of salinity on the increased production of nonprotein nitrogen in halophytes

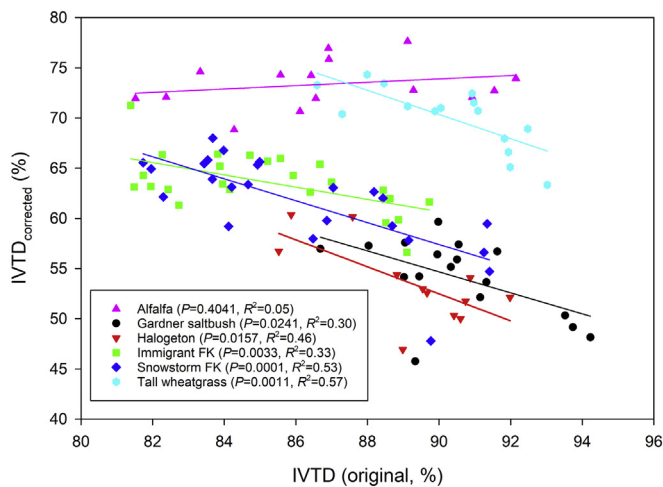


Figure 4. Linear relationships between uncorrected in vitro true digestibility (IVTD) and IVTD corrected for ash (IVTD_{corrected}) (as % of DM) of plants grown in hydroponics with increasing amounts of NaCl.

(Masters et al. 2007; Norman et al. 2013), but this study represents one of the few that compared the dose response of CP to increased salinity among different halophytic shrubs. Herein, forage kochia and Gardner's saltbush CP concentrations were similar in the nonsaline conditions, but CP in both was highly affected by increasing salinity levels, though the CP decrease was not as drastic in Gardner's saltbush (see Fig. 1B). Crude protein did not differ between the two forage kochia cultivars at any salinity level, but average forage kochia CP was decreased by 41% of the control at the 600 mM NaCl level (26.1% to 15.4% of DM, respectively) (see Fig. 1B). The correlation between salt concentration and CP in only the forage kochia entries was highly significant ($r = -0.70$; $P = 0.0001$), suggesting that this negative response was largely due to the dilution effects of increasing salt concentrations. However, CP of just the organic matter in forage kochia shoots was also reduced by 31% of the control at 600 mM NaCl (31.6–21.9% of DM, respectively), thus also supporting structural/compositional changes to the OM. In contrast to our overall results, Masters et al. (2010) evaluated six genotypes of river saltbush (*Atriplex amnicola*) and found no clear trend between shoot CP and salinity ranging from 0 mM NaCl to 400 mM NaCl. Forage kochia and Gardner's saltbush are noted for their ability to extend the grazing season into the fall and winter by providing a source of protein at a time when rangeland grasses have gone dormant and no longer meet livestock nutritional requirements. Due to the hydroponic setting and the use of seedlings in this study, it is difficult to draw concrete conclusions about how salinity affects forage kochia CP in actual rangeland situations. Nevertheless, the data suggest that highly saline environments reduce forage kochia CP, which may help explain CP differences frequently observed when forage kochia is evaluated across various rangeland sites (Waldron et al. 2013).

A significant ($P = 0.001$) dose response with lesser (more favorable) NDF_{corrected} as salinity increased was observed in Gardner's saltbush (20% to 12.9% from 0 mM to 600 mM salinity, respectively) (see Fig. 2A). Forage kochia NDF_{corrected} concentrations ranged from 32.4% to 30% and were not affected by salinity or entry ($P > 0.05$) (see Fig. 2A). Ben Salem et al. (2010) reviewed the nutritional value of oldman saltbush (*Atriplex nummularia*) when grown at diverse locations with a range of saline soils and, like our observations for Gardner's saltbush, reported a large range of NDF values (ranging from 45% to 30% DM). However, Masters et al. (2010) reported that there was no clear trend between greater NaCl treatments and NDF in river saltbush, supporting our results in forage kochia and further suggesting that NDF in at least some

halophytic chenopod shrubs does not respond to increased doses of salinity.

Effect of Increasing Salinity on Digestibility and Metabolizable Energy of Forage Kochia

O'Connell et al. (2006) indicated that the most critical aspect influencing profitability of shrubs on saline rangelands was their digestibility and ME. Our results indicate that increasingly saline environments do effect forage kochia digestibility, especially in Snowstorm, but only have a minor to negligible effect on ME. However, regardless of the salinity level, forage kochia exhibited greater digestibility and subsequent ME than Gardner's saltbush (see Fig. 3A and 3B), thus supporting recommendations of using forage kochia to improve the forage base of saline rangelands (Waldron et al. 2010b; Smith et al. 2016). In comparing the two forage kochia cultivars, Immigrant had significantly greater ($P < 0.05$) IVTD_{corrected} than Snowstorm at 300 mM and 600 mM salinity (see Fig. 3A). Immigrant ME was also not affected by salinity, whereas Snowstorm ME was reduced by the 600-mM treatment (see Fig. 3B). These results diverge from a previous report of field-grown Snowstorm exhibiting greater digestibility than Immigrant (Waldron et al. 2013) and, inasmuch as herein Snowstorm biomass had greater salt concentrations than Immigrant (see Fig. 1A), may be an example of how digestibility estimates not corrected for ash (i.e., salt) can be inflated.

The hydroponic nature of our study precluded extensive comparison to other researcher's field-based estimates. Nevertheless, our forage kochia IVTD_{corrected} values (ranging from 65% to 56%) were similar to ash-corrected digestibility estimates of 60% to 50% for saltbush plants that had comparable concentrations of salt (i.e., their saltbush plants comprised up to 28% ash) when grown in a saline pasture (soil Ece 23 dS/m) (Norman et al. 2004). Our results are also consistent with those of Masters et al.'s (2010) evaluation of the nutritional value of river saltbush plants when grown with irrigation treatments of 0, 50, 100, 200, and 400 mM NaCl. They reported that digestibility decreased from $\approx 65\%$ to 55% DM across these salinity levels in 50% of the plants. Furthermore, they reported a reduction in organic matter digestibility (e.g., IVTD_{Dom}) at high salinity levels and concluded that the lack of relationship between NDF and IVTD_{Dom} indicated that the salt concentration effect on digestibility was the result of structural and/or compositional changes to the organic matter within the plants. We also observed that NDF and IVTD_{Dom} were not associated (see Table 1), but in contrast found that IVTD_{Dom} increased as salinity level increased. Nevertheless, changes in IVTD_{Dom}, whether positive or negative, support the conclusion that increasing salt concentrations in halophytes results in structural and/or compositional changes.

Many common in vitro methods of assessing digestibility, such as IVTD, subject the DM to enzymatic or acid digestion and measure residual indigestible material. However, within halophytes the large soluble ash component artificially inflates estimated digestibility using these methods (Norman et al. 2013). Herein, we have shown that forage kochia is not exempt from this limitation (Fig. 4). Some authors have reported that organic matter digestibility (e.g., IVTD_{Dom}) is a more useful indicator of digestibility and energy (Masters et al. 2007), but in our study IVTD_{Dom} was highly correlated with the inflated IVTD estimates (see Table 1). Furthermore, we found that IVTD_{Dom} and IVTD_{corrected} were negatively correlated within forage kochia ($r = -0.41$, $P = 0.003$; data not shown) and across all species were not correlated (see Table 1). As a result, we conclude that digestibility corrected for ash (i.e., IVTD_{corrected}) is a more favorable estimate of digestibility in forage kochia, as compared with uncorrected IVTD or IVTD_{Dom}. Furthermore, it is probable that previous residue-based-only (i.e., uncorrected) IVTD estimates of digestibility in forage kochia and

Gardner's saltbush are inflated, and we recommend that future estimates be corrected for ash as described herein.

Data on the forage quality of halophytic shrubs are limited, and this is the first to investigate the role of salt on forage kochia nutritive value. These data are limited to immature plants in controlled environments, and therefore, additional field-based, mature plant evaluations are needed. Furthermore, adding salt to ruminant diets is known to decrease the efficiency and rate of digestibility, and therefore some authors recommend additional correction is needed to account for these apparent effects on digestibility kinetics (Norman et al. 2010; Norman et al. 2013). Inasmuch as forage kochia is valued for its ability to improve digestion rate of low-quality feedstuffs (Waldron et al. 2010b), additional research on the effect of salt to the digestion kinetics of forage kochia is also needed.

Implications

Forage kochia is a perennial, chenopod half-shrub well adapted to semiarid and arid rangelands and steppes, where it is used as forage for ruminant livestock. It is noted for its ability to produce edible forage in saline environments, but the influence of these saline environments on its forage quality had not been determined until now. In this study, it was discovered that forage kochia exhibited a dose response for salt concentration, crude protein, and digestibility in relation to increasing salinity. Salt concentrations reached a maximum of 19% of forage kochia DM when growing in 600 mM NaCl solution, which may have potential negative consequences to voluntary intake by ruminants grazing forage kochia. Crude protein did not differ between two forage kochia cultivars, but average forage kochia CP was decreased by 41% of the control at 600 mM NaCl. This may help explain the range of CP values observed for forage kochia across rangelands with varying soil salinity. Ash-corrected digestibility was decreased by 90 and 49 g kg⁻¹ DM between the control and 600 mM NaCl level, in Snow-storm and Immigrant, respectively. However, forage kochia exhibited lesser salt concentrations and greater digestibility and subsequent metabolizable energy than Gardner's saltbush (another valuable chenopod forage shrub), regardless of the salinity level. This study also confirmed that common residue-based in vitro methods overestimate digestibility and metabolizable energy of forage kochia and other halophytic chenopod shrubs growing in saline environments by not accounting for the soluble salt accumulation in the forage mass. This implies that land managers need to be aware of both soil salinity and plant species composition as they assess the forage potential of rangelands. In conclusion, saline rangelands reduce forage kochia's forage quality, primarily as a result of potentially high concentrations of ingestible salt and reduced digestibility and crude protein. However, this reduction appears to be less than in other halophytic Chenopodiaceae forage shrubs, thus supporting the continued use of forage kochia to improve the forage base of saline rangelands.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rama.2019.12.005>.

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