Title: No Escape: The Influence of Substrate Sodium on Plant Growth and Tissue Sodium Responses

Running title: Plant responses to substrate sodium

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Abstract

1. As an essential micronutrient for many organisms, sodium plays an important role in ecological and evolutionary dynamics. Although plants mediate trophic fluxes of sodium, from substrates to higher trophic levels, we know relatively little about plants' comparative growth and sodium accumulation responses to variation in substrate sodium. We carried out a systematic review to examine how plants respond to variation in substrate sodium concentrations.

2. We compared growth and tissue-sodium responses among 107 cultivars or populations (67 species in 20 plant families), broadly expanding beyond the agricultural and model taxa for which several generalizations previously have been made. We hypothesized *a priori* response models for each population's growth and sodium accumulation responses as a function of increasing substrate NaCl. We used BIC to choose the best model. Additionally, using a phylogenetic signal analysis, we tested for phylogenetic patterning of growth and sodium accumulation responses across plant taxa.

3. The influence of substrate sodium on growth differed across taxa, with most populations experiencing detrimental effects at high concentrations. Irrespective of growth response, tissue concentrations of sodium for most taxa increased as sodium concentrations in the substrate increased. We found no strong associations between growth and types of sodium accumulation responses across taxa. Our phylogenetic signal analyses found that evolutionary history helps predict the distribution of total-plant growth responses across the phylogeny, but not sodium accumulation responses.
4. Our study suggests that saltier plants in saltier soils may prove to be a broadly general pattern for sodium across plant taxa. Regardless of growth responses, sodium accumulation mostly followed an increasing trend and did not have any evident association with growth responses as substrate sodium levels increased. Finally, plant adaptations to substrate sodium vary with a degree of phylogenetic conservatism.

Keywords: biomass accumulation, fitness, halophytes, model selection, plant salt stress responses, plant growth, sodium, sodium accumulation

Introduction

Plants are key conduits in many, especially terrestrial, biogeochemical cycles (Elser & Bennett, 2011; Farago, 1994; Neubauer, Givler, Valentine, & Megonigal, 2005; Yuan & Chen, 2015). They often link soils to consumers and control, limit, or enhance the availability of elements that animals and microbes need. As intermediaries between soils and higher trophic levels, plants vary substantially in their composition of essential micronutrients for animals and decomposers. Elemental composition, stoichiometry and concentrations are principal dimensions of plant chemistry, or phytochemistry (Farago, 1995; Sterner & Elser, 2002). Hunter (2016) envisioned the geographic patterning of phytochemistry as the phytochemical landscape. Accordingly, the phytochemical landscape of micronutrients has considerable effects on plant-herbivore interactions, as well as community and ecosystem dynamics across landscapes that vary in soils, climate, *etc*. (Clay, Yanoviak, & Kaspari, 2014; Kaspari, Yanoviak, & Dudley, 2008; Moore, Lawler, Wallis, Beale, & Foley, 2010). Nonetheless, the composition, formation and intermediary function of the phytochemical landscape remains poorly characterized and understood (Hunter, 2016), especially for certain elements like sodium (Kaspari, 2020).

Sodium is the seventh most abundant element in the Earth's crust (Kaspari, 2020). However, its presence in terrestrial ecosystems is highly heterogeneous, but spatially correlated with xeric conditions, certain geological formations and proximity to a marine coast or source of marine aerosols (Kaspari, 2020; Martin, Coombes, & Dunstan, 2010; Smith, 2013; Stallard & Edmond, 1981). Sodium is unusual as a nutrient for life because although it is a non-essential element for most plants, it is a key and essential element for animals and decomposers (Kaspari, 2020). Although sodium requirements vary among organisms, the availability and intake of sodium are tightly linked to organismal performance across ecosystems and form fundamental components of ecological and evolutionary dynamics (Baxter & Dilkes, 2012; Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009; Sterner & Elser, 2002).

Plant populations and communities are exposed to a wide range of sodic substrates across terrestrial landscapes. Many plants actively avoid or limit sodium intake and most plants tolerate sodium in soils to remarkably high levels (at milli-molar levels) before they show signs of growth defects compared to many other non-essential or toxic cations such as lithium or many heavy metals that induce toxicity symptoms at micro-molar levels (Nawaz, Iqbal, Bliek, & Schat, 2017; Pantha & Dassanayake, 2020; Shahzad et al., 2016; van Zelm, Zhang, & Testerink, 2020; Vithanage et al., 2019). Most plants can tolerate or can be acclimated to survive up to 200 mM NaCl in their growth media, but those plants that can complete their life cycles at salinity levels higher than 200 mM NaCl are generally identified as halophytes (Cheeseman, 2015; Flowers, Galal, & Bromham, 2010; Flowers, Hajibagheri, & Clipson, 1986). Unlike most plants, many halophytes need sodium to thrive and show growth defects under limited sodium (Bose et al., 2017; D. Wang et al., 2012). However, only about 1% of the global flora are considered halophytes; they are distributed in multiple plant clades that reflect their convergent evolution to saline environments (Flowers & Colmer, 2008).

Variation in soil concentrations of sodium salts has direct links to variation in foliar sodium, which in turn influences plant-herbivore interactions and higher trophic-level performance (Bravo, Harms, & Emmons, 2010, 2012; Cheeseman, 2015; Kaspari, 2020; Kaspari, Clay, Donoso, & Yanoviak, 2014;

Snell-Rood *et al*., 2014). Even though most plants do not need sodium, they cannot necessarily avoid it nor escape having to cope with it. As sodium concentration increases in the substrate, its concentration in plant tissue also generally increases, and in turn affects plant fitness, especially in plants highly sensitive to salt stress (Greenway & Munns, 1980; Pantha & Dassanayake, 2020; Yang & Guo, 2018; Zhu, 2001). With increasing sodium, plants have been shown to: decrease biomass accumulation; increase osmotic, oxidative, and ionic stress responses; and arrest growth due to changes in cellular biochemistry (Maathuis, 2014; Zhao, Zhang, Song, Zhu, & Shabala, 2020).

Decades of physiological, biochemical, and genetic studies have contributed to our current understanding of how plants respond to salt stress. Yet these studies have primarily targeted salt stress-sensitive model plants like *Arabidopsis*, salt-sensitive crops, or extremely tolerant halophytes. For example, most crops or *Arabidopsis* ecotypes will show signs of salt-stress at 100 mM NaCl (0.58 %) treatments, whereas some halophytes can survive salinities exceeding seawater strengths (3.5 %) (Debez, Saadaoui, Slama, Huchzermeyer, & Abdelly, 2010; Flowers, 2004; Kazachkova et al., 2018; Zhu, 2000). However, these two extremes in the plant salt-tolerance spectrum represent less than 2% of all angiosperm diversity. Therefore, it is unclear how plants with varying degrees of salt-stress responses growing in diverse salinity conditions fit with the general expectations on how sodium accumulates in plants and how this accumulation affects their growth. To address this broad question, we conducted a systematic review of 49 published studies that includes 67 species and 107 cultivars or populations to identify broad-scale patterns of salt accumulation and growth responses across terrestrial angiosperms. Employing *a priori* response models that we could test against experimental data; we surveyed the relationships between plant biomass growth and substrate NaCl concentration from controlled experiments across taxa. We also characterized relationships between plant tissue sodium accumulation and substrate NaCl concentration across taxa and examined biomass growth responses associate with sodium accumulation. Finally, we assessed phylogenetic patterning of growth and sodium accumulation responses to determine if evolutionary history plays a role in the distribution of these traits.

Materials and Methods

Article search and selection protocol

To determine the effects of experimentally controlled, laboratory- or greenhouse-based substrate sodium chloride (NaCl) treatments on plant biomass and sodium accumulation in their tissues, we searched for peer-reviewed studies using Web of Science in December 2017 and May 2019 following the PRISMA protocol (Moher et al., 2009). We performed an initial search in December 2017 using the search criteria: "sodium AND biomass AND plant AND growth;" a timespan of "All years;" and indexes "Sci Expanded." These criteria yielded 6,503 articles. For a second search in May 2019, we used the keywords: "sodium AND biomass AND plant OR sodium AND growth AND plant OR sodium accumulation AND shoot AND root AND plant OR sodium AND plant AND halophytes AND biomass;" a timespan of "All years;" and indexes "Sci Expanded." This search yielded 6,654 articles. Subsequently, 6,387 duplicates were removed from the dataset, which produced a total of 6,770 non-duplicate articles from the two searches.

The articles fell into five unique categories: effects of sodium on growth, biomass, and tissue sodium accumulation in plants (1,305); salt related responses involving other taxa (animals, fungi, bacteria, protists, etc.) (906); transcriptomics, genomics, proteomics, or other molecular responses (627); influences of other elements and/or compounds (1,750); and other miscellaneous articles (2,183). We retained the 1,305 articles that provided data for growth (biomass accumulation) and sodium accumulation in plant tissues.

In plants, biomass, or biomass growth, are often used as proxies for fitness, because they are often highly correlated with plant fecundity and survivorship. In addition, these fitness metrics can be easily applied across taxa to answer comparable questions across multiple species (Younginger, Sirová, Cruzan, & Ballhorn, 2017). To investigate the relationship between substrate sodium and biomass changes, we further categorized studies into those that quantified both above- and belowground biomass (128); aboveground biomass (20); belowground biomass (3); total biomass (88); or fresh biomass (9). Studies from which quantitative data were not available or accessible (1,057) were excluded at this step. We retained 229 studies that reported sodium concentrations in plants, of which 49 studies also reported above- and belowground biomass for a total of 107 cultivars, strains, or varieties (herein populations) of plants, in 67 species, 43 genera, and 20 families, across 16 orders (Supplementary information: Table S1). Although these controlled experiments were conducted by different groups, in different controlled environments, and at different time scales, each used specific NaCl treatments between control and salt-treated plants for a uniform duration specific to each study, keeping all other macro- and micronutrients constant. The plant material subjected to NaCl treatments was mostly seedlings (80.37%), with the remaining studies conducted on cuttings (13.08%), rootstocks/grafts (3.74%), and bulbs (2.80%). Prior to analysis, we updated nomenclatural changes for all species considered in this study using Tropicos (www.tropicos.org) and NCBI taxonomical databases (Supplementary information: Table S6).

Data extraction and compilation

Articles differed substantially in their data representation, ranging from tables to graphical illustrations. We directly extracted data from tables, whereas measurements in figures were extracted using WebPlotDigitizer (Rohatgi, 2019). Treatments of NaCl were converted when necessary to mM. We focused on the mean responses of plants across treatments compared to their relevant control group as defined in each published study.

For biomass growth of above- (B_A), belowground (B_B), or total dry mass (B_T), we extracted and converted when necessary all measurements in grams. Above- and belowground biomass summed together equaled total plant biomass. We calculated relative biomass difference (RBD) for above-, belowground, or total biomass as:

$$RBD = \frac{Treatment\ biomass}{Control\ biomass} - 1$$

Values of RBD greater than zero mean that growth under the treatment condition exceeded the growth observed for control plants. A negative or zero RBD indicates that growth paused or slowed in the salt-treated plants compared to the control plants. While we note that growth itself cannot be negative, negative RBD values may represent salt-induced shedding of leaves or similar plant responses that may directly affect the total biomass of experimental plants. RBD values corresponding to their raw experimental values for each study are given in Supplementary Information: Table S2.

Using the same methods described above, we extracted sodium concentrations per dry mass of above-, belowground or total tissues. It is important to note that some plants may have expelled sodium, by means of salt glands or other adaptations. Tissue sodium concentration was considered as reported by each study. Acceptable sodium concentration measurements included weight by weight basis (*i.e.,* mg/g, mg/kg), molality (*i.e.,* µM, mM or M(mol/L)), molarity (*i.e.,* mol/g), percentage (%), or parts per million (ppm). We converted all measurements when necessary, to percentage (%) values. Measurements of electric conductivity (S/m or psu) were excluded because, unless stated, they do not necessarily reflect sodium concentrations accurately since electrical conductivity results from multiple elemental ions (Carter & Gregorich, 2007). Above- (Na_A) and belowground (Na_B) tissue sodium concentrations (%) were used to calculate total plant sodium concentration (Na_T, %) using the formula:

$$Na_T = \left(\frac{B_A}{B_T} * Na_A\right) + \left(\frac{B_B}{B_T} * Na_B\right)$$

All extracted raw data for sodium accumulation have been organized in Supplementary information: Table S3.

Model design, selection and population classification

We postulated a set of *a priori* potential response models for both RBD (Table 1) and sodium accumulation (Table 2) as functions of substrate NaCl treatments. Each *a priori* model prediction was described by a mathematical function for the shape of the response curve. Three pairs of responses shared an underlying mathematical function. For growth (Table 1), the function for a straight line accounted for both linear increase and linear decrease models; the slope of the line was used to classify the respective response - positive slope indicated linear increase and negative slope indicated linear decrease. Also, the quadratic function accounted for both hump-shaped and non-linear decrease models. For sodium accumulation (Table 2), the quadratic function accounted for hump-shaped and non-linear increase. In these quadratic-function cases, we used the vertex value (a) to classify cases as hump-shaped (when a was negative) or non-linear decrease and non-linear increase (when a was positive).

We used an Information Criterion (IC) approach to select the model that best fit the data extracted for each population, using three different ICs: Akaike Information Criterion (AIC), the AIC small-sample corrected version (AICc), and Bayesian Information Criterion (BIC). We used the R package '*AICcmodavg*' to calculate AIC, AICc and BIC values (Mazerolle, 2020). Although we examined results from all three metrics, we based our conclusions on BIC, since this metric gave consistent results across the data sampled, it is more specific (reduced Type-I error or lower false-positive rate), and is considered a more conservative test, as advocated by Dziak, Coffman, Lanza, Li, and Jermiin (2020). AIC is mainly recommended for larger datasets and does not account for sample size. Furthermore, for AICc, the penalization that is given to the AIC formula increases the chances of overfitting the data due to the extremely small sample sizes for the data analyzed (Bolker, 2018; Dziak et al. 2020). The models from Tables 1 and 2 that best fit each response (*i.e.*, the smallest BIC value) were used to designate a response shape for each population's above-, belowground and total plant biomass growth and sodium accumulation, respectively. Since we based our conclusions on BIC, we provide the corresponding likelihood values, ΔBIC, and BIC weights for each model chosen; we also share results from the other two IC metrics for comparison (Supplementary Information: Tables S4, S5, S7 and S8).

Fisher's Exact test contingency analysis with simulated p-values in R-Studio following recommendations from Broman and Caffo (2003) was used to test for significant differences between growth and Na accumulation. This test assumes that each population can be treated independently. This assumption may not be valid if the responses in certain groups are dependent on phylogenetic relationships (see next section for our analyses to test for such a bias).

To determine whether sodium accumulation differed by growth responses between above- and belowground tissues, for each growth response category we performed a Wilcoxon test for paired values of above- vs. belowground tissue sodium concentrations. For this test we divided treatments into non-saline (0 mM treatment of NaCl) and saline treatments (30-300 mM treatment of NaCl). For the saline group, the highest treatments for each population were selected within the treatment range of 30-300 mM of NaCl to keep sample size equal among non-saline and saline groups for adequate comparisons.

Phylogenetic patterns among responses

We performed a phylogenetic signal analysis to assess whether phylogenetic relationships may have influenced growth and Na accumulation responses in the diverse set of taxa used in our systematic review. Phylogenetic signal is the tendency of closely related species to resemble each other more in trait values than species drawn at random (Blomberg, Garland, & Ives, 2003; Münkemüller et al., 2012). We used a subset of the rooted and dated ALLMB phylogeny from Smith and Brown (2018) for our phylogenetic signal analyses; this phylogeny consists of a backbone from Magallón, Gómez-Acevedo, Sánchez-Reyes, and Hernández-Hernández (2015) and data from both GenBank and the Open Tree of Life (Smith & Brown, 2018; available from https://github.com/FePhyFoFum/big_seed_plant_trees; Supplementary information: Table S6). The phylogenetic tree of angiosperms was pruned using the '*drop.tip'* function from the *ape* package (Paradis and Schliep 2019; v.5.3) on R (v1.2.1335; RStudio, Inc.) to represent the species relevant to this study. In four cases (*Citrus sinensis, Solanum nigrum, Triglochin bulbosa,* and *Tripleurospermum maritimum*), subspecies were used as proxies in the phylogeny. For the genus *Narcissus*, we used the species *N. tazetta* for tree pruning (LoPresti, Pan, Goidell, Weber, & Karban, 2019). Additionally, for species that had multiple populations represented in our response dataset, we averaged population responses and selected the best models that fit the extracted data to assign overall responses for growth and sodium accumulation for each species (*Aeloropus lagopoides, Beta vulgaris, Brassica rapa, Cajanus cajan, Eucalyptus camaldulensis, Gossypium hirsutum, Helianthus annuus, Lotus creticus, Narcissus, Olea europaea, Oryza sativa, Phaseolus vulgaris, Solanum lycopersicum,* and *Solanum melongena*). A polytomy at the node for *Citrus* was resolved using the *phytools* package (Revell 2012) function '*resolveNode'* and '*multi2di'* function from the *ape* package (Paradis and Schliep 2019) in R Studio.

We tested for phylogenetic signals for the discrete characters of above-, belowground and total plant growth and sodium accumulation response, respectively, using the Maddison and Slatkin (1991) method in the '*phylo.signal.disc'* function from Bush et al. (2016). This method estimates the minimum trait transitions at each node and compares this to a distribution sampled from a null model (Head et al., 2018; Paleo-López et al., 2016). We used 1000 randomizations to infer a significant result if the number of observed trait changes was significantly (alpha=0.05) less than the median of the null model distribution.

Results

Increasing substrate NaCl has varied effects on total plant growth responses

Using model selection for each of our chosen 107 populations, we classified relative total plant growth responses as shown in Table 1 (Supplementary information: Table S1). Growth was negatively affected as sodium increased in the substrate for most taxa. However, 14 taxa showed a linear increase or initial increase (*i.e*., hump shaped) growth response for treatments ≥250 mM NaCl. Growth was severely reduced in all populations that were exposed to NaCl concentrations >500 mM as compared to 0 mM of NaCl (Fig. 1). None of the populations that we classified as having linear increase or threshold decline biomass responses were exposed to treatments >320 mM NaCl.

Plant growth based on relative biomass difference showed similar trends in response to increased salinity regardless of the tissue sampled from above- or belowground (Supporting information S1: Figure S1a, b). Interestingly, the overall growth patterns of above or belowground tissue mirrored the patterns observed at the total plant level as visualized by similarity in the alluvial plot (Fig. 2a).

Total plant sodium increases as substrate sodium increases

Using model selection for each of the 107 populations, we classified total plant sodium accumulation responses into 6 groups shown in Table 2 (Supplementary Information: Table S1). The total sodium concentration within a plant increased as the substrate concentration of sodium increased (Fig. 1b). However, the level of sodium accumulation was highly variable among populations and between above and belowground tissues (Supporting Information S1: Figure S1c, d). Notably, the aboveground sodium concentrations were generally higher than in belowground tissues for most populations (Supporting Information S1: Figure S1c, d). Additionally, regardless of the variation observed, both relative above- ($p < 0.001$) and belowground ($p < 0.001$) responses were similar to relative total sodium accumulation responses (Fig. 2b).

Crop species do not adequately represent general plant responses

In our study, crop species represent 57.9% (62) of the populations surveyed with only 7 of them surpassing 200 mM experimental exposure to substrate NaCl (Fig. 3). Growth responses were generally more variable in non-crop populations with hump-shaped growth responses being more prominent in non-crops (26.7 %) as compared to crop (4.8%) populations (Fig. 3a). Moreover, percent differences in internal sodium concentration varied more in non-crops plants as compared to crop populations (*i.e.,* variability in sodium held within the plant was higher in non-crops) (Fig. 4).

Plant growth responses do not predict sodium accumulation responses

Total plant biomass growth responses were largely independent of the type of sodium accumulation response, which we illustrate using an alluvial plot ($p = 0.43$; Fig. 5). Furthermore, irrespective of the growth response, tissue sodium concentrations increased monotonically (*i.e.,* increase in plant sodium continues at a steady positive rate as sodium in the substrate increases or increase to a plateau for most taxa) (77%) as sodium concentrations in the substrate increased (Fig. 1 and 5).

Only those populations with hump-shaped growth responses differed significantly in sodium accumulation between above- and belowground tissues across saline treatments (Wilcoxon test: n= 17, Z=1.9, p>0.046). There were no statistically significant differences for any other biomass growth responses between sodium accumulation of above- versus belowground tissues across saline treatments. Additionally, for non-saline treatments, there was no statistically significant difference for any biomass growth response groups when above-and belowground sodium accumulation was compared (Fig. 6).

Phylogenetic relationships predict biomass growth but not sodium accumulation responses

Biomass growth, both above- and belowground, showed significant phylogenetic signal (*i.e*., phylogenetic relationships help explain the distribution of the trait across the phylogenetic tree in our dataset; $p = 0.031$ and $p = 0.046$, respectively; Fig. 7). We recovered 28 observed evolutionary transitions (*i.e.,* the change from one discrete trait to another) with a randomization median of 35 for aboveground biomass growth response. Belowground biomass growth response showed 33 observed evolutionary transitions and a randomization median of 37 transitions. We found significant phylogenetic signal for total biomass response ($p = 0.012$) with 29 observed evolutionary transitions and 34 median randomization transitions. Most of the species in the order Caryophyllales, especially in the family Amaranthaceae, expressed a hump-shaped biomass growth response as sodium increased in the substrate. However, hump-shaped responses were also found in other plant orders, reflecting potential independent evolutionary origins, though further testing is necessary.

Sodium accumulation responses (both above- and belowground) were not phylogenetically organized in any plant orders and did not show significant phylogenetic signal ($p = 0.37$ and $p = 0.184$, respectively; Fig. 8). For aboveground sodium accumulation response, there were 36 observed evolutionary transitions while the randomization median was 37. We found 35 observed evolutionary transitions and 37 randomized median transitions for belowground sodium accumulation response. No phylogenetic signal was found for total sodium accumulation response ($p = 0.161$) and we recovered 38 observed transitions with a randomized median of 40 transitions. For the orders most sampled, Caryophyllales and Poales, responses for sodium accumulation differed substantially across and within genera, with no apparent pattern observed. Plants appeared to accumulate sodium in different ways and patterns regardless of their biomass growth responses.

Discussion

Increasing substrate sodium influences plant growth and sodium accumulation in variable ways

Saline soils are known to hinder plant growth, in general, and crop losses are reported when soil salinity is above a crop−specific threshold (Bernstein, 1975; Zhao et al., 2020; Zörb, Geilfus, & Dietz, 2019). While our analysis is aligned with this general consensus on the negative impact of soil salinity on plant growth, it sheds light on how plant growth varied in response to substrate NaCl levels across plant taxa that ranged from highly studied crops to scarcely examined wild species (Table 1 and Fig. 2 a, b). Despite the overall trend of decreased biomass concurrent to increasing substrate NaCl levels, several taxa in the order Caryophyllales (*e.g*., families Amaranthaceae, Plumbaginaceae and Portulacaceae) showed a hump-shaped or linear increases in biomass growth to increasing substrate NaCl (Figs. 1a and 7). Most halophytes are non-randomly distributed and the order Caryophyllales holds the greatest number of recorded halophytes among angiosperms (Flowers et al., 2010). Halophytes not only are tolerant of high NaCl, but also use Na^+ and Cl^- ions for osmotic adjustment in an energetically favorable manner and are equipped with structural and physiological traits which aid the compartmentalization of salts to promote growth while avoiding ionic or osmotic stress until threshold NaCl levels are reached (Munns, Passioura, Colmer, & Byrt, 2020; Slama, Abdelly, Bouchereau, Flowers, & Savouré, 2015). This set of characteristics would account for the positive growth we observed within the Caryophyllales taxa in our analysis (Fig.1a and 7). Furthermore, plants that follow these hump-shaped or linear increase growth responses to increasing substrate sodium follow a subsidy-stress gradient, *i.e.,* at low substrate sodium levels overall plant growth is subsidized, reaching a threshold leading to growth inhibition due to salt stress as sodium in the substrate becomes toxic (Odum, Finn, & Franz, 1979).

The use of sodium as an inexpensive osmolyte has convergently evolved in many halophytes as well as other plants adapted to water deficit stress and are found in multiple orders of plants. For example, even at low sodium levels in the soil, the xeric adapted plant, *Zygophyllum xanthoxylum* (Zygophyllaceae), accumulates high concentrations of sodium in shoots, resulting in large mesophyll cells leading to leaf succulence (Xi et al., 2018). All plants that followed these trajectories in our analyses (Fig. 7) are considered salt tolerant, as classified in the eHALOPH database (Santos, Al-Azzami, Aronson, & Flowers, 2016) and by the respective authors in each study (Supplementary Information S1). Regardless, even among those salt-tolerant taxa, plant biomass eventually decreased at the highest NaCl concentrations (Fig. 1a).

The taxa that showed linear or non-linear decreases (Fig. 1a and 7) as NaCl increased in the substrate are non-halophytes highly sensitive to salt stress where growth is inhibited by excess salts (Munns et al., 2020; van Zelm et al., 2020). Moreover, we found that closely related lineages resembled each other with respect to biomass growth responses (*i.e.*, significant phylogenetic signal indicating shared physiological responses within clades); thus, the patterns observed in this trait are at least somewhat explained by shared evolutionary history (Fig. 7). However, phylogenetic patterns do not account for sodium accumulation responses (Fig. 8).

In plants, tissue sodium concentrations are generally linked with increasing substrate sodium concentrations (Fig. 1b). However, plant sodium accumulation seemed to be uncoupled from biomass growth responses and any discernible phylogenetic signal among taxa (Figs. 5 and 8). Similar patterns were observed when aboveground sodium accumulation was compared in the species *Plantago maritima* and *P. media* as NaCl in the substrate was increased (Maathius, 2014; note that these populations – among others in the literature – were not included in the current study since they did not meet the criteria for our selection). The variation in responses by each species was mainly due to differential and discrete tolerance thresholds and external sodium concentrations (Maathuis, 2014), which might explain the idiosyncratic variation that is observed among taxa use in this study in terms of sodium accumulation responses (Figs. 1b and 8).

Additionally, the accumulation of higher amounts of sodium in aboveground (Supporting Information S1: Fig. S1c) than belowground (Supporting Information S1: Fig. S1d) tissues is apparent when comparing sodium accumulation responses for each population across increasing treatments of substrate NaCl (Fig. 1b). This observation agrees with the current understanding that sodium, once in the transpiration stream, is retained in the shoots as phloem re-circulation to roots is considerably less compared to xylem loading from roots to shoots (Munns, 2002; Munns & Tester, 2008). Sodium accumulation in the shoots is dependent on the local tissue and species-specific tolerance capacity. Plants are known to store excess sodium in older leaves to protect younger growing tissue from salt toxicity and sustain growth until species-specific tolerance levels are reached (Munns & Tester, 2008). Alternatively, a few halophytes have developed salt glands to remove sodium from shoots against a concentration gradient – a unique adaptation that is found in several plant orders (Dassanayake & Larkin, 2017).

Once sodium enters the roots, plants have transporters that preferentially export sodium back to the soil at an energy cost. However, this capacity to export sodium at the soil-root interphase is easily exceeded even among halophytes and accumulation of sodium inside the plant is unavoidable when external sodium concentrations increase (Zhao et al., 2020). Therefore, other sodium transporters that facilitate ionic balance throughout the plant organs play critical roles in sustaining growth or survival during salt stress (Apse & Blumwald, 2007; Yamaguchi, Hamamoto, & Uozumi, 2013). Our systematic review agrees with previous studies investigating single or small groups of taxa subjected to salt stress to highlight that almost all plants accumulated sodium monotonically (or nearly monotonically) as sodium increased in the substrate (Figs. 1b and 5). Plants that expressed the biomass growth hump-shaped response accumulated significantly higher concentrations of sodium in above- than belowground tissues. Alternatively, populations characterized by the other growth responses did not differ significantly in above- vs. belowground sodium accumulation in saline treatments but not in non-saline treatments (Fig. 6). We discussed earlier that the hump-shaped response was preferentially represented by taxa in the order Caryophyllales, and that this clade is an evolutionary hotspot for halophytes, but this response is not confined to the order (Fig. 7). Furthermore, Caryophyllales species often are shoot sodium hyperaccumulators; they are enriched in plants that develop salt glands; and have a higher tolerance to higher tissue sodium levels compared to predominantly salt-sensitive orders (Dassanayake & Larkin, 2017; Flowers et al., 2010; White et al., 2017).

Domesticated plants species tend to occupy a narrow range of variation among salt stress responses

Our systematic review demonstrated a clear dichotomy between salt tolerance (deduced from growth responses) during increased external sodium in crops compared to wild species or plants that have not been subjected to domestication. All wild species tend to have a higher capacity to tolerate higher tissue sodium than crop or domesticated species (Fig. 2 a, b). The exception to this is seen with crops in Caryophyllales, such as *Beta vulgaris, Salicornia bigelovii,* and *Spinacia oleracea* (Choo, Song, & Albert, 2001; Wu, Liang, Feng, & Zhang, 2013; Yamada, Kuroda, & Fujiyama, 2016). Recent studies have illustrated how crop species have lost traits related to salt tolerance their ancestral wild relatives had before and during domestication (Quan et al., 2018; Rozema et al., 2015; Z. Wang et al., 2021, 2020).

The individual studies used for our systematic review are limited to small and variable sample sizes among populations, differing treatment concentrations of NaCl, and include a mixture of crop (44.1%) and non-crop (55.9%) plant species. Salt stress responses in plants are known to vary in how the salt treatment is given (acclimated treatment vs salt shock), duration of the treatment, the age of the plants, plant growth conditions (*e.g.,* light levels, presence of other stresses, and grown hydroponically or in soil, tidal systems, submerged systems), plant habit (*e.g.,* herb vs tree, creeper vs upright), life history traits (*e.g.,* annual vs perennial, frequency of flowering), morphological traits of the plants (*e.g.,* presence or absence of salt glands, ability to produce succulent leaves, structural adaptations in roots), among many other genetic and environmental factors (Polle & Chen, 2015; Zhao et al., 2020). Plant survival compared to growth may use different adaptive traits among plants and biomass may not be the only indicator nor the optimal indicator to measure salt responses among different groups of plants. Therefore, systematic, and rigorous studies need to be performed to understand overall mechanisms underlying salt stress responses across taxa, as discussed in the next sections.

Characterizing responses promotes our understanding of plant-salt stress

The models used in this study provide a useful approach to quantify and categorize individual plant population responses to variation in NaCl in the substrate. These models describe the response trajectories of biomass growth and sodium accumulation responses and could be used extensively across taxa of interest. By using an Information Criterion approach, one can select the best-fit model for each population, given that our formulated models (*e.g.,* linear decrease, hump-shaped, *etc*.) effectively describe natural patterns (Brewer, Butler, & Cooksley, 2016), within and among species (Table 1 and 2). For many purposes, it may be more useful to categorize plants by their responses across a range of sodium conditions, as opposed to performance above and below strict thresholds as is often done with halophytic or salt tolerant plants (see Grigore, Ivanescu, and Toma, (2014) for a review on definitions and descriptions related to halophytes).

Experimental design to achieve broader understanding

Many studies have tested the effects of NaCl on plant growth and yield, especially in crop species (Cheeseman, 2015). However, because of differences in methodology, it is a challenge to make comparisons and contrasts of results across studies. We make several observations and recommendations for future studies:

a. Often, there is a lack of enough replication and/or treatments. For us, this prevented effective response pattern identification in some cases, especially in studies that presented only three treatments with few replicates.
b. The determination of treatments was often arbitrary. Limitations are imposed using independent categorical variables (ANOVA-based approach) instead of applying treatments as independent numeric discrete or continuous variables (regression-based approach). Experimental designs that cover a wide range of treatments may provide more accurate estimates. A regression-based approach allows one to better fit non-linear responses which encompasses most of the responses we measured in our study (Inouye, 2001; Whitlock & Schluter, 2014). Additionally, when resources are limited, experimental design should prioritize increasing the number of treatments over increasing number of replicates per treatment. Furthermore, functional growth analysis (*i.e.,*

the assessment of absolute growth rate and relative growth rate) should be performed to better comprehend how plants manage resources at different life stages or across multiple environmental stresses, especially in the context of biomass growth and ionic accumulation (Cheeseman & Wickens, 1986; Tessmer, Jiao, Cruz, Kramer, & Chen, 2013).

c. Most of the plants in the studies selected were not exposed to the highest levels of sodium they could potentially encounter in nature. Lack of these data thwarts the complete description of responses associated with increasing substrate NaCl within and across taxa. Linear increase responses are highly unlikely across all NaCl concentrations observed in nature. This type of response in our study likely results from lack of high NaCl treatments. Under the full range of NaCl, these taxa would most likely have hump-shaped responses. Additionally, we observed that in non-saline treatments (0 mM substrate NaCl), substantially large amounts of sodium were found in some plant taxa. The reason for this could have been the lack of attention to the ionic salts used in the Hoagland solution; some salts are combined with sodium (*i.e.,* EDTA, Na_2MoO_4 $2H_2O$, etc). Another reason could be the use of tap water instead of distilled or deionized water. Generally, a combination of copper, calcium, magnesium, and sodium is found in tap water on average at 1%, with some regional variation (Patterson, Pehrsson and Perry, 2013).

d. Many of the plants in the studies selected were grown under controlled conditions using watering regimes and nutrient mixes that do not closely reflect conditions in nature. Future research should focus on plant morphological, physiological, and adaptive responses to treatment solutions and/or substrates that truly match conditions (water availability, nutrient stoichiometry, etc.) potentially found in nature.

e. Studies generally focus on biomass to the exclusion of other fitness-related traits. Even though biomass is an appropriate proxy for fitness measurements in plants (Younginger et al., 2017), observations on flower production, survivorship, seed set, and seed germination success should be quantified, to provide a more complete understanding of sodium's influence on whole-plant performance and fitness (Primack & Kang, 1989).

f. Studies also should consider that salt stress is often combined with water deficit and heat stress, or other nutrient stresses in natural habitats. Additionally, biotic stresses such as herbivory and diseases can compound the overall plant response to salt stress, with special consideration of wild taxa. The net outcome of plant performance under these natural conditions needs to be assessed compared to responses observed under controlled environments to be able to model plant responses at community or ecosystem scales.

Moving toward an ecological - evolutionary perspective: from the lab to the field

We focused on plant performance and sodium accumulation strategies in controlled settings as reported in the literature, which emphasizes the physiological aspects of substrate sodium rather than the ecological and selective effects of sodium on plant performance, including fitness, under environmental conditions in nature. More importantly, this systematic review suggests the general no-escape-from-sodium hypothesis, *i.e.,* that generally plants' tissue sodium levels reflect (at least in a ranked fashion) substrate/solution sodium levels irrespective of their growth responses to sodium (potentially with key and interesting exceptions). We still have a long way to go to be able to fully test this hypothesis, especially under the natural field conditions that truly matter for plant evolution, ecology, and farming.

Moreover, assessments of the phytochemical landscape of sodium across large geographical areas is increasing, with examples in *Ficus* in Central and South America (Bravo & Harms, 2017), *Asclepias* (milkweeds) in Minnesota (Mitchell et al., 2020), among roadside plant communities in Massachusetts (Bryson & Barker, 2002), and across global grasslands (Borer et al., 2019). These examples demonstrate that aboveground plant sodium accumulation co-varies closely with some abiotic factors, including but not limited to: effective distance from nearest coast/saline habitat; road salt pollution; and concentration of sodium in the soil. However, experimental designs that include comprehensive plant growth meta-data, phenotyping, and careful selection of target plants to allow rigorous, yet broad comparisons are needed. These recommendations would help advance our understanding of the complexity of the formation of the phytochemical landscape of sodium and its ecological and evolutionary consequences for plant performance, sodium accumulation and plant-herbivore interactions.

In conclusion, understanding the influence of sodium in the substrate on plant performance (growth, fitness) and tissue sodium accumulation is essential to understand ecological and evolutionary dynamics of plants across terrestrial environments. Our study highlights that plant adaptations to substrate sodium vary with a degree of phylogenetic conservatism. Regardless of growth responses, sodium accumulation mostly followed an increasing trend and did not have any apparent association to growth responses as substrate sodium levels increased. In any case, saltier plants in saltier soils may prove to be a broadly general pattern for sodium, which begs the future research question: how do plants respond to the other elements in their substrates?

References

Abdallah, S. B., Aung, B., Amyot, L., Lalin, I., Lachâal, M., Karray-Bouraoui, N., & Hannoufa, A. (2016). Salt stress (NaCl) affects plant growth and branch pathways of carotenoid and flavonoid biosyntheses in *Solanum nigrum*. *Acta Physiologiae Plantarum*, *38*(3), 1–13. doi: 10.1007/s11738-016-2096-8

Al Sherif, E. A. (2009). *Melilotus indicus* (L.) All., a salt-tolerant wild leguminous herb with high potential for use as a forage crop in salt-affected soils. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *204*(10), 737–746. doi: 10.1016/j.flora.2008.10.004

Apse, M. P., & Blumwald, E. (2007, May 25). Na^+ transport in plants. *FEBS Letters*, Vol. 581, pp. 2247–2254. doi: 10.1016/j.febslet.2007.04.014

Ashraf, M., & Ahmad, S. (2000). Influence of sodium chloride on ion accumulation, yield components and fibre characteristics in salt-tolerant and salt-sensitive lines of cotton (*Gossypium hirsutum* L.). *Field Crops Research*, *66*(2), 115–127.

Ashraf, M., Nazir, N., & McNeilly, T. (2001). Comparative salt tolerance of amphidiploid and diploid *Brassica* species. *Plant Science*, *160*(4), 683–689. doi: 10.1016/S0168-9452(00)00449-0

Assaha, D. V. M., Ueda, A., & Saneoka, H. (2013). Comparison of growth and mineral accumulation of two solanaceous species, *Solanum scabrum* Mill. (huckleberry) and *S. melongena* L. (eggplant), under salinity stress. *Soil Science and Plant Nutrition*, *59*(6), 912–920. doi: 10.1080/00380768.2013.858300

Barhoumi, Z., Djebali, W., Smaoui, A., Chaïbi, W., & Abdelly, C. (2007). Contribution of NaCl excretion to salt resistance of *Aeluropus littoralis* (Willd) Parl. *Journal of Plant Physiology*, *164*(7), 842–850. doi: 10.1016/j.jplph.2006.05.008

Bayuelo-Jiménez, J. S., Debouck, D. G., & Lynch, J. P. (2003). Growth, gas exchange, water relations, and ion composition of *Phaseolus* species grown under saline conditions. *Field Crops Research*, *80*(3), 207–222. doi: 10.1016/S0378-4290(02)00179-X

Baxter, I., & Dilkes, B. P. (2012). Elemental Profiles Reflect Plant Adaptations to the Environment. *Science*, *336*(6089), 1661–1663. https://doi.org/10.1126/science.1219992

Ben Hamed, K., Chibani, F., Abdelly, C., & Magne, C. (2014). Growth, sodium uptake and antioxidant responses of coastal plants differing in their ecological status under increasing salinity. *Biologia*, *69*(2), 193–201. doi: 10.2478/s11756-013-0304-1

Bernstein, L. (1975). Effects of Salinity and Sodicity on Plant Growth. *Annual Review of Phytopathology, 13*(1), 295–312. doi: 10.1146/annurev.py.13.090175.001455

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*(4), 717–745. doi: 10.1111/j.0014-3820.2003.tb00285.x

Bolker, B. M. (2008). *Ecological models and data in R.* Princeton University Press. doi: 10.1111/j.1442-9993.2010.02210.x

Borer, E. T., Lind, E. M., Firn, J., Seabloom, E. W., Anderson, T. M., Bakker, E. S., … Stevens, C. J. (2019). More salt, please: global patterns, responses and impacts of foliar sodium in grasslands.

Ecology Letters, *22*(7), 1136–1144. doi: 10.1111/ele.13270

Bose, J., Munns, R., Shabala, S., Gilliham, M., Pogson, B., & Tyerman, S. D. (2017). Chloroplast function and ion regulation in plants growing on saline soils: Lessons from halophytes. *Journal of Experimental Botany, 68*(12), 3129–3143. https://doi.org/10.1093/jxb/erx142

Bravo, A., & Harms, K. E. (2017). The biogeography of sodium in Neotropical figs (Moraceae). *Biotropica*, *49*(1), 18–22. doi: 10.1111/btp.12398

Bravo, A., Harms, K. E., & Emmons, L. H. (2010). Puddles created by geophagous mammals are potential mineral sources for frugivorous bats (Stenodermatinae) in the Peruvian Amazon. *Journal of Tropical Ecology*, *26*(2), 173–184. doi: 10.1017/S0266467409990472

Bravo, A., Harms, K. E., & Emmons, L. H. (2012). Keystone resource (*Ficus*) chemistry explains lick visitation by frugivorous bats. *Journal of Mammalogy*, *93*(4), 1099–1109. doi: 10.1644/11-MAMM-A-333.1

Brewer, M. J., Butler, A., & Cooksley, S. L. (2016). The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. *Methods in Ecology and Evolution*, *7*(6), 679–692. doi: 10.1111/2041-210X.12541

Broman, K. W., & Caffo, B. S. (2003). Simulation-based P values: Response to North et al. *American Journal of Human Genetics*, *72*, p. 496. doi: 10.1086/346175

Bryson, G. M., & Barker, A. V. (2002). Sodium accumulation in soils and plants along Massachusetts roadsides. *Communications in Soil Science and Plant Analysis*, *33*(1–2), 67–78. doi: 10.1081/CSS-120002378

Bush, S. E., Weckstein, J. D., Gustafsson, D. R., Allen, J., DiBlasi, E., Shreve, S. M., … Johnson, K. P. (2016). Unlocking the black box of feather louse diversity: A molecular phylogeny of the hyper-diverse genus *Brueelia*. *Molecular Phylogenetics and Evolution*, *94*, 737–751. doi: 10.1016/j.ympev.2015.09.015

Carter, M. R., & Gregorich, E. G. (2007). *Soil Sampling and Methods of Analysis* (Second Edi). CRC Press.

Chartzoulakis, K. S., Therios, I. N., Misopolinos, N. D., & Noitsakis, B. I. (1995). Growth, ion content and photosynthetic performance of salt-stressed kiwifruit plants. *Irrigation Science*, *16*(1), 23–28. doi: 10.1007/BF00208392

Cheeseman, J. M. (2015). The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. *New Phytologist*, *206*(2), 557–570. doi: 10.1111/nph.13217

Cheeseman, J. M., & Wickens, L. K. (1986). Control of Na^+ and K^+ transport in *Spergularia marina*. III. Relationship between ion uptake and growth at moderate salinity. *Physiologia Plantarum, 67*(1), 15–22. doi: 10.1111/j.1399-3054.1986.tb01256.x

Choo, Y. S., Song, S. D., & Albert, R. (2001). Effects of salinity on growth and patterns of ions and organic solutes in five sedges (*Carex* spp.) with different ecological demands. *Flora*, *196*(1), 71–80. doi: 10.1016/S0367-2530(17)30014-2

Clay, N. A., Yanoviak, S. P., & Kaspari, M. (2014). Short-term sodium inputs attract microbi-detritivores and their predators. *Soil Biology and Biochemistry*, *75*, 248–253. doi: 10.1016/j.soilbio.2014.04.021

Dassanayake, M., & Larkin, J. C. (2017). Making plants break a sweat: The structure, function, and evolution of plant salt glands. *Frontiers in Plant Science, 8*(March), 1–20. doi: 10.3389/fpls.2017.00406

Debez, A., Saadaoui, D., Slama, I., Huchzermeyer, B., & Abdelly, C. (2010). Responses of *Batis maritima* plants challenged with up to two-fold seawater NaCl salinity. *Journal of Plant Nutrition and Soil Science*, *173*(2), 291–299. doi: 10.1002/jpln.200900222

Dziak, J. J., Coffman, D. L., Lanza, S. T., Li, R., & Jermiin, L. S. (2020). Sensitivity and specificity of information criteria. *Briefings in Bioinformatics*, *21*(2), 553–565. doi: 10.1093/bib/bbz016

Elser, J., & Bennett, E. (2011). A broken biogeochemical cycle. *Nature, 478*(7367), 29–31. https://doi.org/10.1038/478029a

Ebrahimi, R., & Bhatla, S. C. (2011). Effect of sodium chloride levels on growth, water status, uptake, transport, and accumulation pattern of sodium and chloride ions in young sunflower plants. *Communications in Soil Science and Plant Analysis*, *42*(7), 815–831. doi: 10.1080/00103624.2011.552657

Farago, M. E. (1995). Plants and the chemical elements: Biochemistry, uptake, tolerance and toxicity. In *Environmental Pollution* (Vol. 87). doi: 10.1016/0269-7491(95)90037-3

Ferreira, R. G., Távora, F. J. A. F., & Hernandez, F. F. F. (2001). Distribuição da matéria seca e composição química das raízes, caule e folhas de goiabeira submetida a estresse salino. *Pesquisa Agropecuaria Brasileira*, *36*(1), 79–88. doi: 10.1590/s0100-204x2001000100010

Flowers, T. J. (2004). Improving crop salt tolerance. *Journal of Experimental Botany, 55*(396), 307–319. https://doi.org/10.1093/jxb/erh003

Flowers, T. J., & Colmer, T. D. (2008). Salinity tolerance in halophytes. *New Phytologist*, *179*(4), 945–963. doi: 10.1111/j.1469-8137.2008.02531.x

Flowers, T. J., Galal, H. K., & Bromham, L. (2010). Evolution of halophytes: Multiple origins of salt tolerance in land plants. *Functional Plant Biology, 37*(7), 604–612. https://doi.org/10.1071/FP09269

Flowers, T. J., Hajibagheri, M. A., & Clipson, N. J. W. (1986). Halophytes. *Quarterly Review of Biology*, *61*(3), 313–337. https://doi.org/10.1086/415032

Gebauer, J., El-Siddig, K., Salih, A. A., & Ebert, G. (2004). *Tamarindus indica* L. seedlings are moderately salt tolerant when exposed to NaCl-induced salinity. *Scientia Horticulturae*, *103*(1), 1–8.

doi: 10.1016/j.scienta.2004.04.022

Gorai, M., Vadel, A. M., Neffati, M., & Khemira, H. (2007). The effect of sodium chloride salinity on the growth, water status and ion content of *Phragmites communis* Trin. *Pakistan Journal of Biological Sciences*, *10*(13), 2225–2230. doi: 10.3923/pjbs.2007.2225.2230

Greenway, H., & Munns, R. (1980). Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology*, *31*(1), 149–190. doi: 10.1146/annurev.pp.31.060180.001053

Grigore, M. N., Ivanescu, L., & Toma, C. (2014). Halophytes: An integrative anatomical study. In *Halophytes: An Integrative Anatomical Study*. Springer International Publishing. doi: 10.1007/978-3-319-05729-3

Gul, B., Ansari, R., Aziz, I., & Khan, M. A. (2010). Salt tolerance of *Kochia scoparia*: A new fodder crop for highly saline arid regions. *Pakistan Journal of Botany*, *42*(4), 2479–2487. Retrieved from http://inis.iaea.org/Search/search.aspx?orig_q=RN:42055250

Gulzar, S., Khan, M. A., & Ungar, I. A. (2003). Effects of salinity on growth, ionic content, and plant-water status of *Aeluropus lagopoides*. *Communications in Soil Science and Plant Analysis*, *34*(11–12), 1657–1668. doi: 10.1081/CSS-120021303

Hamilton, E. W., McNaughton, S. J., & Coleman, J. S. (2001). Molecular, physiological, and growth responses to sodium stress in C^4 grasses from a soil salinity gradient in the Serengeti ecosystem. *American Journal of Botany*, *88*(7), 1258–1265. doi: 10.2307/3558337

Head, C. E. I., Koldewey, H., Pavoine, S., Pratchett, M. S., Rogers, A. D., Taylor, M. L., & Bonsall, M. B. (2018). Trait and phylogenetic diversity provide insights into community assembly of reef-associated shrimps (Palaemonidae) at different spatial scales across the Chagos Archipelago. *Ecology and Evolution*, *8*(8), 4098–4107. doi: 10.1002/ece3.3969

Hunter, M. D. (2016). Linking Trophic Interactions with Ecosystem Nutrient Dynamics on the Phytochemical Landscape. In *The Phytochemical Landscape*. Princeton University Press. doi: 10.1515/9781400881208-009

Inouye, B. D. (2001). Response surface experimental designs for investigating interspecific competition. *Ecology*, *82*(10), 2696–2706. doi: 10.1890/0012-9658(2001)082[2696:RSEDFI]2.0.CO;2

Kafi, M., & Rahimi, Z. (2011). Effect of salinity and silicon on root characteristics, growth, water status, proline content and ion accumulation of purslane (*Portulaca oleracea* L.). *Soil Science and Plant Nutrition*, *57*(2), 341–347. doi: 10.1080/00380768.2011.567398

Kaspari, M. (2020). The seventh macronutrient: how sodium shortfall ramifies through populations, food webs and ecosystems. *Ecology Letters*, *23*(7), 1153–1168. doi: 10.1111/ele.13517

Kaspari, M., Clay, N. A., Donoso, D. A., & Yanoviak, S. P. (2014). Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. *Ecology*, *95*(4), 795–800. doi:

10.1890/13-1274.1

Kaspari, M., Yanoviak, S. P., & Dudley, R. (2008). On the biogeography of salt limitation: A study of ant communities. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(46), 17848–17851. doi: 10.1073/pnas.0804528105

Kaspari, M., Yanoviak, S. P., Dudley, R., Yuan, M., & Clay, N. A. (2009). Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(46), 19405–19409. https://doi.org/10.1073/pnas.0906448106

Kazachkova, Y., Eshel, G., Pantha, P., Cheeseman, J. M., Dassanayake, M., & Barak, S. (2018). Halophytism: What Have We Learnt From *Arabidopsis thaliana* Relative Model Systems? *Plant Physiology, 178*(3), 972–988. https://doi.org/10.1104/pp.18.00863

Kchaou, H., Larbi, A., Gargouri, K., Chaieb, M., Morales, F., & Msallem, M. (2010). Assessment of tolerance to NaCl salinity of five olive cultivars, based on growth characteristics and Na^+ and Cl^- exclusion mechanisms. *Scientia Horticulturae*, *124*(3), 306–315. doi: 10.1016/j.scienta.2010.01.007

Keling, H., & Zhujun, Z. (2010). Effects of different concentrations of sodium chloride on plant growth and glucosinolate content and composition in pakchoi. *African Journal of Biotechnology*, *9*(28), 4428–4433. Retrieved from https://www.ajol.info/index.php/ajb/article/view/82700

Khan, M. A., Gul, B., & Weber, D. J. (2001). Effect of salinity on the growth and ion content of *Salicornia rubra*. *Communications in Soil Science and Plant Analysis*, *32*(17–18), 2965–2977. doi: 10.1081/CSS-120000975

Khan, M. A., Ungar, I. A., & Showalter, A. M. (2000a). Effects of Salinity on Growth, Water Relations and Ion Accumulation of the Subtropical Perennial Halophyte, *Atriplex griffithii* var. stocksii. *Annals of Botany*, *85*(2), 225–232. doi: 10.1006/anbo.1999.1022

Khan, M. A., Ungar, I. A., & Showalter, A. M. (2000b). Effects of sodium chloride treatments on growth and ion accumulation of the halophyte *Haloxylon recurvum*. *Communications in Soil Science and Plant Analysis*, *31*(17–18), 2763–2774. doi: 10.1080/00103620009370625

Khan, M. A., Ungar, I. A., & Showalter, A. M. (2000c). The effect of salinity on the growth, water status, and ion content of a leaf succulent perennial halophyte, *Suaeda fruticosa* (L.) Forssk. *Journal of Arid Environments*, *45*(1), 73–84. doi: 10.1006/jare.1999.0617

Kim, S., Rayburn, A. L., Voigt, T., Parrish, A., & Lee, D. K. (2012). Salinity effects on germination and plant growth of prairie cordgrass and switchgrass. *Bioenergy Research*, *5*(1), 225–235. doi: 10.1007/s12155-011-9145-3

LoPresti, E. F., Pan, V., Goidell, J., Weber, M. G., & Karban, R. (2019). Mucilage-bound sand reduces seed predation by ants but not by reducing apparency: a field test of 53 plant species. *Ecology*, *100*(10), 1–11. doi: 10.1002/ecy.2809

Maathuis, F. J. M. M. (2014). Sodium in plants: perception, signalling, and regulation of sodium fluxes. *J Exp Bot*, *65*(3), 849–858. doi: 10.1093/jxb/ert326

Maddison, W. P., & Slatkin, M. (1991). Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution*, *45*(5), 1184. doi: 10.2307/2409726

Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015). A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist*, *207*(2), 437–453. doi: 10.1111/nph.13264

Manivannan, P., Jaleel, C. A., Sankar, B., Kishorekumar, A., Murali, P. V, Somasundaram, R., & Panneerselvam, R. (2008). Mineral uptake and biochemical changes in *Helianthus annuus* under treatment with different sodium salts. *Colloids and Surfaces B: Biointerfaces*, *62*(1), 58–63. doi: 10.1016/j.colsurfb.2007.09.019

Martin, A. R., Coombes, P. J., & Dunstan, R. H. (2010). Investigating the influences of season and coastal proximity on the elemental composition of harvested rainwater. *Water Science and Technology*, *61*(1), 25–36. doi: 10.2166/wst.2010.775

Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).* R package. Retrieved from https://cran.r-project.org/package=AICcmodavg.

Mitchell, T. S., Agnew, L., Meyer, R., Sikkink, K. L., Oberhauser, K. S., Borer, E. T., & Snell-Rood, E. C. (2020). Traffic influences nutritional quality of roadside plants for monarch caterpillars. *Science of The Total Environment*, *724*, 138045. doi: 10.1016/j.scitotenv.2020.138045

Moghaieb, R. E. A., Saneoka, H., Ito, J., & Fujita, K. (2001). Characterization of salt tolerance in tomato plant in terms of photosynthesis and water relations. *Soil Science and Plant Nutrition*, *47*(2), 377–385. doi: 10.1080/00380768.2001.10408400

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., Altman, D., Antes, G., … Tugwell, P. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine*, *6*(7), e1000097. doi: 10.1371/journal.pmed.1000097

Moore, B. D., Lawler, I. R., Wallis, I. R., Beale, C. M., & Foley, W. J. (2010). Palatability mapping: A koala's eye view of spatial variation in habitat quality. *Ecology*, *91*(11), 3165–3176. doi: 10.1890/09-1714.1

Mori, S., Yoshiba, M., & Tadano, T. (2006). Growth response of *Suaeda salsa* (L.) Pall to graded NaCl concentrations and the role of chlorine in growth stimulation. *Soil Science and Plant Nutrition*, *52*(5), 610–617. doi: 10.1111/j.1747-0765.2006.00076.x

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756.

doi: 10.1111/j.2041-210X.2012.00196.x

Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, Cell & Environment, 25*(2), 239–250. doi: 10.1046/j.0016-8025.2001.00808.x

Munns, R., Passioura, J. B., Colmer, T. D., & Byrt, C. S. (2020). Osmotic adjustment and energy limitations to plant growth in saline soil. *New Phytologist, 225*(3), 1091–1096. doi: 10.1111/nph.15862

Munns, R., & Tester, M. (2008). Mechanisms of Salinity Tolerance. *Annual Review of Plant Biology, 59*(1), 651–681. doi: 10.1146/annurev.arplant.59.032607.092911

Naidoo, G. (1994). Growth, water and ion relationships in the coastal halophytes *Triglochin bulbosa* and *T. striata*. *Environmental and Experimental Botany*, *34*(4), 419–426. doi: 10.1016/0098-8472(94)90024-8

Nawaz, I., Iqbal, M., Bliek, M., & Schat, H. (2017). Salt and heavy metal tolerance and expression levels of candidate tolerance genes among four extremophile *Cochlearia* species with contrasting habitat preferences. *Science of The Total Environment, 584–585*, 731–741. https://doi.org/10.1016/j.scitotenv.2017.01.111

Nedjimi, B. (2009). Salt tolerance strategies of *Lygeum spartum* L.: A new fodder crop for Algerian saline steppes. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *204*(10), 747–754. doi: 10.1016/j.flora.2008.11.004

Nedjimi, B. (2014). Effects of salinity on growth, membrane permeability and root hydraulic conductivity in three saltbush species. *Biochemical Systematics and Ecology*, *52*, 4–13. doi: 10.1016/j.bse.2013.10.007

Neubauer, S. C., Givler, K., Valentine, S. K., & Megonigal, J. P. (2005). Seasonal patterns and plant-mediated controls of subsurface wetland biogeochemistry. *Ecology, 86*(12), 3334–3344. https://doi.org/10.1890/04-1951

Odum, E. P., Finn, J. T., & Franz, E. H. (1979). Perturbation theory and the subsidy-stress gradient. *BioScience*, *29*(6), 349–352. doi: 10.2307/1307690

Paleo-López, R., Quintero-Galvis, J. F., Solano-Iguaran, J. J., Sanchez-Salazar, A. M., Gaitan-Espitia, J. D., & Nespolo, R. F. (2016). A phylogenetic analysis of macroevolutionary patterns in fermentative yeasts. *Ecology and Evolution*, *6*(12), 3851–3861. doi: 10.1002/ece3.2097

Pantha, P., & Dassanayake, M. (2020). Living with Salt. *The Innovation, 1*(3), 100050. https://doi.org/10.1016/j.xinn.2020.100050

Paradis, E., & Schliep, K. (2019). *ape* 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics, 35*(3), 526–528. doi: 10.1093/bioinformatics/bty633

Parida, A. K., Veerabathini, S. K., Kumari, A., & Agarwal, P. K. (2016). Physiological, anatomical and metabolic implications of salt tolerance in the halophyte *Salvadora persica* under hydroponic culture condition. *Frontiers in Plant Science*, *7*. doi: 10.3389/fpls.2016.00351

Patterson, K. Y., Pehrsson, P. R., & Perry, C. R. (2013). The mineral content of tap water in United States households. *Journal of Food Composition and Analysis, 31*(1), 46–50. doi: 10.1016/j.jfca.2013.03.004

Polle, A., & Chen, S. (2015). On the salty side of life: Molecular, physiological and anatomical adaptation and acclimation of trees to extreme habitats. *Plant, Cell and Environment, 38*(9), 1794–1816. doi: 10.1111/pce.12440

Primack, R. B., & Kang, H. (1989). Measuring fitness and natural selection in wild plant populations. *Annual Review of Ecology and Systematics*, *20*(1), 367–396. doi: 10.1146/annurev.es.20.110189.002055

Quan, R., Wang, J., Hui, J., Bai, H., Lyu, X., Zhu, Y., … Huang, R. (2018). Improvement of salt tolerance using wild rice genes. *Frontiers in Plant Science, 8*(January), 1–11. doi: 10.3389/fpls.2017.02269

Qureshi, T. M., Ashraf, M. Y., Bano, A., & Hussain, F. (2007). Ion partitioning, K/Ca and K/Na ratios of *Eucalyptus camaldulensis* grown under NaCl salinity. *Pakistan Journal of Botany*, *39*(7), 2565–2574.

Rejili, M., Vadel, A. M., Guetet, A., & Neffatti, M. (2007). Effect of NaCl on the growth and the ionic balance K^+/Na^+ of two populations of *Lotus creticus* (L.) (Papilionaceae). *South African Journal of Botany*, *73*(4), 623–631. doi: 10.1016/j.sajb.2007.06.006

Renault, S., Croser, C., Franklin, J. A., & Zwiazek, J. J. (2001). Effects of NaCl and Na_2SO_4 on red-osier dogwood (*Cornus stolonifera* Michx) seedlings. *Plant and Soil*, *233*(2), 261–268. doi: 10.1023/A:1010512021353

Revell, L. J. (2012). *phytools*: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution, 3*(2), 217–223. doi: 10.1111/j.2041-210X.2011.00169.x

Rohatgi, A. (2019). *WebPlotDigitizer*. San Francisco, CA. Retrieved from https://automeris.io/WebPlotDigitizer

Rozema, J., Cornelisse, D., Zhang, Y., Li, H., Bruning, B., Katschnig, D., … van Bodegom, P. (2015). Comparing salt tolerance of beet cultivars and their halophytic ancestor: Consequences of domestication and breeding programmes. *AoB PLANTS, 7*(1), 1–12. doi: 10.1093/aobpla/plu083

Ruiz, D., Martínez, V., & Cerdá, A. (1997). Citrus response to salinity: growth and nutrient uptake. *Tree Physiol.*, *17*(3), 141–150.

Sanadhya, P., Agarwal, P., & Agarwal, P. K. (2015). Ion homeostasis in a salt-secreting halophytic grass. *AoB Plants*, *7*, plv055. doi: 10.1093/aobpla/plv055

Santos, J., Al-Azzami, M., Aronson, J., & Flowers, T. J. (2016). eHALOPH a database of salt-tolerant plants: Helping put halophytes to work. *Plant and Cell Physiology*, *57*(1), e10. Retrieved from https://www.sussex.ac.uk/affiliates/halophytes/index.php

Shaheen, S., Naseer, S., Ashraf, M., & Akram, N. A. (2013). Salt stress affects water relations, photosynthesis, and oxidative defense mechanisms in *Solanum melongena* L. *Journal of Plant Interactions*, *8*(1), 85–96. doi: 10.1080/17429145.2012.718376

Shahzad, B., Tanveer, M., Hassan, W., Shah, A. N., Anjum, S. A., Cheema, S. A., & Ali, I. (2016). Lithium toxicity in plants: Reasons, mechanisms and remediation possibilities – A review. *Plant Physiology and Biochemistry, 107,* 104–115. https://doi.org/10.1016/j.plaphy.2016.05.034

Shereen, A., Ansari, R. U., Yasmin, S., Raza, S., Mumtaz, S., Khan, M. A., & Mujtaba, S. M. (2007). Physiological responses of rice (*Oryza sativa* L.) to saline stress. *Pakistan Journal of Botany*, *39*(7), 2527–2534.

Slama, I., Abdelly, C., Bouchereau, A., Flowers, T., & Savouré, A. (2015). Diversity, distribution and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. *Annals of Botany, 115*(3), 433–447. doi: 10.1093/aob/mcu239

Smith, D. B. (2013). *Geochemical and Mineralogical Maps for Soils of the Conterminous United States*. U.S. Department of the Interior, U.S. Geological Survey.

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*(3), 302–314. doi: 10.1002/ajb2.1019

Snell-Rood, E. C., Espeset, A., Boser, C. J., White, W. A., & Smykalski, R. (2014). Anthropogenic changes in sodium affect neural and muscle development in butterflies. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(28), 10221–10226. doi: 10.1073/pnas.1323607111

Sohail, M., Saied, A. S., Gebauer, J., & Buerkert, A. (2009). Effect of NaCl salinity on growth and mineral composition of *Ziziphus spina-christi* (L.) willd. *Journal of Agriculture and Rural Development in the Tropics and Subtropics*, *110*(2), 107–114.

Stallard, R. F., & Edmond, J. M. (1981). Geochemistry of the Amazon. 1. Precipitation chemistry and the marine contribution to the dissolved load at the time of peak discharge. *Journal of Geophysical Research*, *86*(C10), 9844–9858. doi: 10.1029/JC086iC10p09844

Sterner, R. W., & Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press.

Taffouo, V. D., Nouck, A. H., Dibong, S. D., & Amougou, A. (2010). Effects of salinity stress on seedlings growth, mineral nutrients and total chlorophyll of some tomato (*Lycopersicum esculentum* L.) cultivars. *African Journal of Biotechnology*, *9*(33), 5366–5372. doi: 10.5897/AJB10.798

Tammam, A. A., Alhamd, M. F. A., & Hemeda, M. M. (2008). Study of salt tolerance in wheat (*Triticum aestium* L.) cultivar Banysoif 1. *Australian Journal of Crop Science, 1*(3). 115-125.
Tessmer, O. L., Jiao, Y., Cruz, J. A., Kramer, D. M., & Chen, J. (2013). Functional approach to high-throughput plant growth analysis. BMC Systems Biology, 7(Suppl 6), S17. doi: 10.1186/1752-0509-7-S6-S17
Tounsi, S., Feki, K., Hmidi, D., Masmoudi, K., & Brini, F. (2017). Salt stress reveals differential physiological, biochemical and molecular responses in *T. monococcum* and *T. durum* wheat genotypes. *Physiology and Molecular Biology of Plants*, *23*(3), 517–528. doi: 10.1007/s12298-017-0457-4
Turan, M. A., Elkarim, A. H. A., Taban, N., & Taban, S. (2010). Effect of salt stress on growth and ion distribution and accumulation in shoot and root of maize plant. *African Journal of Agricultural Research*, *5*(7), 584–588. doi: 10.5897/AJAR09.677
van Zelm, E., Zhang, Y., & Testerink, C. (2020). Salt Tolerance Mechanisms of Plants. *Annual Review of Plant Biology, 71*(1), 403–433. https://doi.org/10.1146/annurev-arplant-050718-100005
Veatch-Blohm, M. E., Sawch, D., Elia, N., & Pinciotti, D. (2014). Salinity tolerance of three commonly planted *Narcissus* cultivars. *HortScience*, *49*(9), 1158–1164. doi: 10.21273/hortsci.49.9.1158
Vithanage, M., Kumarathilaka, P., Oze, C., Karunatilake, S., Seneviratne, M., Hseu, Z.-Y., Gunarathne, V., Dassanayake, M., Ok, Y. S., & Rinklebe, J. (2019). Occurrence and cycling of trace elements in ultramafic soils and their impacts on human health: A critical review. *Environment International, 131*(June), 104974. https://doi.org/10.1016/j.envint.2019.104974
Waheed, A., Hafiz, I. A., Qadir, G., Murtaza, G., Mahmood, T., & Ashraf, M. (2006). Effect of salinity on germination, growth, yield, ionic balance and solute composition of Pigeon pea (*Cajanus cajan* (L.) Millsp). *Pakistan Journal of Botany*, *38*(4), 1103–1117.
Wang, D., Wang, H., Han, B., Wang, B., Guo, A., Zheng, D., Liu, C., Chang, L., Peng, M., & Wang, X. (2012). Sodium instead of potassium and chloride is an important macronutrient to improve leaf succulence and shoot development for halophyte *Sesuvium portulacastrum*. *Plant Physiology and Biochemistry, 51,* 53–62. https://doi.org/10.1016/j.plaphy.2011.10.009
Wang, Z., Hong, Y., Zhu, G., Li, Y., Niu, Q., Yao, J., … Zhu, J. (2020). Loss of salt tolerance during tomato domestication conferred by variation in a Na^+ /K^+ transporter. *The EMBO Journal, 39*(10). doi: 10.15252/embj.2019103256
Wang, Z., Hong, Y., Li, Y., Shi, H., Yao, J., Liu, X., … Zhu, J. (2021). Natural variations in *SlSOS1* contribute to the loss of salt tolerance during tomato domestication. *Plant Biotechnology Journal, 19*(1), 20–22. doi: 10.1111/pbi.13443
White, P. J., Bowen, H. C., Broadley, M. R., El-Serehy, H. A., Neugebauer, K., Taylor, A., … Wright, G.

(2017). Evolutionary origins of abnormally large shoot sodium accumulation in nonsaline environments within the Caryophyllales. *New Phytologist*, *214*(1), 284–293. doi: 10.1111/nph.14370

Whitlock, M. C., & Schluter, D. (2014). *The Analysis of Biological Data*. Macmillan Learning.

Wu, G. Q., Jiao, Q., & Shui, Q. Z. (2015). Effect of salinity on seed germination, seedling growth, and inorganic and organic solutes accumulation in sunflower (*Helianthus annuus* L.). *Plant, Soil and Environment*, *61*(5), 220–226. doi: 10.17221/22/2015-PSE

Wu, G. Q., Liang, N., Feng, R. J., & Zhang, J. J. (2013). Evaluation of salinity tolerance in seedlings of sugar beet (*Beta vulgaris* L.) cultivars using proline, soluble sugars and cation accumulation criteria. *Acta Physiologiae Plantarum*, *35*(9), 2665–2674. doi: 10.1007/s11738-013-1298-6

Xi, J. J., Chen, H. Y., Bai, W. P., Yang, R. C., Yang, P. Z., Chen, R. J., … Wang, S. M. (2018). Sodium-related adaptations to drought: New insights from the xerophyte plant *Zygophyllum xanthoxylum*. *Frontiers in Plant Science*, *871*. doi: 10.3389/fpls.2018.01678

Yamada, M., Kuroda, C., & Fujiyama, H. (2016). Growth promotion by sodium in amaranthaceous plants. *Journal of Plant Nutrition*, *39*(8), 1186–1193. doi: 10.1080/01904167.2015.1069341

Yamaguchi, T., Hamamoto, S., & Uozumi, N. (2013). Sodium transport system in plant cells. *Frontiers in Plant Science*, *4*(OCT), 1–7. doi: 10.3389/fpls.2013.00410

Yang, Y., & Guo, Y. (2018). Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytologist, 217*(2), 523–539. https://doi.org/10.1111/nph.14920

Yokaş, I., Tuna, A. L., Bürün, B., Altunlu, H., Altan, F., & Kaya, C. (2008). Responses of the tomato (*Lycopersicon esculentum* Mill.) Plant to exposure to different salt forms and rates. *Turkish Journal of Agriculture and Forestry*, *32*(4), 319–329. doi: 10.3906/tar-0711-21

Younginger, B. S., Sirová, D., Cruzan, M. B., & Ballhorn, D. J. (2017). Is biomass a reliable estimate of plant fitness? *Appl Plant Sci*, *5*(2). doi: 10.3732/apps.1600094

Yuan, Z. Y., & Chen, H. Y. H. (2015). Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. *Nature Climate Change, 5*(5), 465–469. https://doi.org/10.1038/nclimate2549

Yue, L. J., Li, S. X., Ma, Q., Zhou, X. R., Wu, G. Q., Bao, A. K., … Wang, S. M. (2012). NaCl stimulates growth and alleviates water stress in the xerophyte *Zygophyllum xanthoxylum*. *Journal of Arid Environments*, *87*, 153–160. doi: 10.1016/j.jaridenv.2012.06.002

Zhao, C., Zhang, H., Song, C., Zhu, J. K., & Shabala, S. (2020). Mechanisms of Plant Responses and Adaptation to Soil Salinity. *The Innovation, 1*(1), 100017. https://doi.org/10.1016/j.xinn.2020.100017

Zhu, J. K. (2000). Genetic analysis of plant salt tolerance using arabidopsis. *Plant Physiology, 124(*3), 941–948. https://doi.org/10.1104/pp.124.3.941

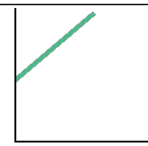
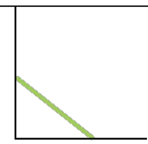
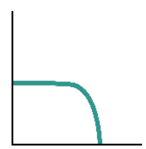
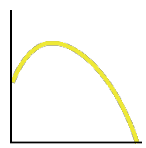
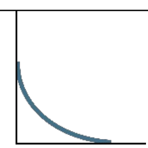
Zhu, J. K. (2001). Plant salt tolerance. *Trends in Plant Science, 6*(2), 66–71. https://doi.org/10.1016/S1360-1385(00)01838-0

Zörb, C., Geilfus, C. M., & Dietz, K. J. (2019). Salinity and crop yield. *Plant Biology, 21*(S1), 31–38. doi: 10.1111/plb.12884

Zouhaier, B., Najla, T., Abdallah, A., Wahbi, D., Wided, C., Chedly, A., & Abderrazak, S. (2015). Salt stress response in the halophyte *Limoniastrum guyonianum* Boiss. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *217*, 1–9. doi: 10.1016/j.flora.2015.09.003

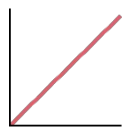
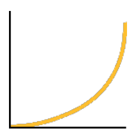
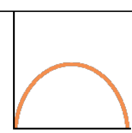
Tables

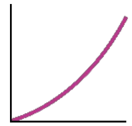
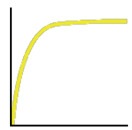
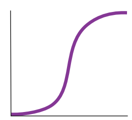
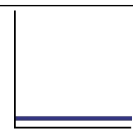
Table 1: *A priori* response predictions for relative biomass growth and models used to classify populations in plants exposed to increasing concentrations of NaCl in the substrate.

Model ID	Equation	Classification	*A priori* representation	Criterion of classification	Total plant responses	Aboveground responses	Belowground responses	Biological significance
I	$y=mx+b$	Linear increase		m	3 (2.8%)	3 (2.8%)	5 (4.7%)	Salt induced linear growth response.
		Linear decrease		$-m$	40 (37.4%)	34 (31.8%)	31 (29%)	Salt sensitive linear decrease in relative growth.
II	$y=-e^x$	Threshold decline		-*e*	11 (10.3%)	11 (10.3)	15 (14%)	Salt insensitive growth at lower Na concentrations changed to rapid growth inhibition as external Na increases.
III	$y=ax^2+b$	Hump-shaped		$-a$	18 (16.8%)	18 (16.8%)	17 (15.9%)	Salt induced growth enhancement switches to growth inhibition as external Na increases.
		Non-linear decrease		a	32 (29.9%)	33 (30.8%)	29 (27.1%)	Decelerating growth inhibition in response to increasing substrate salt.

IV	$y=b$	Zero slope			3 (2.8%)	3 (2.8%)	5 (4.7%)	Salt-insensitive growth.

Table 2: *A priori* response predictions for sodium accumulation responses and models used to classify populations in plants exposed to increasing concentrations of NaCl in the substrate.

Model ID	**Equation**	**Classification**	***A priori* representation**	**Criterion of classification**	**Total plant responses**	**Aboveground responses**	**Belowground responses**	**Biological significance**
I	$y=mx+b$	Linear increase			35 (32.7%)	39 (36.4%)	35 (32.7%)	Plants steadily and monotonically increase accumulation of sodium as sodium in the substrate increases.
II	$y=e^x$	Exponential increase		*e*	13 (12.1%)	12 (11.2%)	11 (10.3%)	Monotonic exponential increase in accumulation of sodium as sodium in the substrate increases.
III	$y=a x^2+b$	Hump-shaped		$-a$	12 (11.2%)	5 (4.7%)	14 (13.1%)	Accumulation of sodium increases to a maximum and then decreases as sodium in the substrate increases; this is a non-monotonic change, since the directionality of

								change reverses.
		Non-linear increase		a	7 (6.5%)	5 (4.7%)	6 (5.6%)	Monotonic increase in accumulation of sodium is non-linear as sodium in the substrate increases.
IV	$y=a-be^{-}$	Asymptotic increase			22 (20.6%)	24 (22.4%)	20 (18.7%)	Monotonic increase in accumulation of sodium at a decreasing rate, which then either approaches saturation or reaches a plateau, as sodium in the substrate increases.
V	$y=\frac{1}{1+e^{-x}}$	Sigmoidal increase			17 (15.9%)	16 (15%)	14 (13.1%)	Monotonic increase in accumulation of sodium is sigmoidal as sodium in the substrate increases.
VI	$y=b$	Zero slope			1 (0.9%)	1 (0.9%)	2 (1.9%)	Accumulation of sodium is unaffected by sodium in the substrate.

Figures

Figure 1

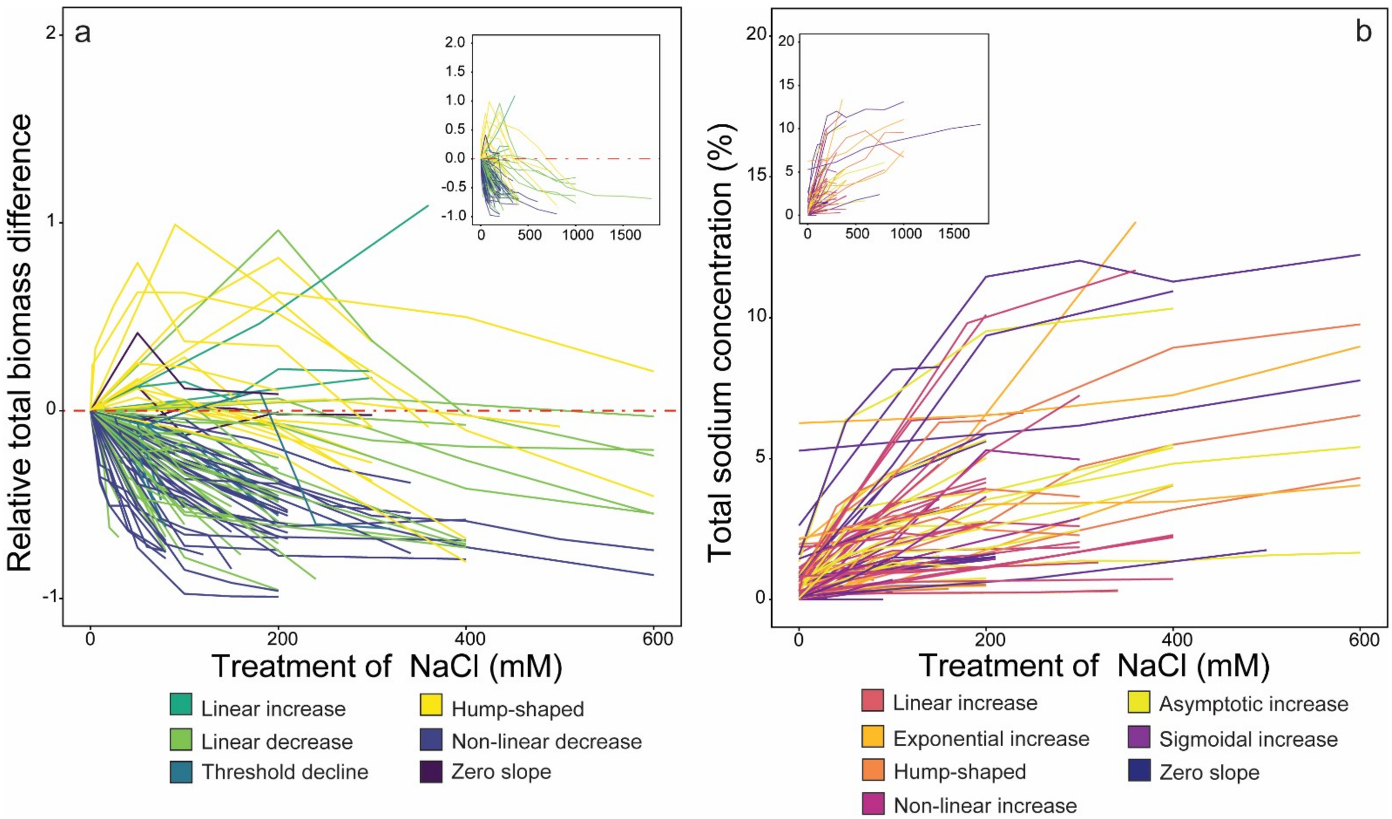
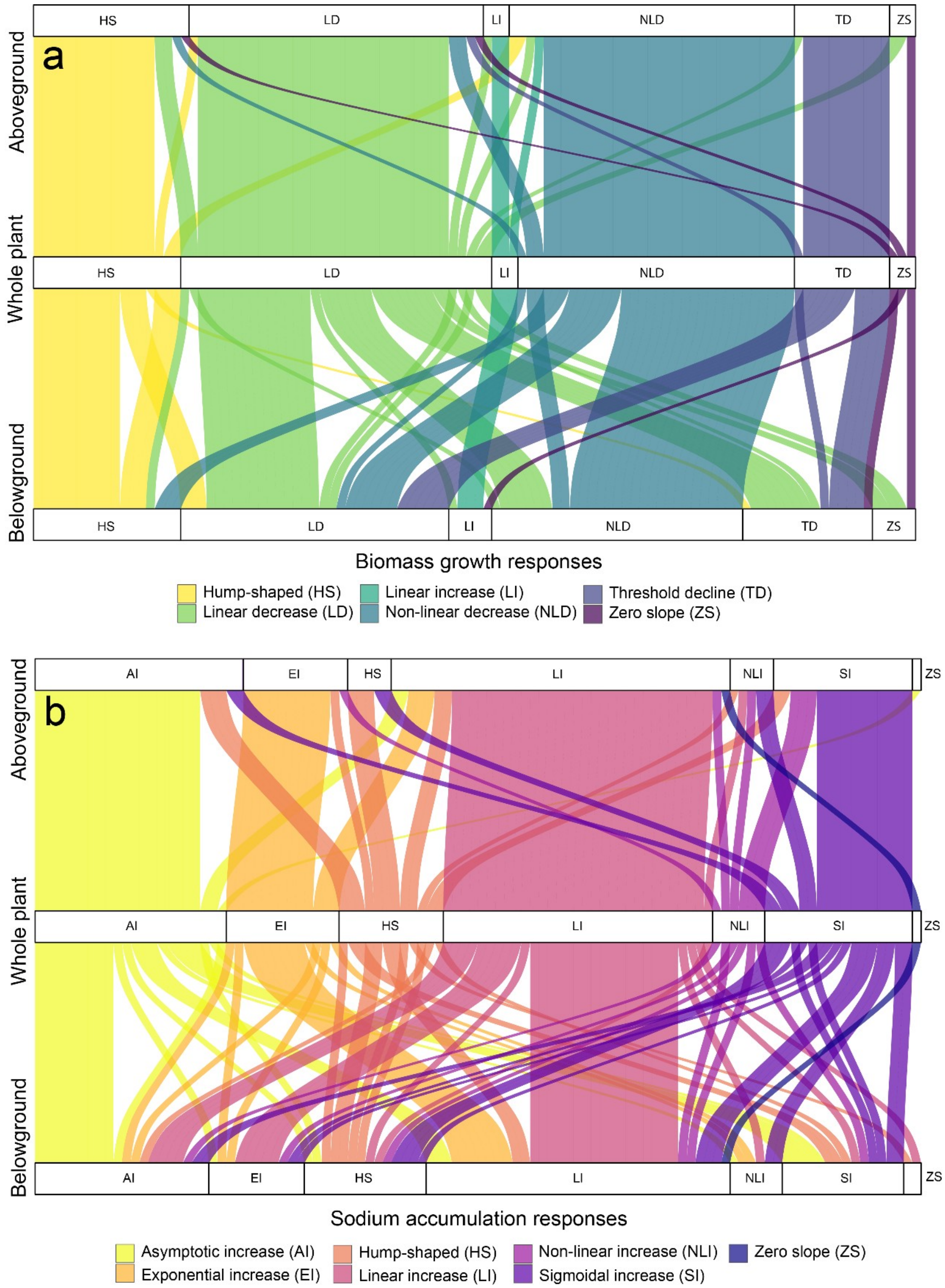


Figure 2



a
Aboveground
Whole plant
Belowground
HS
LD
LI
NLD
TD
ZS
Biomass growth responses
Hump-shaped (HS)
Linear decrease (LD)
Linear increase (LI)
Non-linear decrease (NLD)
Threshold decline (TD)
Zero slope (ZS)
b
AI
EI
HS
LI
NLI
SI
ZS
Sodium accumulation responses
Asymptotic increase (AI)
Exponential increase (EI)
Hump-shaped (HS)
Linear increase (LI)
Non-linear increase (NLI)
Sigmoidal increase (SI)
Zero slope (ZS)

Figure 3

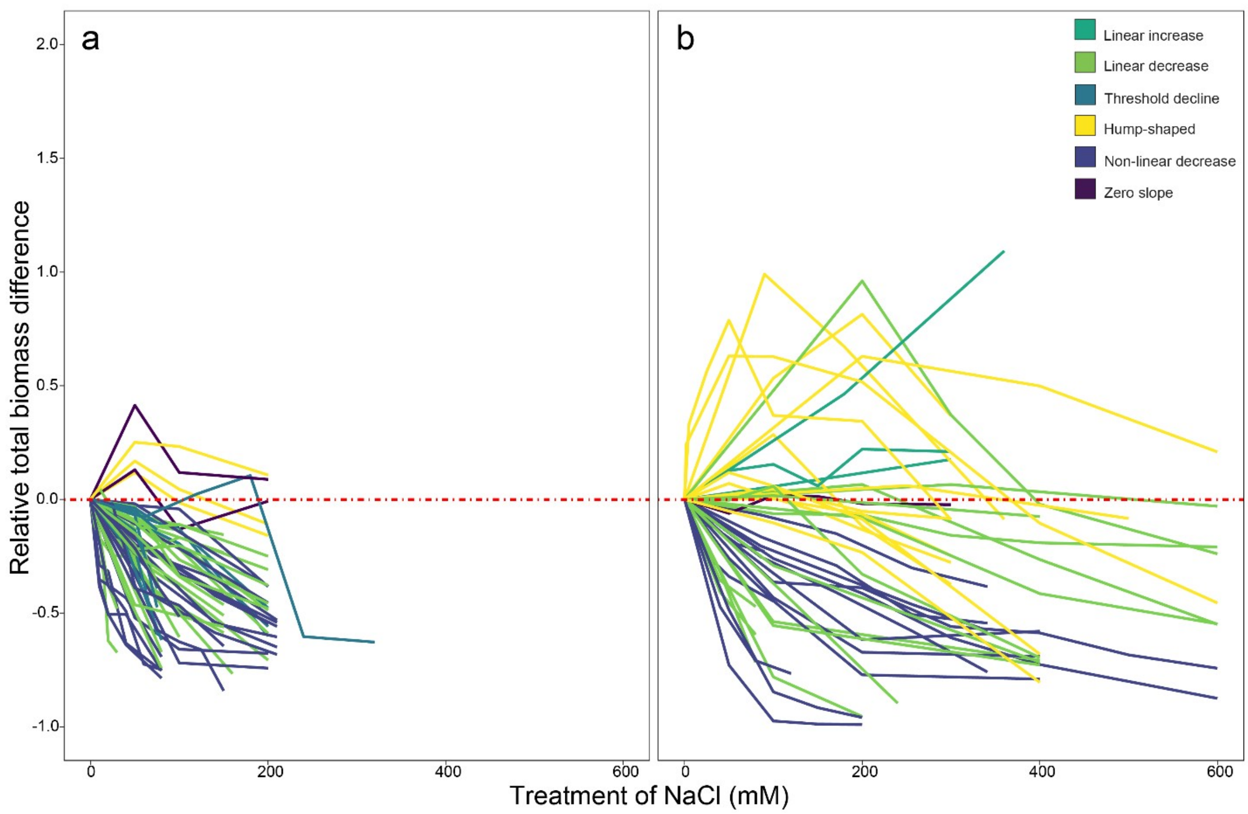

a
b
Linear increase
Linear decrease
Threshold decline
Hump-shaped
Non-linear decrease
Zero slope
Relative total biomass difference
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
0
200
400
600
Treatment of NaCl (mM)

Figure 4

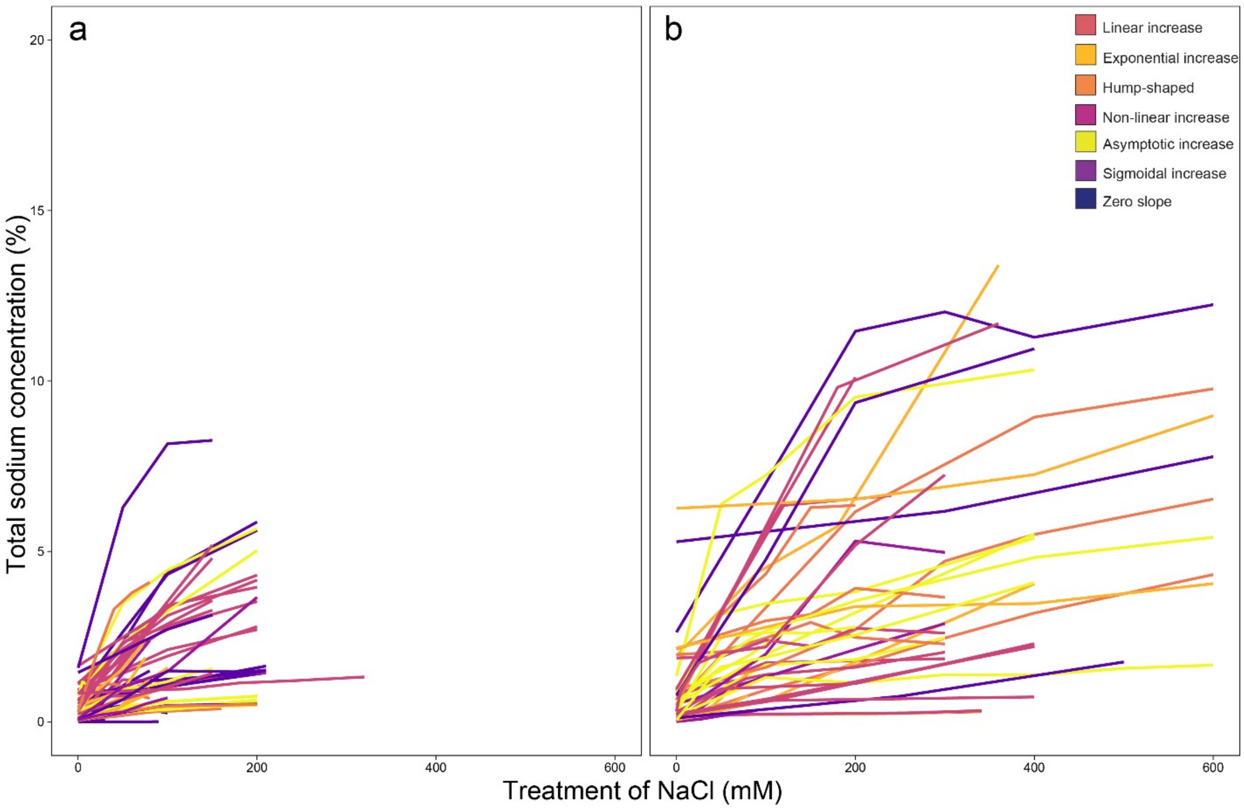


Figure 5

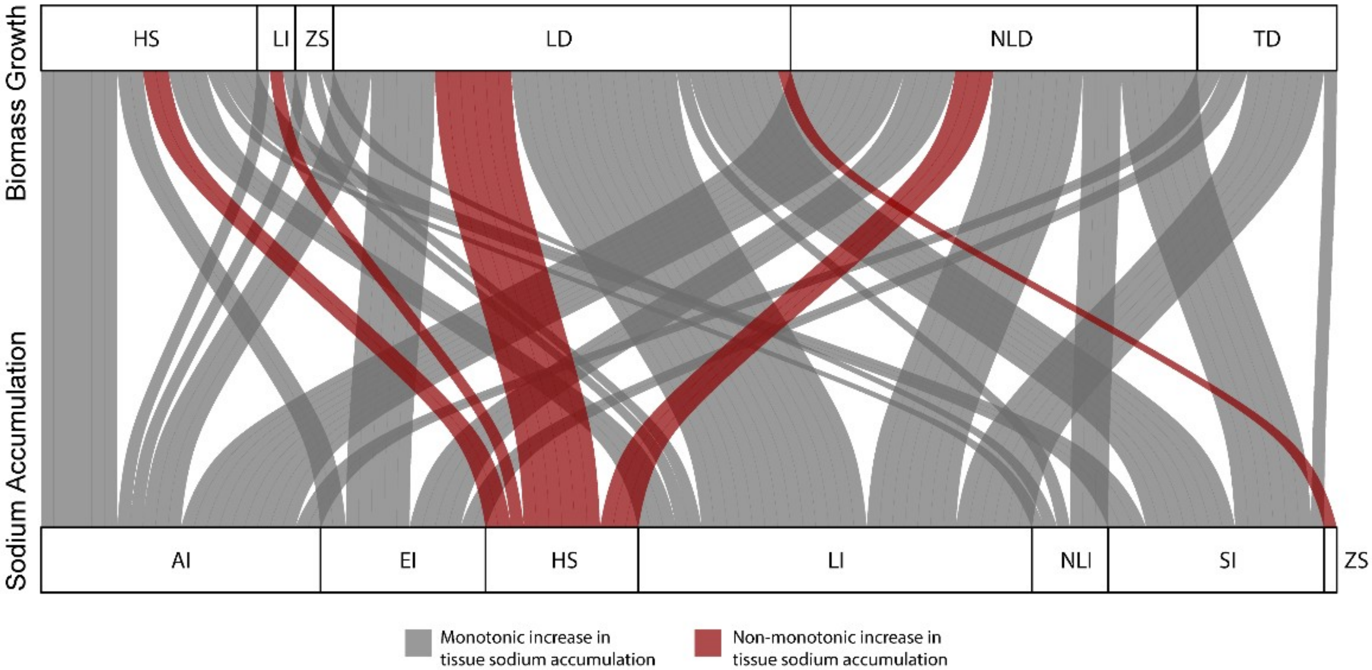

Biomass Growth
HS
LI
ZS
LD
NLD
TD
Sodium Accumulation
AI
EI
HS
LI
NLI
SI
ZS
Monotonic increase in tissue sodium accumulation
Non-monotonic increase in tissue sodium accumulation

Figure 6

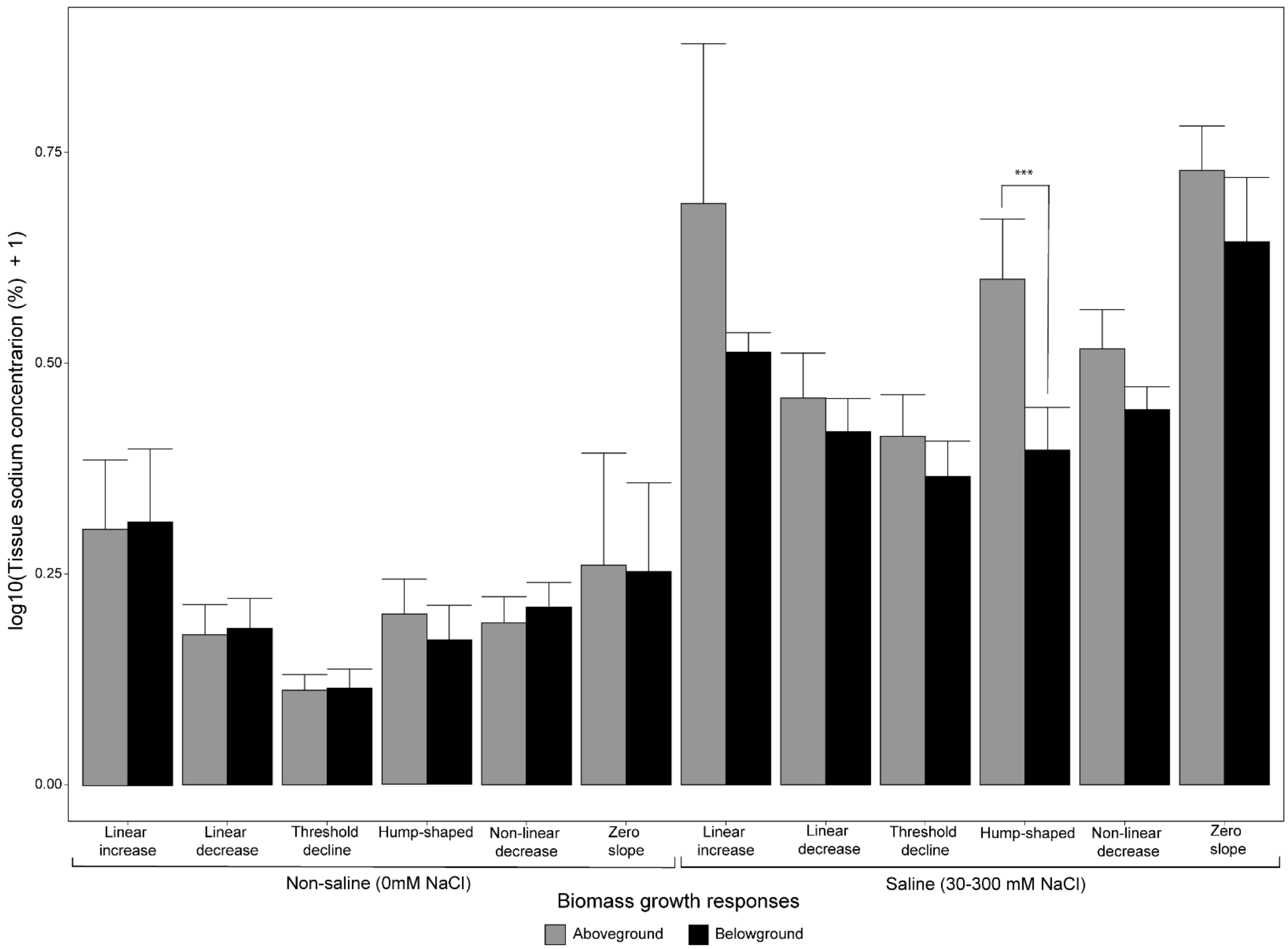

log10(Tissue sodium concentrarion (%) + 1)
0.00
0.25
0.50
0.75
***
Linear increase
Linear decrease
Threshold decline
Hump-shaped
Non-linear decrease
Zero slope
Linear increase
Linear decrease
Threshold decline
Hump-shaped
Non-linear decrease
Zero slope
Non-saline (0mM NaCl)
Saline (30-300 mM NaCl)
Biomass growth responses
Aboveground
Belowground

Figure 7

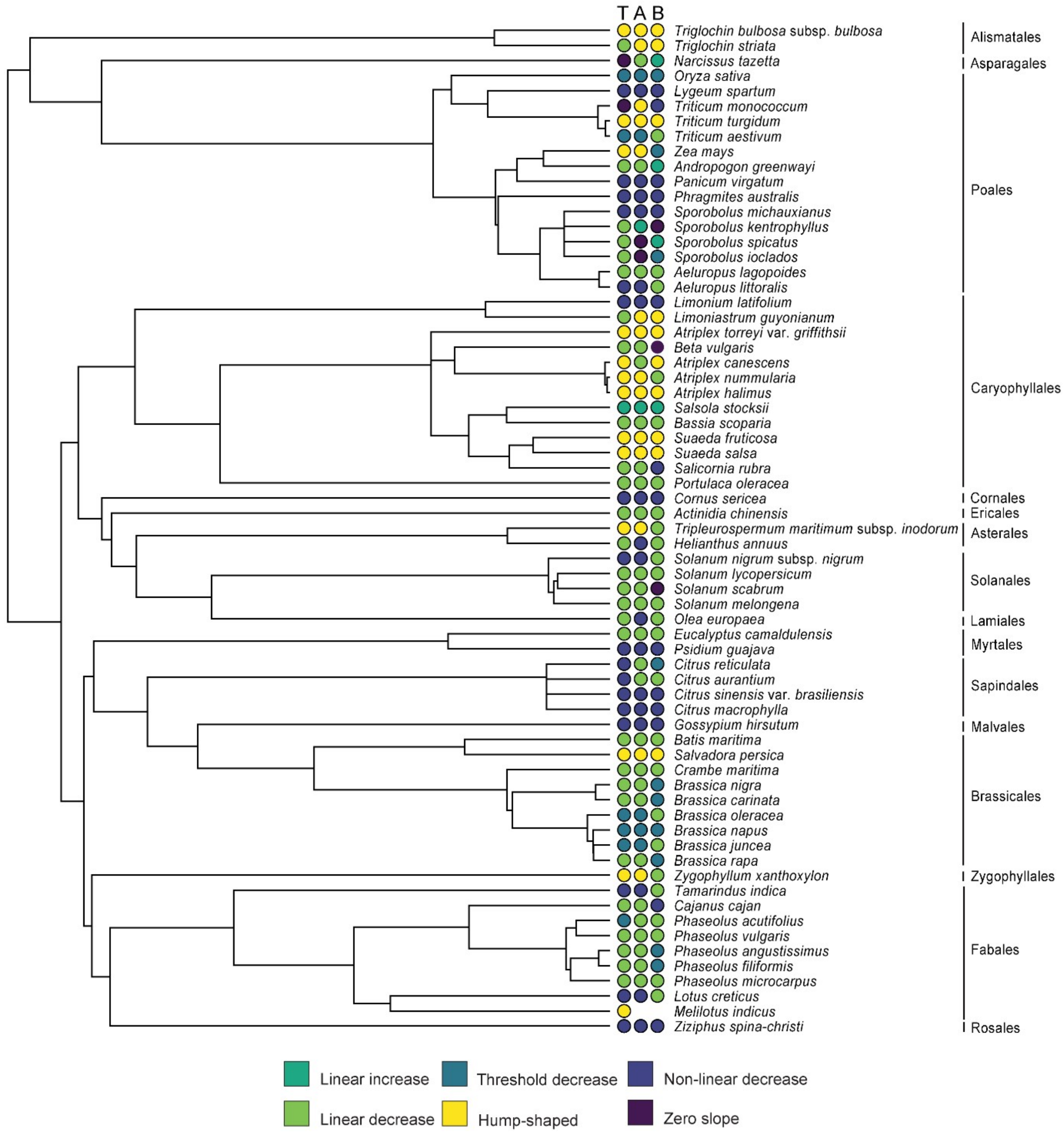

T A B
Triglochin bulbosa subsp. bulbosa
Triglochin striata
Narcissus tazetta
Oryza sativa
Lygeum spartum
Triticum monococcum
Triticum turgidum
Triticum aestivum
Zea mays
Andropogon greenwayi
Panicum virgatum
Phragmites australis
Sporobolus michauxianus
Sporobolus kentrophyllus
Sporobolus spicatus
Sporobolus ioclados
Aeluropus lagopoides
Aeluropus littoralis
Limonium latifolium
Limoniastrum guyonianum
Atriplex torreyi var. griffithsii
Beta vulgaris
Atriplex canescens
Atriplex nummularia
Atriplex halimus
Salsola stocksii
Bassia scoparia
Suaeda fruticosa
Suaeda salsa
Salicornia rubra
Portulaca oleracea
Cornus sericea
Actinidia chinensis
Tripleurospermum maritimum subsp. inodorum
Helianthus annuus
Solanum nigrum subsp. nigrum
Solanum lycopersicum
Solanum scabrum
Solanum melongena
Olea europaea
Eucalyptus camaldulensis
Psidium guajava
Citrus reticulata
Citrus aurantium
Citrus sinensis var. brasiliensis
Citrus macrophylla
Gossypium hirsutum
Batis maritima
Salvadora persica
Crambe maritima
Brassica nigra
Brassica carinata
Brassica oleracea
Brassica napus
Brassica juncea
Brassica rapa
Zygophyllum xanthoxylon
Tamarindus indica
Cajanus cajan
Phaseolus acutifolius
Phaseolus vulgaris
Phaseolus angustissimus
Phaseolus filiformis
Phaseolus microcarpus
Lotus creticus
Melilotus indicus
Ziziphus spina-christi
Alismatales
Asparagales
Poales
Caryophyllales
Cornales
Ericales
Asterales
Solanales
Lamiales
Myrtales
Sapindales
Malvales
Brassicales
Zygophyllales
Fabales
Rosales
Linear increase
Threshold decrease
Non-linear decrease
Linear decrease
Hump-shaped
Zero slope

Figure 8

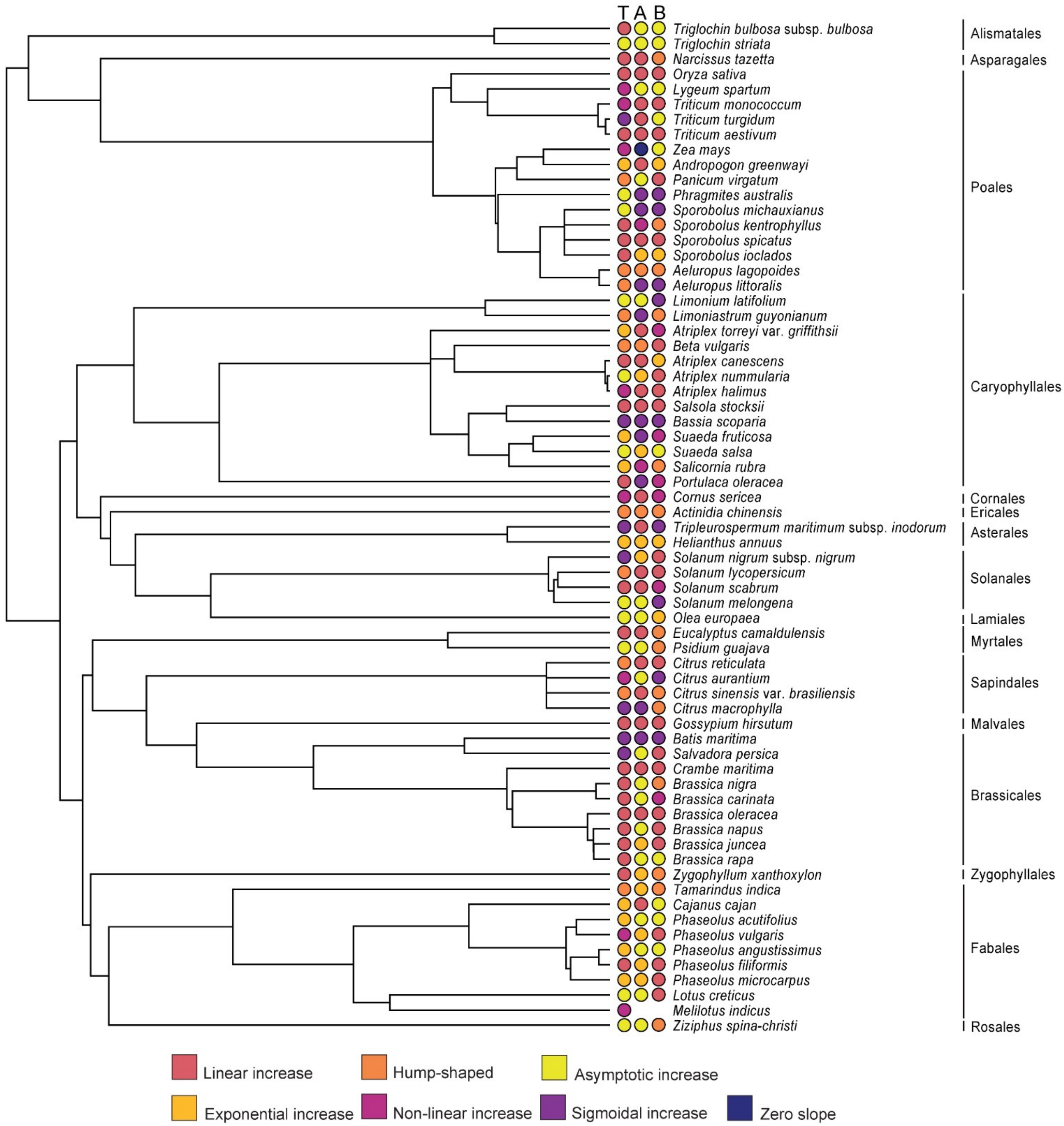


Figure Captions:

Figure 1: Populations' responses to increasing substrate NaCl concentrations. Total relative biomass growth responses (a) across NaCl treatments for each population sampled in the study. Negative and positive values represent a growth inhibition or an increase, respectively, in growth relative to control NaCl substrate concentrations. Also, the effect of NaCl treatments on total plant sodium accumulation (b) across increasing NaCl substrate concentrations for each population. The main data shown cover the range from 0 to 600 mM treatments of NaCl. An inset with the complete dataset and treatments is included with each panel. Colors represent the responses that describe biomass growth and sodium accumulation responses, as in Tables 1 and 2.

Figure 2: Alluvial plot describing the association between above-and belowground phenotype responses to total plant biomass (a) and sodium accumulation (b). Thickness of each connector indicates the proportion of populations in each response group. Responses for growth (a) where abbreviated as follows: Hump-shape (HS), linear decrease (LD), linear increase (LI), non-linear decrease (NLD), threshold decline (TD) and zero slope (ZS). For sodium accumulation responses (b) were abbreviated as follows: Asymptotic increase (AS), exponential increase (EI), hump-shaped (HS), linear increase (LI), non-linear increase (NLI), sigmoidal increase (SI) and zero slope (ZS).

Figure 3: Growth responses to increasing substrate NaCl for (a) crop and (b) non-crop populations.

Figure 4: Sodium accumulation responses to increasing substrate NaCl for (a) crop and (b) non-crop populations.

Figure 5: Alluvial plot describing the associations between biomass growth and sodium accumulation responses. Sodium accumulation responses were either monotonically increasing (grey) or not (maroon). Thickness of each connector indicates the proportion of populations in each response group. Responses for growth (a) where abbreviated as follows: Hump-shape (HS), linear decrease (LD), linear increase (LI), non-linear decrease (NLD), threshold decline (TD) and zero slope (ZS). For sodium accumulation responses (b) were abbreviated as follows: Asymptotic increase (AS), exponential increase (EI), hump-shaped (HS), linear increase (LI), non-linear increase (NLI), sigmoidal increase (SI) and zero slope (ZS).

Figure 6: Mean log-transformed tissue sodium concentration (%) (and SE) for above- and belowground tissues across biomass growth responses for non-saline (0 mM NaCl) and saline treatments (30-300 mM NaCl). Significant differences ($p<0.001$, Wilcoxon Test) for above- and belowground mean response comparisons are indicated by asterisks (***).

Figure 7: Total (T), above- (A) and belowground (B) and plant biomass growth responses mapped onto a phylogeny. Tips represent species pruned from rooted and dated ALLMB phylogeny from Smith and Brown (2018). Plant orders are indicated to the right of the phylogeny.

Figure 8: Total (T), above- (A) and belowground (B) plant sodium accumulation response mapped onto a phylogeny. Tips represent species pruned from rooted and dated ALLMB phylogeny from Smith and Brown (2018). Plant orders are indicated to the right of the phylogeny.

Appendix

Supporting information S1: Figure S1: Populations' responses to increasing substrate NaCl concentrations. Above-(a) and belowground (b) relative biomass growth responses across NaCl treatments for each population sampled in the study. Negative and positive values represent a growth inhibition or an increase, respectively, in growth relative to control NaCl substrate concentrations. Also, the effect of NaCl treatments on above- (c) and belowground (d) sodium accumulation across increasing NaCl substrate concentrations for each population. The main data shown cover the range from 0 to 600 mM treatments of NaCl. An inset with the complete dataset and treatments is included with each panel. Colors represent the responses that describe biomass growth and sodium accumulation responses, as in Tables 1 and 2.

Supporting information: Table S1: Summary of populations' responses. Each population response was classified using a model selection approach related to *a priori* predictions.

Supporting information: Table S2: Biomass growth raw data extracted from each study for each population considered in the study.

Supporting information: Table S3: Sodium accumulation raw data extracted from each study for each population considered in the study.

Supporting information: Table S4: Model Selection results for each population response for biomass growth. AIC, AICc, and BIC results for each population are recorded here along with likelihood, delta, and weights for each model.

Supporting information: Table S5: Model Selection results for each population response for sodium accumulation. AIC, AICc, and BIC results for each population are recorded here along with likelihood, delta, and weights for each model.

Supporting information: Table S6: Compiled data used for phylogenetic signal analysis.

Supporting information: Table S7: Model selection responses for biomass growth for above- and belowground tissues. Only BIC results are included along with likelihood, delta, and weight for each model.

Supporting information: Table S8: Model selection responses for sodium accumulation for above- and belowground tissues. Only BIC results are included along with likelihood, delta, and weight for each model.

Conflict of interest

The authors have no competing interest to declare.

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Author contributions

L.Y.S. and K.E.H. conceived the main ideas for this study. L.Y.S., K.E.H. and B.D.E. designed methodology; L.Y.S. collected the data; L.Y.S., B.D.E. and P.B.H. analyzed the data; M.D. gave essential comments for manuscript completion; L.Y.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data are available in: 10.6084/m9.figshare.14558457