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Sodium addition increases leaf herbivory and fungal damage across four grasslands

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Abstract

1. Sodium (Na) is an essential element for all animals, but not for plants. Soil Na supplies vary geographically. Animals that primarily consume plants thus have the potential to be Na limited and plants that uptake Na may be subject to higher rates of herbivory, but their high Na content also may attract beneficial partners such as pollinators and seed dispersers.
2. To test for the effects of Na biogeochemistry on herbivory, we conducted distributed Na press experiments (monthly Na application across the growing season) in four North American grasslands.
3. Na addition increased soil and plant Na concentrations at all sites. Grasses in Na addition plots had significantly higher herbivore damage by leaf miners and fungal pathogens than those in control plots. Forbs with higher foliar Na concentrations had significantly more chewing insect herbivore and fungal damage.
4. While no pattern was evident across all species, several forb species had higher Na concentrations in inflorescences compared to leaves, suggesting they may allocate Na to attract beneficial partners.
5. The uptake of Na by plants, and animal responses, has implications for the salinification in the Anthropocene. Increased use of road salt, irrigation with saline groundwater, rising sea levels and increasing temperatures and evapotranspiration rates with climate change can all increase inputs of Na into terrestrial ecosystems.
6. Our results suggest increasing terrestrial Na availability will benefit insect herbivores and plant fungal pathogens.

KEYWORDS
herbivore, insect damage, ionomics, leaf pathogens, nutrient limitation, pollination, prairie, salt

1 | INTRODUCTION

Sodium (Na) is an essential element used in every animal cell; conversely, most plants do not require Na. As a consequence of this dissimilarity in nutritional requirements, increasing Na availability favours herbivores both over plants and over predators which have sufficient access to Na through consuming animal tissue (Kaspari, 2020). Na limitation is predominant in plant consumers like elephants (Holdo et al., 2002), koalas (Au et al., 2017), grasshoppers (Joern et al., 2012) and termites (Kaspari et al., 2014). Plant consumers obtain Na from a variety of sources. At small spatial scales, saline-rich puddles (Boggs & Dau, 2004), animal excreta (Clay et al., 2014) and flesh are all important sources of Na (Clay et al., 2017; Simpson et al., 2006). At larger spatial scales, Na aerosol deposition (National Atmospheric Deposition Program, 2019) and soil sediments (Jones & Hanson, 1984) can increase regional Na availability.

While Na is not metabolically essential for most plants, plant tissue can be an important source of Na for plant consumers. In a study across 26 grasslands, Na content of plant tissue varied 100,000-fold, and herbivores selectively removed high Na content plants from N- and P-fertilized plots (Borer et al., 2019). In another study distributed across 54 grasslands, insect abundance increased in Na pulse experiments, especially in those with low background Na availability (Kaspari et al., 2020; Welti et al., 2019). While less is known about the nutritional requirements of fungi relative to animals (Camenzind et al., 2018; Scharnagl et al., 2017), certain fungi have been found to concentrate Na relative to their environment (Cromack et al., 1977); thus plant-associated fungal pathogens and symbionts may also benefit from higher levels of Na in plant tissues. Plants that do accumulate Na are likely targeted by consumers, with far ranging consequences from driving ungulate movements across the Serengeti (Griffith et al., 2017), to herbivore preference for these plants leading to altered plant community composition (Borer et al., 2019; Bui, 2013), to subsequent increases in predators and parasitoids tracking increases in herbivores (Clay et al., 2014; Welti, Kuczynski, et al., 2020).

For the majority of plants that do not require Na metabolically, Na uptake presents an evolutionary paradox. One possible solution is that Na uptake results in increased attraction of beneficial partners such as pollinators, seed dispersers or mycorrhizae (Kaspari, 2020). Like herbivores, pollinating insects are attracted to Na-enhanced resources. For example, bees show strong preferences for NaCl-spiked water compared to both deionized water and solutions containing other minerals (Bonoan et al., 2017; Lau & Nieh, 2016). Ants, common seed dispersers in grassland systems, are also frequently Na limited (Clay et al., 2017; Kaspari et al., 2020; Prather, Roeder, et al., 2018). If plants can manipulate Na uptake or allocation and use this Na to attract beneficial partners, they may distribute Na to inflorescences, food bodies and extra-floral nectaries (Kaspari, 2020).

Such Na-based drivers of plant–consumer interactions are important given that human activity continues to alter terrestrial Na availability. Climate change induced rising temperatures and increasing evapotranspiration will alter the hydrological cycle and are predicted to increase terrestrial Na deposition rates (Daliakopoulos et al., 2016). Crop irrigation with saline water is a substantial issue, with much as 20% of irrigated land globally, an area the size of France, being salt-spoiled (Qadir et al., 2014), and with production on still more land suppressed by Na accumulation (National Research Council, 2005). The combination of overuse of groundwater and rising sea levels is predicted to greatly exacerbate future land salinification (Daliakopoulos et al., 2016). Additionally, road salt application adds substantial amounts of Na to roads and nearby areas in freeze-prone climates. For example, the state of Massachusetts (USA) recommends adding 109 kg of salt/lane mi/freezing event (Massachusetts Department of Transportation, 2019). Elevated global $p\mathrm{CO}_2$ can, in contrast, lead to nutrient dilution (Loladze, 2014; Welti, Roeder, et al., 2020; Ziska et al., 2016), decreasing Na concentrations in plant tissues. While human activity has greatly altered the geography of terrestrial Na availability, we are only beginning to understand how these changes affect ecological communities (Kaspari, 2020). Ongoing changes to terrestrial Na availability are likely to affect herbivory rates which themselves modify plant productivity (Jia et al., 2018; Prather, Laws, et al., 2018), diversity (Koerner et al., 2018; La Pierre et al., 2015; Seager et al., 2013) and decomposition (Kaspari et al., 2014; Lemoine & Smith, 2019; Wang et al., 2018).

Here we examine the relationship between plant foliar Na content and damage by three groups of consumers, namely foliar fungal pathogens, phloem-feeding and chewing insects. We test two hypotheses pertaining to the role of Na uptake in plant–insect interactions, using a distributed Na press experiment in four central North American grasslands. In community ecology, press experiments simulate a continuously altered state, in this case, Na addition being frequently applied; pulse experiments, in contrast, are single perturbations aimed at measuring the magnitude of response and time to recovery (Bender et al., 1984). To address what costs plants may incur in increasingly saline environments, we hypothesize that (H1), all else equal, plants that uptake more Na in leaves will experience increased herbivory rates. However, herbivory costs may be offset by the benefits of attracting pollinators and dispersers. Thus we hypothesize that (H2) plants will have higher concentrations of Na in inflorescences relative to leaves. While previous work has demonstrated Na limitation of herbivore abundance (e.g. Au et al., 2017; Kaspari, 2020; Welti et al., 2019), here we examine the cost for plants of living in high Na environments—specifically, that of enhanced herbivory.

2 | MATERIALS AND METHODS

2.1 | Site description

We conducted a press experiment of Na fertilization in the summer of 2018 at four inland grasslands in the continental United States. The four sites consist of Selman Living Laboratory (SLL), a mixed-grass prairie operated as biological station by the University of Central Oklahoma in western Oklahoma, Konza Prairie (KNZ), a tallgrass prairie operated as biological station by Kansas State University and owned by the Nature Conservancy in northeastern Kansas, Platte River Prairie (PRP), a restored Nature Conservancy tallgrass prairie in southern Nebraska, and Niobrara Valley Preserve (NVP), a Nature Conservancy mixed-grass prairie in northern Nebraska. The two more northern sites (those in Nebraska) have much sandier soils than the Oklahoma and Kansas sites as a result of sediment erosion from the Rocky Mountains. These sites vary in annual cumulative precipitation increasing from west to east (NVP: 510 mm; SLL: 690 mm; PRP: 711 mm; KNZ: 835 mm) and mean annual temperature increasing from north to south (NVP: 9°C; PRP:

10°C; KNZ: 12°C; SLL: 15°C). However, KNZ experienced an extreme drought in early 2018 with the first 6 months, typically the wettest half of the year for this site, having <200 mm of cumulative precipitation.

2.2 | Experimental design

At each of the four grasslands, we setup an experiment with 20 plots, each 7 m × 7 m, and 7 m apart in a 2 × 10 grid. Plot treatments alternated so that every other plot was a control followed by a Na addition plot, with 10 plots in each treatment. Sodium applications consisted of 10 g NaCl/m^2, or 490 g NaCl (196 g Na) dissolved in 1 L water per plot and were applied monthly for 5 months (May–September). While it is difficult to compare our level of Na application to saline irrigation additions as our additions compared much higher concentrations but much less water, soil salinity levels in June at the site with the highest Na concentrations (SLL: 158 ppm ± 19 *SE*) only reached moderate saline hazard levels (Daliakopoulos et al., 2016). The level of Na addition is additionally comparable to the amount of Na that would be made available to the biotic community by a bison urinating on a plot (Steinauer & Collins, 1995). Control plots were treated with 1 L of water at the time of each Na addition.

2.3 | Plant and soil sampling

We clipped all above-ground plant biomass from a 0.1 m × 1 m clip strip in the same location in the interior of each plot in July and categorized plants into grasses, forbs and litter. Grasses and forbs were dried for 48 hr at 60°C, weighed, and all samples with >2 g of dry biomass were ground and analysed for chemistry.

In order to compare inflorescence and leaf Na levels, we additionally sampled all forbs that were flowering within each plot during monthly sampling in June, July and August. Forb sampling varied with availability of flowering plants, but when possible, we sampled the 10 leaves from 10 individual plants, selecting the fifth leaf from top. When 10 individual flowering plants were not available, the next leaves from top (e.g. sixth and seventh) were sampled from the same individuals. Inflorescences were taken haphazardly from as many flowering plants of the same species within each plot as possible, with the goal of collecting enough tissue for elemental chemistry (>2 g dried material). Samples of forb inflorescences and leaves were collected during the day, between 9:00 and 15:00. We note that whole inflorescences were used, in order to have sufficient tissue to conduct the same elemental chemistry quantification as was conducted on leaf tissue. However, this is only a rough estimate of nutrient availability to pollinators who primarily consume nectar and pollen. We choose to examine plant nutrient concentrations rather than total plant nutrients because insect herbivores in mixed to tallgrass prairie are more likely limited by nutrient concentrations than plant biomass (Whiles & Charlton, 2006), and because measuring total nutrient concentrations would require removal of flowering forbs from plots, potentially altering insect activity.

We collected soils for chemistry from each plot in June. We collected all plant and soil samples before the monthly Na application (i.e. they were collected one month after the last Na application). Soils were collected using a small hand trowel from depths of 1 to 10 cm.

Grass and forb samples from clip strips, inflorescences and leaves from flowering forbs, and soils were analysed for C and N using combustion analysis and for metals using hot plate digestion and inductively coupled plasma atomic emission spectroscopy by the Cornell Nutrient Analysis Laboratory (https://cnal.cals.cornell.edu/).

2.4 | Herbivory scoring

Our herbivory measurements followed a protocol created by the Nutrient Network (NutNet) where leaves are given a damage score of 0–4 for each of five herbivory categories: invertebrate chewing, invertebrate sucking or leaf mining, fungal damage and vertebrate damage (https://nutnet.org/index.php/methods/leaf-damage; James, 1971). Scores correspond to percent damage with **0** = no visible damage, **1** = 0> and <1% damage, **2** = 1> and <5% damage, **3** = 5> and <25% damage and **4** = >25% damage. Examples of leaf damage adapted from James (1971) referenced by this protocol and ourselves when scoring leafs for 1%, 5%, 25% and 50% damage levels for a grass and a forb are provided in Supporting Information (Figure S1). Vertebrate damage was rarely detected (present on scored forbs in 3.5% of plots), and thus we do not include it in our analyses.

Forb herbivory was scored on the 10 forb leaves collected alongside inflorescence collection. We scored grasses for herbivory at the end of the growing season in September. At each of the four sites, we identified a dominant grass species that was present in each of the 20 plots and scored 10 blades of grass from this species haphazardly sampled from 10 plants within each plot (800 total blades). The scored grass species consisted of *Bothriochloa laguroides* (SLL), *Andropogon gerardii* (KNZ), *Eragrostis trichodes* (PRP) and *Panicum oligosanthes* (NVP). For analysis of both grass and forb herbivory, the average of the herbivory score of the 10 leaves/species/plot was considered one replicate.

2.5 | Analyses

All analyses were conducted in program R version 4.0.3 (R Core Team, 2020). To first check whether plants and soils in Na+ plots differed from controls, we used Welch's *t*-test, a test that corrects for heterogeneity of variance, with each site to test for differences between soil, grass and forb Na concentrations, grass and forb biomass, and grass and forb concentrations of carbon (C), nitrogen (N), phosphorus (P) and potassium (K). Plant Na concentrations, in addition to plant N, P and K exhibited log-skewed distributions and were log10 transformed prior to all analyses. We measured other macronutrients in addition to plant Na to test whether Na fertilization altered other plant macronutrients (e.g. Wakeel, 2013).

Our analyses of the effects of Na addition on grass and forb herbivory differed due to differences in the data structure. Grass herbivory was conducted within the same month, and sampling was conducted evenly across all 20 plots within a site, albeit with different grass species at each site due to plant distributions. To examine the effects of Na addition on grass herbivory/damage, we calculated the Cohen's *D* effect size (Cohen, 1988) of each herbivory/ damage category (chewing invertebrates, leaf miners and fungal) and for each site. To calculate an overall effect of each damage category, we used mixed models, one for each damage type as the response variable, with a fixed variable treatment, and a random variable of site.

Forbs were collected and scored for herbivory when flowering during three monthly site visits, resulting in an uneven distribution of samples across treatments, species, sites and time. Additionally, following herbivory scoring on forbs, we measured their elemental chemistry. To test for the effect of leaf Na concentrations on forb herbivory/damage, we used mixed models for each of the three damage types (chewing invertebrates, leaf miners and fungal) as response variables, a fixed effect of leaf Na concentrations, and random variables of site, month and plant species. As the relationship between fungal damage and leaf Na appeared unimodal, we additionally included a second-order polynomial effect of leaf Na in the fungal damage model. Mixed models were conducted using the R package LME4 (Bates et al., 2015). To further investigate differences in the relationships between leaf Na concentrations and herbivory/damage across months and sites, we conduct additional individual regressions within each location and sampling time in a supplemental analysis.

To examine if forbs allocated higher concentrations of Na to flowers compared to leaves, we regressed the concentration of Na (ppm) in inflorescences over that in leaves for all species. We further examine the relationship between leaf and inflorescence Na concentrations for species with three or more samples of both leaf and inflorescence chemistry.

3 | RESULTS

3.1 | Soil sodium, plant sodium and plant biomass

In the control plots, the two sandier Nebraska sites on average had fourfold lower soil Na content (PRP: 19 ppm ± 1 *SE*; NVP: 25 ppm ± 2 *SE*) than the more clay-rich soils of the two southern sites (SLL: 96 ppm ± 11 *SE*; KNZ: 87 ppm ± 17 *SE*; Figure S2). Soil Na increased in soil treatment plots by an average of 1.6-fold across all sites (Figure S2; SLL: 158 ppm ± 19 *SE*; KNZ: 146 ppm ± 20 *SE*; PRP: 24 ppm ± 1 *SE*; NVP: 42 ppm ± 3 *SE*). Na fertilization did not affect above-ground grass or forb biomass (Figure S3A,B; Table 1A,B). Across all sites, in Na+ plots, grasses and forbs averaged Na concentrations ninefold and 17-fold higher than those in control plots (Figure S3C,D; Table 1C,D). Grass and forbs in the two

TABLE 1 Control and treatment means, replicate number (*n*), Welch's *t*-test statistic (*t*), degrees of freedom (*df*) and *p*-value (*p*) for differences from each site between control and Na fertilization for grass biomass (A), forb biomass (B), grass Na (C) and forb Na (D). Grass and forb Na were log transformed to reduce heteroskedasticity. The lower number of replicates at Platte River Prairie (PRP) was caused by the spread of poison ivy across the plots, preventing sampling. The lower replicate numbers for forb Na and SLL grass Na are due to too little plant biomass being collected in the plot to conduct elemental analysis. Boxplots of all comparisons are provided in Figure S3. Sites are listed from southern most (SLL) to northern most (NVP)

Site	Control mean	Treatment mean	Control *n*	Treatment *n*	*t*	*df*	*p*
(A) Grass biomass (g/m^2)							
SLL	245	43	10	10	−1.6	9.1	0.14
KNZ	167	198	10	10	1.2	16.1	0.23
PRP	256	269	7	6	0.1	9.4	0.91
NVP	137	137	10	10	0.01	17.1	0.99
(B) Forb biomass (g/m^2)							
SLL	29	14	10	10	−0.9	13.9	0.37
KNZ	28	35	10	10	0.4	13.7	0.68
PRP	87	136	7	6	0.9	9.6	0.4
NVP	14	24	10	10	0.8	11.7	0.43
(C) Grass Na (ppm)							
SLL	34	103	8	9	3.7	15	0.002
KNZ	12	65	10	10	4.9	14.4	<0.001
PRP	22	243	7	6	5.1	6.3	0.002
NVP	12	324	10	10	7.3	9	<0.001
(D) Forb Na (ppm)							
SLL	25	167	6	4	1.8	3.1	0.17
KNZ	25	366	8	6	3.6	6.3	0.01
PRP	42	752	7	6	8.5	10.2	<0.001
NVP	16	575	5	6	6	6.7	<0.001

sandy northern grasslands had higher Na uptake with Na addition (Figure S3C,D; Table 1C,D). However, Na addition had little to no effect on grass or forb concentrations of C, or the macronutrients N, P or K (Figures S4 and S5). Flowering forb species collected across months tended to have higher concentrations of Na in both leaves and inflorescences, with the caveat that due to the relative rarity of forbs, few forb species offered replicated samples across plots within a month or between months (Figure S6; Table S1).

3.2 | Grass damage

Mixed models across the four sites found leaf miner herbivory scores (Est. = 0.41, *SE* = 0.05, *df* = 75, $p < 0.001$), fungal damage (Est. = 0.46, *SE* = 0.06, *df* = 75, $p < 0.001$) and chewing herbivory (Est. = 0.16, *SE* = 0.05, *df* = 75, $p = 0.002$) on dominant grass species were higher in Na+ plots than control plots. Fungal damage was the most common leaf damage category on grasses (present on 95% of blades; mean score 1.65 ± 0.05 *SE*), with chewing herbivory (present on 25% of blades; mean score 0.37 ± 0.04 *SE*) and leaf miner herbivory (present on 36% of blades; mean score 0.36 ± 0.04 *SE*) both being less common. *Andropogon gerardii* at KNZ and *Dichanthelium oligosanthes* at NVP had overall higher herbivory than *Bothriochloa laguroides* at SLL and *Eragrostis trichodes* at PRP (Figure 1). Across the four sites, higher herbivory scores on grasses were driven by increased leaf miner and fungal damage. Grasses on control and Na+ plots generally did not differ in the amount of chewing damage, with the exception of higher chewing damage on *Dichanthelium oligosanthes* at NVP Na+ plots (Figure 1).

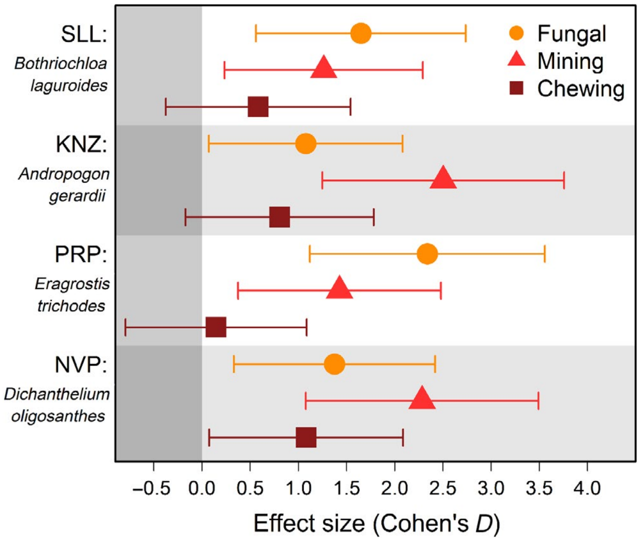


FIGURE 1 Effect sizes (Cohen's *D*) revealed little differences in chewing herbivory, but increased leaf miner herbivory and fungal damage on Na+ plots. Error bars represent 95% CI. Ten leaf blades were scores from each plot; the mean plot score for each damage type is used as independent replicates (200 blades scored per site; *n* = 10 for each treatment within each site). Sites are listed from southern most (SLL) to northern most (NVP)

3.3 | Forb damage

Across all sampled leaves, 94% exhibited herbivory or fungal damage. Fungal damage was the most common leaf damage category on forbs (present on 91% of leaves; mean score 0.95 ± 0.06 *SE*), followed by chewing herbivory (present 68% of leaves; mean score 0.57 ± 0.06 *SE*) and leaf miner herbivory (present on 76% of leaves; mean score 0.51 ± 0.05 *SE*).

Chewing herbivory scores increased with leaf Na in our overall mixed model with included month, site and plant species as random variables (Figure 2a; Est. = 0.389 ± 0.086 *SE*, *df* = 124.9, $p < 0.001$). Within sites, chewing herbivory scores on forbs increased at our most well-sampled site, PRP. No such relationship was found at other sites (Figure S7A). Over time, chewing herbivory increased with leaf Na in June and August, but not in July (Figure S8A). Leaf miner herbivory scores were not correlated with leaf Na across all samples (Figure 2b; Est. = 0.014 ± 0.066 *SE*, *df* = 115.5, $p = 0.83$), nor at any individual site (Figure S7B) or within any sampling month (Figure S8B). Fungal damage scores had a unimodal relationship with leaf Na across all samples (Figure 2c; first-order polynomial term: Est. = 2.012 ± 0.55 *SE*, *df* = 128.6, $p < 0.001$; second-order polynomial term: Est. = −1.248 ± 0.585 *SE*, *df* = 118.2, $p = 0.033$). This unimodal relationship was driven by four plant samples with the highest leaf Na concentrations (all samples with >1,100 ppm Na), all in the genus *Asclepias* and comprising one sample of *Asclepias syriaca* and three of *Asclepias viridis* (Figure 2). Split by sampling site, fungal damage exhibited a unimodal relationship with leaf Na at KNZ, a positive relationship at PRP and no relationship at SLL and NVP (Figure S7C). Split by month, fungal damage over leaf Na was unimodal in June and July, but not in August (Figure S8C).

3.4 | Floral versus foliar chemistry

Interspecific variation in Na content of forb inflorescences (*n* = 121 plots) and leaves (*n* = 138 plots) regularly varied 1,000-fold. Na in leaves in control plots (*n* = 71; mean: 69 ppm ± 40 *SE*) varied from 4 ppm (*Helianthus pauciflorus*) to 2,876 ppm (*Asclepias viridis*). Leaves in Na+ plots (*n* = 67; mean: 390 ppm ± 143 *SE*) varied from 9 ppm (*Psoralea tenuiflora*) to 9,353 ppm (*Asclepias viridis*).

Inflorescence Na in control plots (*n* = 62; mean: 98 ppm ± 26 *SE*) varied from 5 ppm (*Solidago missouriensis*) to 902 ppm (*Asclepias viridis*). Inflorescence in Na+ plots (*n* = 59; mean: 178 ppm ± 38 *SE*) varied from 7 ppm (*Achillea millefolium*) to 1,316 ppm (also *Achillea millefolium*).

The overall relationship across all sites, months and plant species between inflorescence and leaf Na concentrations had a slope lower than a 1:1 ratio (Est. = 0.546 ± 0.066SE, $R^2 = 0.37$, $F_{1,117} = 68$, $p < 0.001$), with no general support for our hypothesis that inflorescence tissues consistently contain higher Na concentrations than leaves (Figure 3). However, several species tended to have higher inflorescence than leaf Na, notably *Amorpha canescens* (*n* = 3, average inflorescence to leaf Na ppm ratio [I:L] = 6.8), *Calylophus*

FIGURE 2 Herbivory on forbs across all sites, sampling period, treatments and plant species are regressed over Na concentrations (ppm) of leaves for chewing herbivory (a), leaf miner herbivory (b) and fungal damage (c). Each point represents the mean of 10 leaves collected and scored from each plant species within a site and sampling period. Forb herbivory split by site and sampling date are depicted in Figures S7 and S8 respectively

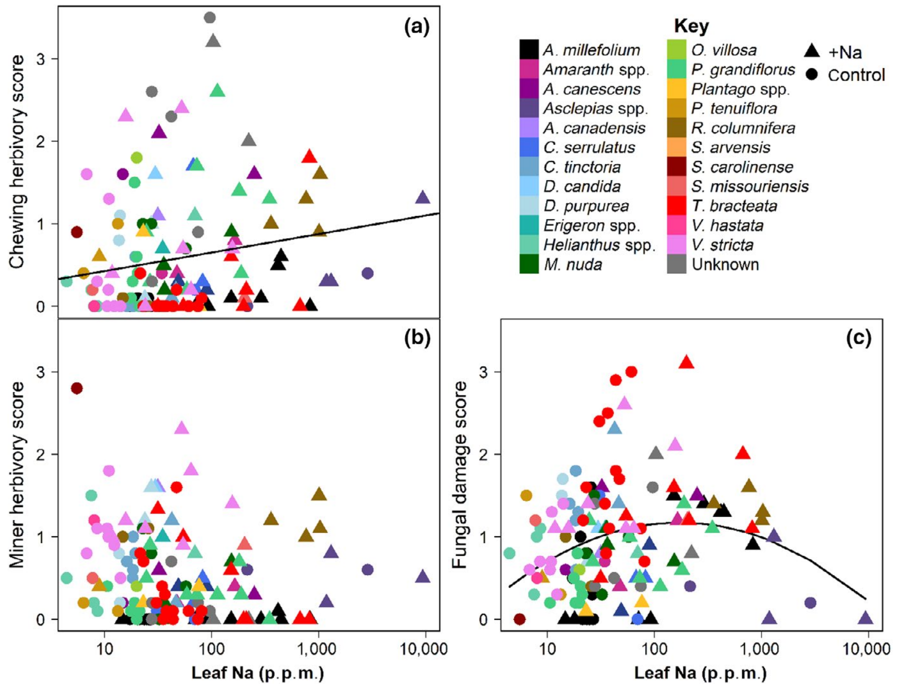
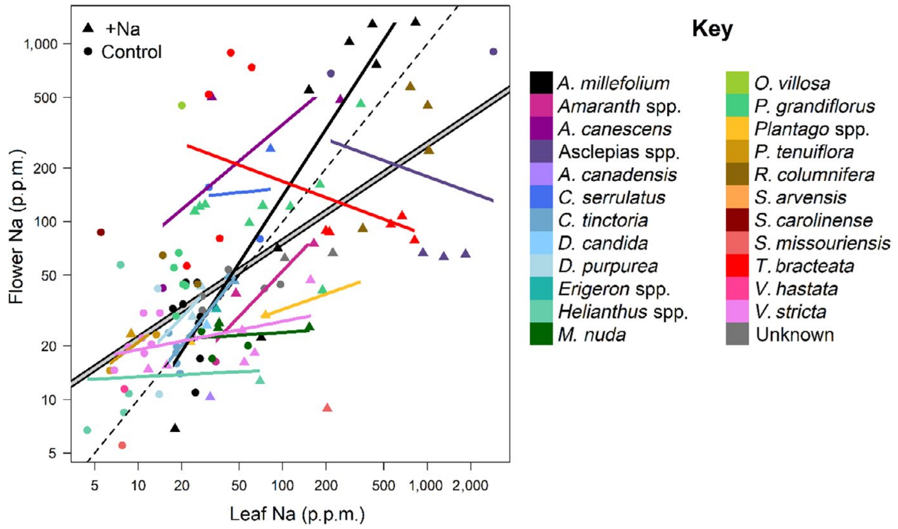


FIGURE 3 Inflorescence (Flower) Na (ppm) plotted over leaf Na (ppm) for all samples. Dashed line represents the 1:1 ratio of inflorescence and leaf Na. The thick grey line with a black edge denotes the overall regression relationship for all species. For plant species with three or more samples, we plot the regression line of the relationship between inflorescence and leaf Na, using colour to denote plant species



serrulatus ($n = 3$; I:L = 3.1), *Penstemon grandiflorus* ($n = 14$; I:L = 2.3) and *Psoralea tenuiflora* ($n = 3$; I:L = 2.2). With the exception of one species (*Achillea millefolium*), increases in leaf Na tended to reduce the ratio of Na in inflorescences to leaves (Figure 3).

4 | DISCUSSION

We document support for the hypothesis that plants with higher Na concentrations suffer increased consumption by both insect herbivores and fungal pathogens. Na-fertilized grasses had both higher leaf miner herbivory and more fungal damage compared to grasses in control plots. In forbs, higher leaf Na led to increased chewing herbivore and fungal damage. Across all sampled plants, we did not find strong evidence for our second hypothesis, that plants accumulate Na in flowers relative to leaves to attract mutualists. However, with the caveat of low sample sizes, some plant species had up to 22-fold Na in inflorescences compared to leaves, suggesting interspecific differences in which some species allocate Na to attract pollinators. In other plant species where the ratio of Na concentrations in leaves and inflorescences is close to 1, irrespective of overall Na content, the correlation between leaf and inflorescence Na presents a potential trade-off for plants. A ratio of one implies no Na allocation to particular plant tissues; thus increased Na levels are expected to increase both herbivory and pollination.

Increased herbivory with increasing Na levels was a consistent response across both grasses and forbs. The increase in fungal damage with increased foliar Na in both grasses and forbs is of particular interest, as we know little about the use of Na by fungi. Foliar fungal damage in our study was common, occurring on over 90% of both forb and grass leaves. In comparison, a survey of grassland plants in the Swiss alps found 24% of leaves had fungal damage (Fischer et al., 2012). Na may also interfere with the uptake of other nutrients in plants (Kronzucker et al., 2013), potentially changing foliar nutrient composition or reducing plant's ability to defend themselves in ways that favour fungal pathogens. There is mixed evidence on the role of Na shortfall constraining fungi metabolism (Camenzind et al., 2018; China et al., 2018; Cromack et al., 1977). While our results suggest a benefit of Na fertilization to foliar fungal pathogens, the mechanism causing this response remains unclear and would be a fruitful avenue for future studies.

Grasses exhibited stronger damage responses than forbs from leaf miners and fungal pathogens. That difference likely arises from our sampling of one species of grass on all 20 plots, compared to our opportunistic sampling of forbs on the subset of plots where and when we found them in flower. Heterogeneity in damage rates across herbivore types also likely arose from the natural history of the interactions. For example, the lack of enhanced grass chewing damage to Na addition may be due to the difficulty of detection, as chewers may sever the entire grass blade. Moreover, the lack of a relationship between increased foliar Na and leaf miner damage may result from their cloistered feeding within leaves, reducing their ability to select and accumulate on high Na leaves.

The effects of increased Na inputs on plant, animal and fungal responses can be driven by both biotic and abiotic context. For example, herbivore attraction to such Na fertilization can be enhanced by the availability of macronutrients like N and P (Borer et al., 2019; Kaspari et al., 2017; Prather, Laws, et al., 2018; Prather et al., 2020). Additionally, soil Na content can alter rhizobacteria community composition (Astorga-Eló et al., 2020), which in turn can alter plant nutrient uptake and growth. But even with the variety of species and their chemical composition, chewing herbivory and fungal damage increased with forb foliar Na concentrations.

In contrast to our prediction, we did not find strong evidence that forb species allocate additional Na to flowers relative to leaves. Nectar feeders are likely to experience high demand for Na, as through consuming a liquid diet, they must continuously void Na and other electrolytes. Hummingbirds are estimated to replace 14% of their bodies' Na daily (Hiebert & Calder, 1983). Butterflies exhibit puddling behaviour to meet Na needs and will preferentially select puddling sites with higher Na (Arms et al., 1974) and have adapted ways of quickly concentrating ingested Na (Smedley & Eisner, 1995). It is possible that many plants lack the ability to allocate Na to particular tissue or that plant species have variable strategies, preventing detection of Na uptake pattern in our community-level study. Additionally, plants have alternate means of reducing the cost of Na uptake. For example, some plant species are known to store Na in old leaves to reduce the cost of herbivory (Bailey & Scholes, 1997), and the genus with the highest Na levels in our study, like *Asclepias*, may counter the resulting attractiveness to herbivores via a variety of chemical defences (Züst et al., 2015). While more work is needed to examine the strategies of individual plant species, our results suggest more ways for anthropogenic salt—on roads and irrigation water—to stress plants than benefit them.

The biogeography of Na can be added to a list of factors known to influence the rates of herbivory and pathogen damage including plant dominance (Mitchell et al., 2002), productivity (Haddad et al., 2000), diversity (Woodcock & Pywell, 2010), production of secondary compounds (Glendinning, 2002) and plant quality (Lind et al., 2017). The study goes beyond previous work demonstrating Na attracts insects in forests (Clay et al., 2014; Kaspari et al., 2014) and grasslands (Kaspari et al., 2020; Prather, Laws, et al., 2018; Welti, Kuczynski, et al., 2020; Welti et al., 2019) in demonstrating that Na fertilization results in a cost for plants, namely increased herbivory. Due to increased pathogen damage and herbivory of certain plant species, long-term Na fertilization is likely to lead to changes in plant community composition, with cascading effects for all grassland species and ecosystem function (Borer et al., 2014; Bui, 2013; Griffith et al., 2017). Human activities continue to alter the geography of terrestrial Na availability, applying it to crop fields via saline irrigation water, roads via road salt in colder climates (Qadir et al., 2014) and as a result of climate change, increasing Na inputs from sea to land via an altered hydrological cycle and rising sea levels (Daliakopoulos et al., 2016). At the same time, increased $p\text{CO}_2$ is expected to lower foliar Na concentrations at the expense of increased plant carbohydrates in remaining natural areas (Welti, Roeder, et al., 2020). Combined, these drivers predict crop land, coastal areas and roadsides of northern climates will become saltier while inland natural areas are the least likely to have increasing Na inputs. While further work is needed on how the expanding gradient of Na availability will affect ecological systems, our results suggest that moderate increases in Na availability will result in increased herbivory rates, and the abundance of herbivores and plant fungal pathogens.

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AUTHORS' CONTRIBUTIONS

Both the authors designed the study and conducted fieldwork; E.A.R.W. analysed the data and wrote the first draft; M.K. significantly contributed to revisions.

DATA AVAILABILITY STATEMENT

Leaf and inflorescence tissue chemistry, plant herbivory scores, plant biomass and soil sodium content are available from the Dryad

Digital Repository https://doi.org/10.5061/dryad.37pvmcvk4 (Welti & Kaspari, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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