

LETTER

More salt, please: global patterns, responses and impacts of foliar sodium in grasslands

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Abstract

Sodium is unique among abundant elemental nutrients, because most plant species do not require it for growth or development, whereas animals physiologically require sodium. Foliar sodium influences consumption rates by animals and can structure herbivores across landscapes. We quantified foliar sodium in 201 locally abundant, herbaceous species representing 32 families and, at 26 sites on four continents, experimentally manipulated vertebrate herbivores and elemental nutrients to determine their effect on foliar sodium. Foliar sodium varied taxonomically and geographically, spanning five orders of magnitude. Site-level foliar sodium increased most strongly with site aridity and soil sodium; nutrient addition weakened the relationship between aridity and mean foliar sodium. Within sites, high sodium plants declined in abundance with fertilisation, whereas low sodium plants increased. Herbivory provided an explanation: herbivores selectively reduced high nutrient, high sodium plants. Thus, interactions among climate, nutrients and the resulting nutritional value for herbivores determine foliar sodium biogeography in herbaceous-dominated systems.

Keywords

Biogeography, herbivory, nitrogen, phosphorus, potassium, micronutrients, Nutrient Network (NutNet), plant taxonomy.

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INTRODUCTION

Sodium is an essential nutrient for herbivores (Michell 1989; Snell-Rood *et al.* 2014) that can determine animal foraging preferences and movement patterns in space and time (McNaughton 1988; Prather *et al.* 2018). In contrast, sodium is not used for physiological function in most plants, and at high concentrations sodium can be toxic for plants (Mäser *et al.* 2002; Pardo & Quintero 2002; Marschner 2011; Maathuis 2014). Because of this key difference in the mineral nutrition of herbivores and the plants they eat, herbivores must use natural salt licks and seek out and efficiently use the sodium present in plants to meet physiological demands for sodium (Michell 1989). In spite of the essential role of plant sodium content for wild herbivores (Seastedt & Crossley 1981), there is little understanding of the relative importance of the many factors that may control foliar sodium in plants. For example abiotic factors including soil sodium content, soil fertility or climate may determine sodium availability, whereas biotic constraints such as plant species

phylogeny and lifeform or palatability to herbivores may determine the capacity for sodium exclusion and whole tissue losses that may occur with preferential herbivory. Furthermore, these factors may interact and operate globally or regionally to influence foliar sodium, and context may determine whether foliar sodium is likely to interact with herbivory to determine the composition of plant communities in future environments.

Plants access sodium through leaf uptake from atmospheric deposition (Benes *et al.* 1996) or root uptake from soil water (Epstein 1973). Because of the similarity of sodium to the potassium ion that is physiologically critical for plants, cation transporters of roots will transport both sodium and potassium across cell membranes (Pardo & Quintero 2002; Maathuis 2014). Although a relatively small group of plants – mostly C₄ grasses – physiologically requires a small amount of sodium (Brownell & Crossland 1972; Furumoto *et al.* 2011), the sodium cation is present in the foliage of many species and can be used for a variety of critical plant functions, including stomatal opening

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and closing, particularly when potassium is in short supply (Subbarao *et al.* 2003). However, terrestrial sodium is geographically variable (Kaspari *et al.* 2008, 2009; Wicke *et al.* 2011; Vet *et al.* 2014; Doughty *et al.* 2016) because of mineral acquisition from sources such as ocean spray, terrestrial salinisation or road salting practices (Ramakrishna & Viraraghavan 2005; Vet *et al.* 2014), urine (Kaspari *et al.* 2017), loss from leaching (Vitousek & Sanford 1986) and climatic influences, particularly aridity that causes accumulation of sodium via evapotranspiration outstripping precipitation (Raheja 1966). In spite of these general associations, it remains unclear whether foliar sodium varies predictably among plant taxonomic lineages or biogeographically with, for example distance to coast or site aridity and whether site or plant species characteristics effectively predict the foliar sodium content of the most abundant plants.

Although plant sodium is often assumed to simply track soil sodium supply, at biogeographical scales, a growing body of evidence suggests that plant sodium content may not be determined solely via soil sodium supply. Like other soil cations, sodium uptake by plants can be reduced in high pH soils (Tyler & Olsson 2001; Bolan & Brennan 2011), and aridity can lead to increased soil pH (Slessarev *et al.* 2016), suggesting that aridity may either increase foliar sodium via increased soil sodium or reduce it via increased soil pH. Evidence also is accumulating that the supply of macronutrients such as nitrogen can reduce the availability of mineral cations to plants (Lucas *et al.* 2011). Thus, anthropogenic activities that are altering soil pH or increasing macronutrient supply to ecosystems (Franklin *et al.* 2016) may interactively alter the sodium content of foliage and quality of foliage for herbivores (Kaspari *et al.* 2017). Furthermore, herbivores may themselves alter the sodium concentration in plant tissue either by promoting the availability of sodium through recycling (McNaughton *et al.* 1997; Doughty *et al.* 2016), by promoting saline soil conditions (McLaren & Jefferies 2004), or selectively consuming plant species with elevated salt levels in their foliage (Seastedt & Crossley 1981; Welti *et al.* 2019). Thus, herbivory also may promote plant species with relatively high foliar sodium that have traits, such as rapid regrowth, basal meristems or use of sodium to modify osmotic potential under drought, that are beneficial under both saline soil conditions and high grazing intensity (Coughenour 1985; Veldhuis *et al.* 2014; Griffith *et al.* 2017).

Here, we use existing and experimentally created environmental gradients to address the following questions (1) *Patterns of foliar sodium*: Which site (10^4 m²), plot (10^0 m²), and species characteristics predict foliar sodium content? For example does foliar sodium vary predictably among plant taxa, with distance to coast, or along a gradient of soil pH or site aridity? (2) *Responses of foliar sodium to a changing environment*: Does selective herbivory or elevated nutrient supply reduce foliar sodium at the local (plot) scale? (3) *Effects of foliar sodium on grassland species composition*: Does a grassland species' foliar sodium content predict changes in the species' relative abundance in response to herbivory or elevated nutrients?

METHODS

Experimental design and locations

Samples for this study were collected at 26 sites that are part of a long-term, nutrient addition and herbivore-fencing experiment being performed in herbaceous-dominated sites around the world, the Nutrient Network distributed experiment (NutNet, www.nutnet.org). The subset of the NutNet sites that were able to collect tissue samples that comprise the data used in this study spanned Africa, Australia, Europe and North America (Table S1).

Each site had three experimental blocks composed of $10\text{--}5 \times 5$ m plots, each assigned randomly to one of 10 unique treatment combinations. Treatments included a factorial addition of N ($10 \text{ g N m}^{-2} \text{ year}^{-1}$ as timed-release urea [(NH₂)₂CO]), P ($10 \text{ g P m}^{-2} \text{ year}^{-1}$ as triple-super phosphate [Ca(H₂PO₄)₂]), and K ($10 \text{ g K m}^{-2} \text{ year}^{-1}$ as potassium sulphate [K₂SO₄]) plus micronutrients (μ , a mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo [0.05%]), for a total of 8 plots/block. Importantly, no sodium (Na) was added in any treatment. N, P and K were applied annually at each site for 2–4 years (Table S1); the micronutrient mix, μ , was applied once in the first experimental year to avoid toxicity.

For the focal fence and fertilisation experiment, fence treatments were crossed with the control and the all nutrient treatment (N+P+K μ), adding two fenced plots to each block. Fences were built to exclude medium and large mammals and had been in place for 2–4 years at the time of sampling. Fences were 230 cm tall with four strands of barbed wire suspended at equal vertical distances above the lower 90 cm which was surrounded by 1-cm woven wire mesh with a 30-cm outward-facing flange stapled to the ground. At some sites, logistical considerations required slight modifications of the fence design (Fence exceptions table, Table S2). All sampling plots were separated by at least 1 m wide walkways to reduce the impact of treatments on adjacent plots. For additional methods details, see (Borer *et al.* 2014).

Pre-treatment soil collection

Before applying the experimental treatments, three 2.5×10 cm soil cores were collected from each experimental plot, combined, homogenised into a single sample for each 5×5 m plot (roughly 500 g of soil), and dried. Percent soil N from each plot was analysed in a single analytical laboratory using a Costech ECS 4010 CHNSO Analyzer on pulverised soil (Knops lab, University of Nebraska, USA). Extractable soil P, K and micronutrients, including Na, and pH for every soil sample also were quantified in a single analytical laboratory using standard methods (Borer *et al.* 2014) (A&L Laboratories, Memphis, Tennessee, USA). Across our study sites, plot-level soil sodium ranged from 21 ppm (at Val Mustair in Switzerland) to 150 ppm (at Elliott Chaparral, USA).

Plant abundance and biomass estimation

To determine the most abundant plant species in each plot and the change in cover of species in response to the experimental treatments, the percent areal cover of each species was estimated to the nearest 1 percent for each species within a permanently marked 1-m² subplot of each treatment unit.

A metric of site-level net herbivore impact was estimated as the average difference in live plant mass inside and outside of fences within a block during the first year of the treatment. To estimate this, we clipped the aboveground biomass of all plants rooted within a 0.2 m² area of each fenced and control plot. Each sample was divided into growth from the current year and litter from previous years. We used the first year of treatment to estimate herbivore impact on vegetation mass, prior to species-level selection and turnover in response to long-term herbivore exclusion.

Foliar sampling and sodium analysis

Within each plot, the most abundant species were determined as a function of percent cover, and a single healthy leaf was collected from five unique individuals of the species with the greatest cover at the site. Most sites had three to five dominant species present in most plots; however, one site collected eight different species (Val Mustair), because there were not clearly dominant species. All leaves were transported in a cooler, and then dried at 60 °C for 48 h (Firn *et al.* 2019). The collected species represented 5.3% (Val Mustair, Switzerland, a high elevation, highly diverse (25 species/plot) site; this is the site that sampled 8 species) to 52.1% (Saline, KS, USA) of the total plot cover with an average representation of 26% of the total cover across all plots and sites (Table S1). All leaves were then sent to Queensland University of Technology (Dr. J. Firn) for sodium analysis. Dried leaves were ground to a fine powder, then analysed for sodium content with an Agilent 8800 Laser Ablation Inductively Coupled Plasma Mass Spectrometer (LA-ICP-MS), following Duodu *et al.* (Duodu *et al.* 2015) with two exceptions: C, the most abundant naturally occurring element, was used as a standard, and no additional pulverising was performed beyond that required for C analysis. The reference material for sodium was NIST SRM 1570a Trace elements in spinach leaves (USA National Institute of Standards and Technology 2014). Elemental quantification followed the method of Longerich *et al.* (1996), using Iolite, a data reduction software (Paton *et al.* 2010).

Climate data

The WorldClim database provided comparable long-term climate data for all sites (version 1.4; <http://www.worldclim.org/bioclim>). These global climate data were interpolated at high-resolution from data stations with 10–30 years of data (Hijmans *et al.* 2005). We used these data to test whether foliar sodium in the most abundant taxa declined with mean annual precipitation (MAP in mm per year) or increased with a site-level index of aridity (MAP divided by potential evapotranspiration in mm per year) (Barrow 1992). Site-level MAP ranged from 14 at Sheep Station, USA to 1898 mm of annual

precipitation at HJ Andrews LTER; Lookout, USA and the index of aridity ranged from 0.2 at Mount Caroline, Western Australia to 2.4 mm at Val Mustair, Switzerland (Table S1).

Analyses

We explored the relative importance and interactions among the many factors that we hypothesised to constrain foliar sodium. Many of these factors could covary (e.g. annual precipitation, distance to coast and soil pH), and it was possible that there could be multiple models that were similarly informative (i.e. had similar AICc values). For this reason, we used a multi-model approach, which does not try to identify a single best model (Grueber *et al.* 2011). This information theoretic approach starts by calculating all possible subsets of the parameters in the full model, and then uses Akaike's information criterion (AICc) to determine the subset of models sharing similarly high levels of parsimony (Grueber *et al.* 2011). In our case, we included in our high parsimony set all models that fell within 4 AICc units of the model with the lowest AICc value (Grueber *et al.* 2011). Parameter estimates and significance are based on a weighted average of the set of high parsimony models. We present the weighted average parameter value estimate, significance, and the summed AIC weights for all models in which the parameter is included, or *importance*. We used the *dredge* function in the MuMIn R library to calculate the AICc of all possible models and the *model.avg* function in the MuMIn R library to calculate the weighted parameters and statistics.

All models used a random effect structure with site and species within site treated as random intercepts to account for the hierarchical nature of the sampling. To examine biogeographical predictors of foliar sodium, we examined only control plot values, but for the effects of environmental change, we used data from all experimental plots. Experimental treatments were retained in all models. Because of missing soil data, one site (Mt. Caroline) is excluded from experimental analyses. In addition, to avoid bias from having rare species that were found only in one treatment driving the results, for the analysis of the fence and fertilisation experiment (shown in Fig. 4), we include species that are present in Control plots and at least two other treatments (e.g. Control, Fence and Fertilised or Control, Fence and Fence + Fertilised). Similarly, for analysis of the factorial nutrient experiment (Figure S1), we include only species present in Control plots and at least five other treatments. Finally, in analyses of abiotic factors associated with foliar sodium, we tested the leverage of two outlier sites. In particular, we examined the role of a single site (Sheep Station, USA) in driving the association of foliar sodium with soil pH and another site (Lancaster, UK) in determining the importance of distance from the coast in foliar sodium content.

In addition to assessing foliar sodium, we also used multi-model inference to examine the cover response of each plant for which sodium was measured in each plot as a function of the sodium concentration of that species. For assessing the effects of foliar sodium on plant cover in response to the experimental treatments, species with < 0.1% cover in a plot were removed (23 out of 1828 records or 1.3%).

All analyses were performed in R (version 3.3; R Foundation for Statistical Computing).

RESULTS

Patterns of foliar sodium

Foliar sodium in 201 of the most abundant grassland plant species from 26 sites on four continents, including representatives of 32 plant families, varied across five orders of magnitude among sites and the most abundant plant taxa in unmanipulated plots. Foliar sodium ranged from 0.5 ppm in *Phleum pratense* (Poaceae) to 28 271 ppm in *Epilates australis* (Asteraceae, Table S1), and average site-level plant sodium across the most abundant species ranged from 2.7 ppm (at Konza Prairie in the North American Great Plains) to 9,715 ppm (at Burrawan in southeastern Australia). Foliar sodium of the most abundant species in control plots was similar across grasses with C₄ (463 ± 201 ppm) and C₃ (624 ± 159 ppm) photosynthetic pathways ($P = 0.10$). However, across all taxa in unmanipulated (control) plots, foliar sodium varied spatially both within and among sites (Fig. 1); mean foliar sodium content also varied substantially among plant families (Fig. 1, $P < 0.001$, Table S3).

We found that among sites, mean site-scale foliar sodium in control plots increased with soil sodium (Fig. 2, $P = 0.015$; $t = 2.68$), whereas within sites, foliar sodium did not covary with plot-scale soil sodium ($P = 0.51$; $t = 0.64$). In a model that included multiple candidate predictors (site aridity, distance from coast, soil pH, photosynthetic pathway and soil sodium), foliar sodium declined with increasing site-level water availability (increasing AI; $P = 0.001$) and soil pH (Fig. 3, $P = 0.04$, Table S4). However, our model selection

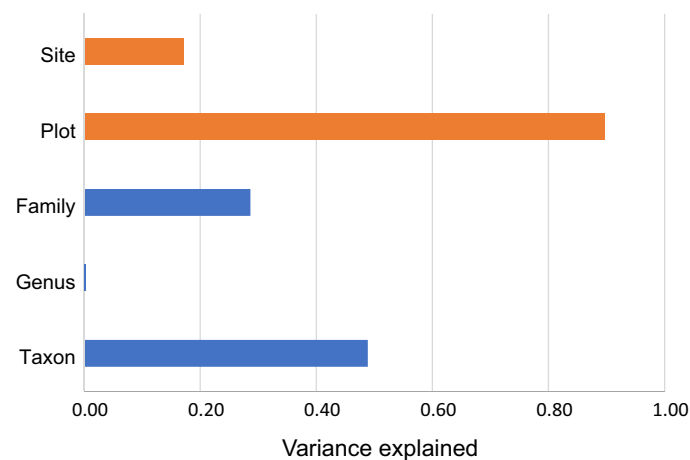


Figure 1 Foliar Na variation across taxonomic and spatial scales: Variance components analysis of foliar sodium in the 85 locally abundant plant taxa from control plots at 26 sites across nested taxonomic and spatial scales. Foliar sodium for 41 species was measured at two or more sites. Variation in foliar sodium associated with plant location is shown in orange; variation associated with taxonomic groups is shown in blue. Variance explained by genus is extremely small, but non-zero ($< 3 \times 10^{-6}$), thus is barely visible in this graph. Table S3 provides the full statistical model associated with this figure.

criteria did not retain soil sodium or photosynthetic pathway in final models. The decline in foliar sodium was similar across both coastal and inland sites except for a single site in the UK with high precipitation and exceptionally high sodium ion deposition relative to most locations on Earth (Vet *et al.* 2014) (Fig 3b, Lancaster, UK). In contrast, for sites with neutral to acidic soils (all except one in this study, Sheep Station, USA), there was no relationship between foliar sodium and soil pH (Fig. 3). Thus, the biogeographical variation in foliar sodium content is explained, in part, by a combination of local conditions, including soil sodium availability and aridity.

Responses of foliar sodium to a changing environment

Nutrients and herbivory interacted to determine the foliar sodium of the most abundant plants, and the strength of this effect depended on aridity but not soil pH (Table S5). In particular, at mesic sites, when herbivores were present, nutrient addition favoured abundant plants with high foliar sodium compared to plants in ambient (control) plots (Fig. 4a, Table S5). As a result, the addition of the full suite of nutrients (N+P+K μ , but not Na) outside of fences weakened the negative effect of increasing water availability (increasing AI) on foliar sodium content (Fig. 4b). The factorial nutrient addition experiment clarified that the interaction between aridity and nutrient supply was primarily driven by the effects of potassium and micronutrients (K μ) and to a lesser extent the effects of nitrogen and phosphorus addition (Table S6, Fig. S1).

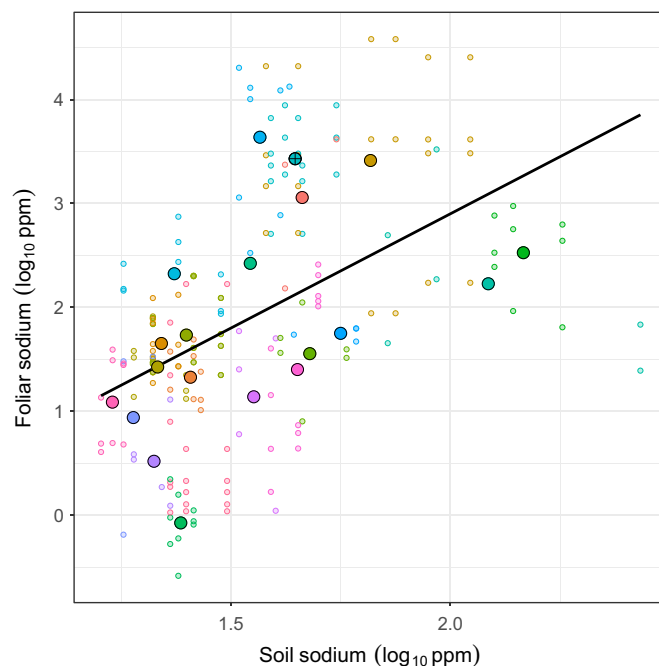


Figure 2 Foliar Na and soil Na: Foliar sodium increases with soil sodium among sites in 85 locally abundant plant taxa from control plots but not among plots or species within sites. Sites have different colours; site means are shown as large points and small points represent species data. Site-level regression is shown as a black line.

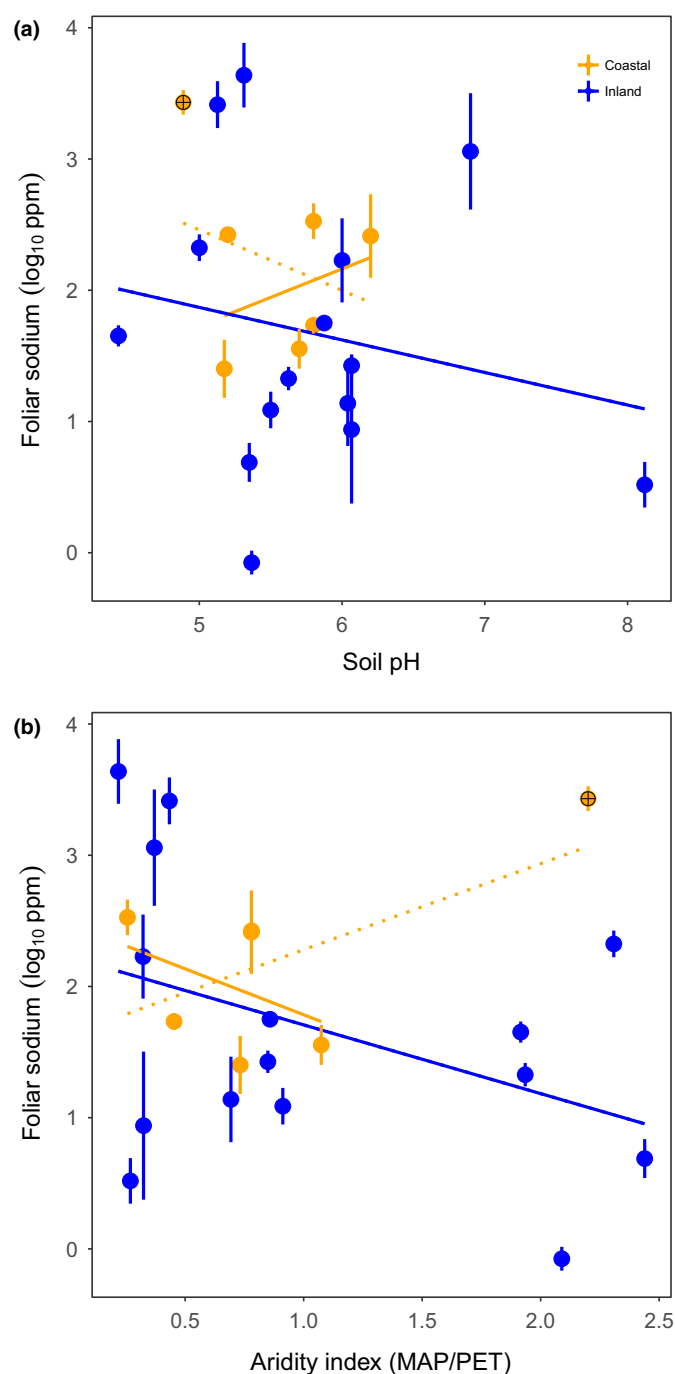


Figure 3 Predictors of foliar Na: The foliar sodium of the most abundant plant species declined across a gradient of (a) plot-scale pH ($z = 2.03$, $P = 0.04$) and (b) site-scale water availability (MAP/PET; $z = 3.24$, $P = 0.001$). Data include the 85 taxa across 22 sites that were growing in control plots. Coastal (orange) and Inland (blue) are divided at 100 km from a coast. The dashed orange line shows the model with all sites included; the solid orange line shows these relationships without a single site in the UK (Lancaster, orange circled site) with high precipitation and coastal salt input. Similarly, the dashed blue line shows the model with all sites included; the solid blue line shows the relationships without the only site with basic soil pH found in US Intermountain West (Sheep Station, blue circled site). Error bars represent $\pm$ SE. Table S4 provides the full statistical model associated with the solid lines shown in this figure.

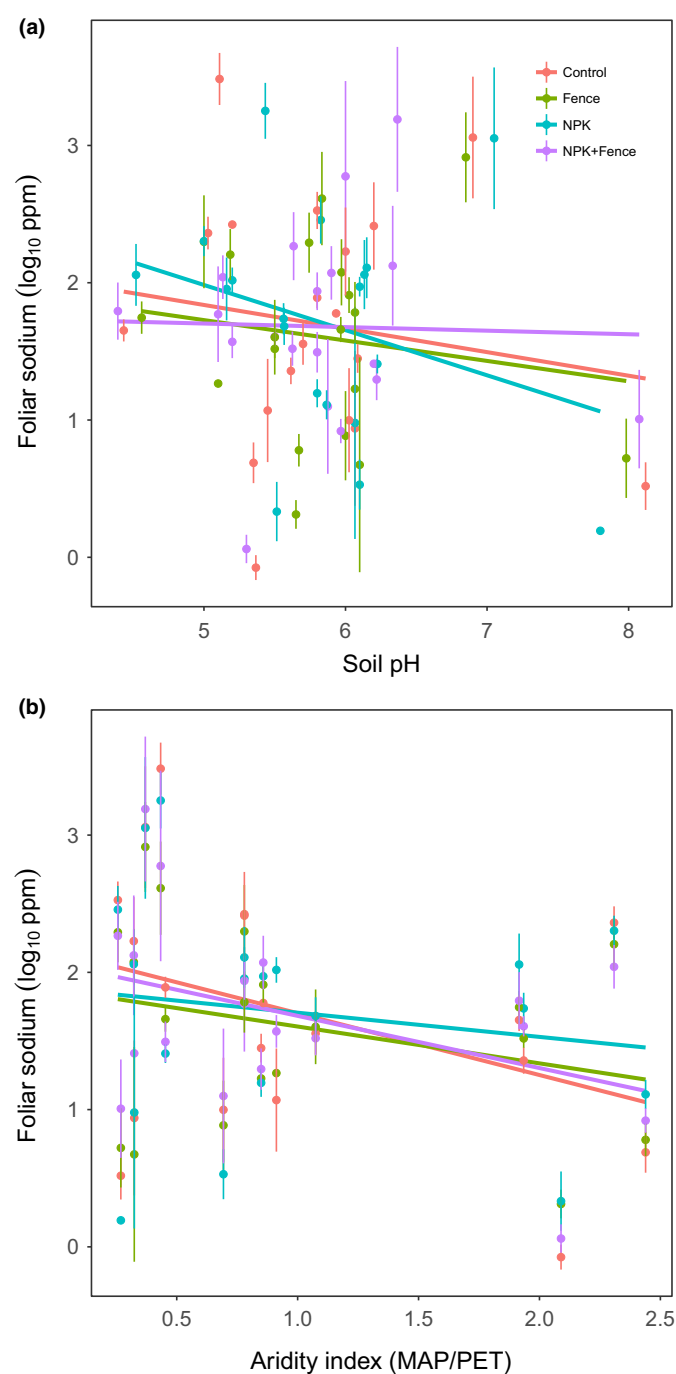


Figure 4 Responses of foliar sodium to changes in herbivory and nutrient supply: Response of foliar Na in 153 locally abundant plant species to a factorial combination of fencing to reduce vertebrate herbivory and fertilisation by a suite of micro- and macronutrients (not including Na⁺) (a) across a gradient in plot-scale pH and (b) across a gradient in site-scale water availability. Foliar sodium is higher than expected from control plots where precipitation is relatively high and nutrients are added ($z = 3.49$, $P = 0.0005$). Error bars represent $\pm$ SE. Table S5 provides details of the full statistical model.

We examined the subset of species that were sampled multiple times among plots and sites to explore the role of intraspecific variability in sodium content in determining these observed responses. Of the 201 species in this experiment, 41

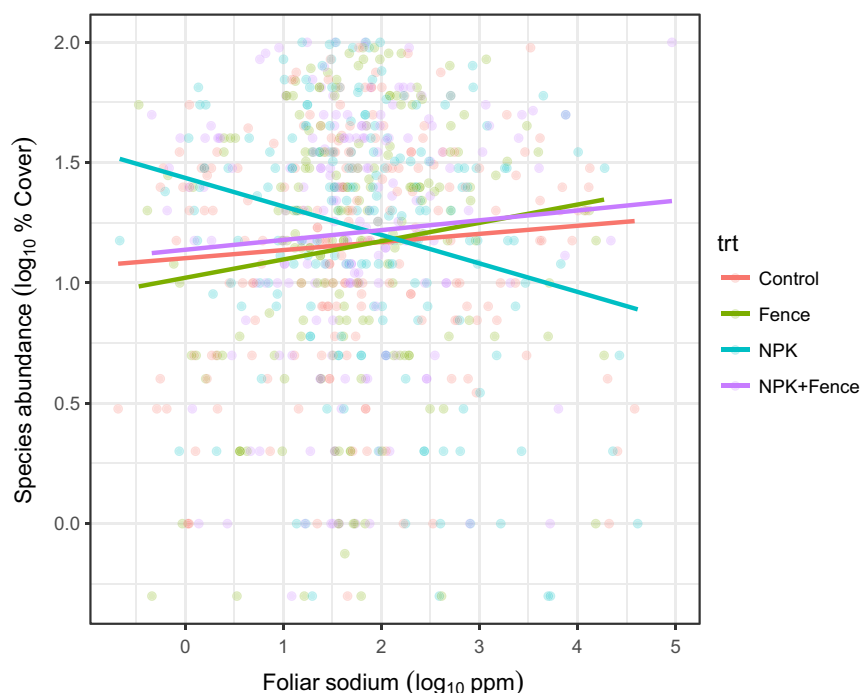


Figure 5 Effects of foliar sodium on grassland species composition: Response of plant abundance to a factorial combination of fencing to reduce vertebrate herbivory and fertilisation by a suite of macro- and micronutrients (not including Na^+) as function of foliar sodium in 153 grassland plant species. Table S9 shows the final model describing species abundance as a function of treatments and foliar sodium.

were among the most abundant (and therefore sampled) in plots at more than one site, and 94 were sampled in both control and treatment plots within sites. Models of the subset of species present among sites and in both control and treatment plots were qualitatively similar to models of the larger dataset for both experiments (Tables S7 and S8), suggesting that some of the observed variation in foliar chemistry is attributable to intraspecific change in foliar sodium content in response to the biotic and abiotic environment.

Effects of foliar sodium on grassland species composition

The sodium content of foliage and plot-scale nutrient supply contributed to the effects of herbivores on changes in the relative abundance of grassland plant species. Fertilisation (with NPK_μ) increased the cover of the most abundant species, and in the presence of herbivores, the abundance of species low in foliar sodium increased in response to fertilisation, whereas high sodium species became less abundant when fertilised (Fig. 5). However, in the absence of herbivores, fertilisation had no consistent effects on species abundances in relation to their foliar sodium concentration (Table S9, Fig. S2). These effects on foliar sodium were independent of the intensity of herbivory among sites (measured as the site-level log ratio of live biomass inside and outside of herbivore exclusion fences ($P > 0.57$ for all main effects and interactions; importance < 0.40 [model not shown])). The factorial nutrient addition experiment clarified that, in the presence of herbivores, the addition of any elemental nutrient caused dominant plant species with relatively high foliar sodium content to decline more than species with lower foliar sodium (Table S10); this effect

was greatest in response to fertilisation with P (Table S10). These results point to selective consumption by herbivores of high nutrient, high sodium plants.

DISCUSSION

This multi-continent, biogeographical study demonstrated that foliar sodium in dominant grassland plants is highly variable among sites and even plots within a site, and there also is significant variation in foliar sodium among families and taxa within families, regardless of geographical location. These patterns likely reflect variation in long-term environmental conditions (e.g. aridity, grazing) that have selected for species with differing strategies for environmental sodium uptake. While there is evidence for phylogenetic conservation of cation transport proteins that can influence sodium uptake (Schachtman & Liu 1999) with predictable differences across photosynthetic pathways (Brownell & Crossland 1972), photosynthetic pathway was not a predictor of foliar sodium in grasses. Nonetheless, the very highest foliar sodium content recorded in this study was 9% (91 818 ppm) in *Eragrostis curvula* (Poaceae, commonly called African Lovegrass) found at Burrawan, Australia. This species has a C_4 photosynthetic pathway, indicating a physiological requirement for sodium, and this site is among the more arid sites in the experiment, suggesting that both photosynthetic pathway (Brownell & Crossland 1972; Furumoto *et al.* 2011) and aridity (Raheja 1966) can be strongly associated with foliar sodium, in some cases. However, the sodium required by C_4 grasses is minimal compared to variation in environmental sodium, so while individual species supported this hypothesis, as a

group, C₄ grasses were not consistently high in foliar sodium.

The results of this globally extensive study demonstrate that the relative abundance of plant species in grasslands is altered by herbivores as a function of sodium content and elemental nutrient supply. In particular, herbivores in grasslands spanning four continents with a variety of herbivore types and densities consistently reduced the cover of plants with high foliar sodium only in high nutrient conditions. The reduction in abundance of sodium-rich plants in fertilised plots is evidence of targeted herbivory of high sodium, protein-rich plants. In particular, herbivores are attracted to plots with elevated nutrients (Mattson 1980) and sodium, and selective consumption reduces the abundance of those species with the highest sodium. These plants are not likely extirpated from the community, since the same species are generally found at higher abundance inside herbivore exclosures, rather they are likely to be in a constant state of regrowth from having their aboveground foliage selectively consumed. Such selective foraging is common in many ecosystems (Belovsky 1981; Jefferies *et al.* 1994; Wallis de Vries & Schippers 1994; Bartolome *et al.* 1998; Doughty *et al.* 2016). These results build from work demonstrating arthropod co-limitation by macronutrients and sodium (Prather *et al.* 2018), suggesting that elevated nutrients may interact with sodium to alter both herbivore and plant communities. Related to this, the impact of herbivores on sodium content of the most abundant plant species was contingent on aridity, with foliar sodium content high and indistinguishable among experimental treatments at arid sites, but declining with increasing water availability. Our arid region results are consistent with previous work that found positive feedbacks generating and maintaining high sodium content grazing lawns because of high evaporation rates under the cropped vegetation (McNaughton 1988). By examining herbivore impacts across a much broader precipitation gradient, we demonstrate that both aridity and herbivory determine foliar sodium biogeography across the world's grasslands, with declining sodium content under increased precipitation and preferential feeding by herbivores.

Our experimental work also demonstrated that the sodium content of locally abundant plants increases with soil sodium at the site-scale; however, when included in models, site aridity was a much more effective predictor of biogeographical variation in foliar sodium than soil sodium. At broad spatial scales, foliar sodium is positively related to soil sodium, as has been observed in previous work (Sutcliffe 1959; Epstein 1973; Pardo & Quintero 2002; Maathuis 2014), but foliar sodium was not strongly predicted by distance to coast, a common surrogate for sodium ion deposition (Vet *et al.* 2014). However, because arid regions are characterised by high evapotranspiration relative to precipitation, these sites tend to accumulate salts over time (Raheja 1966). In contrast, coastal sites may have both high ion input and high precipitation (Vet *et al.* 2014), reducing the environmental pools of ions, including sodium, and causing a mismatch between salt deposition and the location of sodic soils (Wicke *et al.* 2011). In this study, the coastal site with exceptionally high foliar sodium relative to site-scale precipitation (Lancaster, UK) is also situated in a location on Earth with an exceptionally high rate of sodium ion input (Vet *et al.* 2014), suggesting that site

aridity combined with direct measures of site-level sodium ion input rate will likely provide even better predictions of site-level foliar sodium in the most abundant plant taxa. In addition, although we found a decline in foliar sodium with increasing soil pH, this pattern was driven by a single, arid site in the intermountain west of the USA. While this pattern is consistent with expectations of reduced cation uptake in higher pH soils (Tyler & Olsson 2001; Bolan & Brennan 2011), we have only a single site with a pH above neutral. Because soil pH is intimately associated with aridity (Slessarev *et al.* 2016), disentangling the roles of soil pH and aridity in determining grassland plant sodium biogeography will require more thorough sampling, particularly at sites with basic soils spanning a range of aridity. Nonetheless, the strong spatial variation in foliar sodium suggests that environmental context is key in determining foliar sodium which, by extension, implies that future environmental changes may alter foliar sodium for herbivores. Given the importance of dietary sodium for herbivores (Seastedt & D. A. Crossley 1981; McNaughton 1988; McNaughton *et al.* 1997; Kaspari *et al.* 2008; Doughty *et al.* 2016; Welty *et al.* 2019), biogeographical patterns of foliar sodium in abundant grassland plants may arise from interactions with wild herbivores, and likely have significant implications for the distribution and impacts of consumers in grassland ecosystems.

The strong difference in the physiological importance of sodium to grassland plants and wild herbivores has gained increasing attention in ecology, with calls for a greater understanding of the biogeography of sodium (Kaspari *et al.* 2008). This study of both patterns and responses to experimental manipulation, performed at 26 sites spanning wide biotic and abiotic gradients, demonstrates that aridity, soil acidity, nutrient supply and herbivory, interact to influence biogeographical patterns of foliar sodium and its effect on plant abundance. In future environments, climate change is expected to impact global patterns of soil salinity via changes in precipitation and evapotranspiration (Schofield & Kirkby 2003). The current results suggest that the impact of these changes on grassland plant composition will depend on the interactive effects of large-scale changes in aridity and elemental nutrient (N, P) supply and the resulting nutritional value for consumers.

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are listed in Table S11 and data contributors are listed in Table S12.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available on Dryad Digital Repository: <https://doi.org/10.5061/dryad.c742372>

AUTHORSHIP

EB, EL and ES developed and framed the research question; JF led chemical analyses; EB, EL and ES performed statistical analyses. All authors performed the experiment at their sites and collected data used in these analyses; EB, ES and EL also coordinated the experiment. EB wrote the first draft of the manuscript, and all other authors contributed substantially to revisions. See Table S11 for details.

DATA INFORMATION

All data contributors are listed in Table S12.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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