Electrolytes on the prairie: How urine-like additions of Na and K shape the dynamics of a grassland food web

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Abstract
The electrolytes Na and K both function to maintain water balance and membrane potential. However, these elements work differently in plants—where K is the primary electrolyte—than in animals—where ATPases require a balanced supply of Na and K. Here, we use monthly factorial additions of Na and K to simulate bovine urine inputs and explore how these electrolytes ramify through a prairie food web. Against a seasonal trend of increasing grass biomass and decreasing water and elemental tissue concentrations, +K and +Na plots boosted water content and, when added together, plant biomass. Compared to control plots, +Na and +K plots increased element concentrations in above-ground plant tissue early in summer and decreased them in September. Simultaneously, invertebrate abundance on Na and K additions were sequentially higher and lower than control plots from June to September and were most suppressed when grass was most nutrient rich. K was the more effective plant electrolyte, but Na frequently promoted similar changes in grass ionomes. The soluble/leachable ions of Na and K showed significant ability to shape plant growth, water content, and the 15-element ionome, with consequences for higher trophic levels. Grasslands with high inputs of Na and K—via large mammal grazers or coastal aerosol deposition—likely enhance the ability of plants to adjust their above-ground ionomes, with dramatic consequences for the distribution of invertebrate consumers.

KEYWORDS
abundance, fertilization experiment, food web, grassland, ionomics, potassium, resorption, sodium, translocation

INTRODUCTION
The ca. 25 elements required to build life serve different metabolic roles (Frausto da Silva & Williams, 2001; Sterner & Elser, 2002):

1. Carbon (C) with oxygen and hydrogen (OH) provide the carbohydrates (CHOs) that serve both as skeleton and energy source;

2. Nitrogen (N) is a key component of enzymes;

3. Phosphorus (P) contributes to energetic currency and the ribosomes that build cells and tissues; and

4. Metals like zinc, copper, and iron (Zn, Cu, Fe) form the center of enzymes that catalyze chemical reactions.

Potassium (K) and sodium (Na) are two more elements in the ionome (defined here as the vector of essential...
elements found in, or supplying, living tissue, Salt et al., 2008) that play yet another key role as soluble, ionic electrolytes: regulating water balance and maintaining cell integrity (Kaspari, 2020; Sardans & Peñuelas, 2015). Electrolytes are also relatively difficult to store in tissues, easy to leach from soils and—as in all essential elements—shortfall causes pathology (Marschner, 1995; McDowell, 2003). We know much about how N, P, and CHOs regulate ecological abundance (Power, 1992; Stephens & Krebs, 1986; Sterner & Elser, 2002). Electrolytes are, by comparison, understudied (Kaspari, 2021; Sardans & Peñuelas, 2015). Toward a remedy, we explore how electrolyte availability shapes the seasonal ontogeny of a grassland food web.

K and Na in plants

K and Na function differently in plants and animals. K is the chief electrolyte of plants (Marschner, 1995). Plants with more K can grow taller, support more erect leaves, and translocate more minerals from the soil with corresponding higher levels of photosynthesis (De Boer, 1999). Much of what ecologists know about the function of K comes from agronomists (e.g., Ball et al., 2001). For example, when K availability was suppressed in maize, the production of a variety of sugars tripled (Carvalhais et al., 2011) and 4 of 8 grasslands supplemented with K generated more plant biomass (Sardans & Peñuelas, 2015). Adding K should catalyze demand for other essential elements, since relaxing transport costs and increasing access to solar energy can increase demand for the N, P, and other elements needed to build photosynthetic machinery (Jeyasingh et al., 2020; Kaspari, 2021).

In contrast, when Na is metabolically required by plants it is in trace amounts. Instead, Na is generally treated as a toxin (reviewed in Kaspari, 2020). The key known exception (Kronzucker et al., 2013; Subbarao et al., 2003) is in K-poor soils, when Na can substitute for K as an electrolyte. Given Na’s 1000-fold variation in grassland plant tissue (Borer et al., 2019; Welti et al., 2019) and its ability to subsequently attract herbivores to feed on plant tissues and exudates (Welti & Kaspari, 2021) plants may modify their Na supplies to attract mutualists and dissuade enemies (Kaspari, 2020).

K and Na in animals

In animal tissues, Na and K work in tandem as ATPases swap out Na for K across cell membranes (Frausto da Silva & Williams, 2001; Kaspari, 2020). This scenario of co-limitation by Na and K in animals—while plant function is primarily limited only by K—sets up several challenges to consumers.

The first challenge is the ubiquity of Na shortfall in animal populations. This is especially so for herbivores in inland ecosystems far from deposition of oceanic aerosols (Arms et al., 1974; Belovsky, 1978; Blair-West et al., 1968; Borer et al., 2019; Kaspari, 2020; Snell-Rood et al., 2014; Welti et al., 2019). Especially low levels of plant sodium can cause declines in insect abundance (Prather, Laws, et al., 2018; Welti et al., 2019), activity (Prather, Roeder, et al., 2018; Clay et al., 2014), and herbivory (Welti & Kaspari, 2021).

Second, the tandem nature of Na–K ATPases highlights the perils of both shortfalls and imbalance. When the seasonal spring flush of vegetation concentrates K in plant tissue (without compensatory increases in Na) K accumulates in herbivore tissues causing tetany and, in extreme cases, death (Denton, 1982; Jones & Hanson, 1985, for this reason, KCl has been the final poison in executioner’s drug cocktails). This need for balance is reflected in the seasonal foraging of honeybees, which, while always preferring Na, avoid supplemental K when K-rich pollen is abundant (Bonoan et al., 2017).

Third, increases in K that promote plant growth and nutrient transport can also provide more options in combatting herbivores. Fertilization of crops with K can cause “Nutrient Dilution by Growth” (sensu Marschner, 1995) when CHO-rich support tissue dilutes concentrations of other elements like nitrogen (Ball et al., 2001). K supplies also allow plants to better transport plant metabolites; if so, fertilizing with K could further decrease plant palatability by allowing plants to concentrate metabolites associated with plant defense. For example, K-rich plants appear more likely to attract ant defenders (Kaspari et al., 2020) that use K to transport amino acids and sugars to attract ants that, in turn, discourage herbivores (Beattie, 1985).

Loss and gain of K and Na in nature

Both K and Na exist in tissues as soluble ions that are easily lost from plants (where precipitation leaches K from both leaves and soils, Sardans & Peñuelas, 2015) and from animals, where they are a key component of urine (Kaspari, 2021; Steinauer & Collins, 1995). So, unlike the constitutive elements N and P that are easily stored, plants and animals must continuously replenish their K and Na supply. In terrestrial ecosystems, those supplies include large scale Na and K inputs via aerosol deposition (K deposition, for example, varies from...
0.07 to 100 kg ha⁻¹ year⁻¹ (NADP, 2007; Sardans & Peñuelas, 2015)). At smaller grains, animal urine supplies patches of electrolytes from mm² in size from insects to m² sources from herds of ungulates, rock outcrops, and clay licks (Jones & Hanson, 1985; Kaspari, 2020). Indeed, herbivores often “excrete where they eat,” forming dependable Na and K rich grazing lawns (Knapp et al., 1999; McNaughton et al., 1997; Steinauer & Collins, 1995) that support higher densities of some grazing insects (Moran, 2014; Ozment et al., 2021). Plants and animals both create, and then exploit, patches of electrolytes.

Given their unique functional role relative to the well-documented bottom-up effects of N and P on food webs (Lind et al., 2017; Prather et al., 2020; Prather, Laws, et al. 2018) we focus here on how the co-availability of Na and K ramifies through plants to invertebrate consumers. We explore the effect of monthly additions of Na and K—in quantities found in bovine urine—to 49 m² plots of a Great Plains tallgrass prairie, Konza LTER, a site where Na shortfall limits the abundance of insect herbivores (Prather et al., 2021; Welti et al., 2019). We examine the effect of K and Na on plant growth, moisture content, and ionome, and the subsequent effect on the abundance of the invertebrate food web. We test the hypotheses that electrolytes enhance the translocation of the ionome, limit biomass and water content, and that these changes in turn increase the abundance of invertebrates.

**METHODS**

Konza Prairie (KNZ) is a 3487-ha tallgrass prairie and Long-Term Ecological Research (LTER) site in northeast Kansas, USA (39°05’ N, 96°25’ W). In the 2019 growing season, we worked on a watershed (named K1B) which was ungrazed by large ungulates, is burned annually in May, and dominated by the grasses *Sorghastrum nutans* and *Andropogon gerardii*. We used plots initially set up in 2018: 20, 49 m² (7 × 7 m²) plots in two rows of 10 plots, 10 m apart (Appendix S1: Figure S1). In the previous experiment in 2018, we simulated the deposition of the Na content of bovine urine as per (Steinauer & Collins, 1995) with May–August monthly applications of 59 g NaCl as part of an experiment where half the plots received a +Na treatment (59 g NaCl in 3.8 L of tap water) in a stratified design (see Prather et al., 2021). Sampling in 2019 using protocols described below revealed weak evidence for legacy effects on the 10 plots that received treatment in 2018, with clip plots for plant Na ppm 38% lower than 2019 controls plots (Generalized Linear model $p = 0.06$, see Figure 1).

In 2019, we created a factorial application of Na and K, again using concentrations simulating cow urine, generating five plots each of +Na, +K, +NaK, and controls. The 10 plots that had received NaCl in 2018 again received the 59 g of NaCl treatment (Appendix S1: Figure S1). The 10 plots receiving the +K or +Na +K treatment each received both 343 g KCl and 333 g KHCO₃. All treatments were applied dry and scattered evenly by hand. Treatments were applied mid-May then monthly through mid-August. All plant and animal sampling in a given month occurred before that month’s fertilization.

**Plant monitoring**

Plant height, water content, and chemistry were sampled throughout the experiment. From mid-May through mid-September, we sampled plant height using a disc pasture meter (Bransby & Tainton, 1977). A disc pasture meter measures plant height by recording the resting height of a disc supported by the vegetation after being dropped from a set height of 2 m. From a central 2 × 2 m² plot, we took four disc pasture meter readings, one per 1 m².

We analyzed plant ionomes monthly from mid-May through mid-September. In May, due to the low stature and indistinct taxonomy of young grass, we used a 0.1 × 1 m clip strip from a wire frame randomly located in the plot. We clipped plants down to the soil surface, discarding dead litter. In June we haphazardly roamed each plot clipping individuals of the dominant grass *Andropogon gerardii*, until we achieved ca. 5 g wet weight. In July, August, and September, we did the same for the co-dominant *Sorghastrum nutans*.

Samples were weighed, dried at 60°C to a constant weight, then re-weighed to estimate water content, before being shipped Cornell Nutrient Analysis Laboratory ([https://cnal.cals.cornell.edu/](https://cnal.cals.cornell.edu/)) for analysis. We present results ppm elemental chemistry for 15 (B, Ca, Cr, Cu, Fe, K, Mg, Mn, Mo, Na, P, S, Si, and Zn) using hot plate digestion and inductively coupled plasma atomic emission spectroscopy. N was measured with a CN elemental analyzer. We used reviews of plant (Sharma, 2006b) and animal (McDowell, 2003) ionomics to classify elements as universally metabolically essential for plants and animals (C, N, K, Ca, P, Mg, S, Fe, Mn, B, Zn, Cu, Mo) or metabolically essential for just animals (Si, Na, Cr).

**Invertebrate monitoring**

From June through September, and before each month’s fertilization, we sampled invertebrates. We used a
vacuum sampler (henceforth, BugVac, Stewart & Wright, 1995) for 60 seconds for each central 1 \times 1 \text{ m}^2 plot. Invertebrates were put on ice packs in the field and kept frozen until sorted. We counted all invertebrates to record abundance (number m\(^{-2}\)).

**Statistics**

We used SAS 9.4 (SAS_Institute, 2013) for all statistical analysis combining least mean squares regression (PROC REG) and Generalized Linear models (GLMs, PROC
GLIMMIX, using a Gaussian distribution) for inferential statistics and effect sizes (Cohen’s d, Cohen, 1988) to quantify the magnitude of treatment effects. We started using least squares regression to describe the seasonal trajectories of key response variables on control plots. For plants, we quantified height (cm), moisture (%-H2O), and the 15-element plant ionome (ppm); for animals, we quantified abundance.

Next, we used GLM combined with LSMeans (which estimate the marginal means for each effect over a balanced population, SAS Institute, 2013) to assign p-values to distributions of effect sizes and evaluate the three treatments (+Na, +NaK, +K) relative to controls, and month (6, 7, 8, 9 as a categorical variable) as main effects and their interactions. For invertebrates, we added plot (1–20) to account for significant variance as a random factor.

We repeated plant analyses (Appendix S1: Tables S1, S2a, S3a, S4a) using only the July–September Sorghastrum samples to explore if those results were consistent with sampling that incorporated May clip plots, and June samples of Andropogon. All data are available online at Kaspari et al. (2022).

RESULTS

Seasonal dynamics on the five control plots

On the five 7 × 7 m² control plots, plant biomass increased while water content and plant ionome concentrations decreased with month accounting for ca. 2/3 of the seasonal variation in both (Figure 1, Appendix S1: Table S1). Plant height increased five-fold while the moisture content of dominant grasses (Andropogon gerardii in June, Sorghastrum nutans in the remaining months) declined by 12% over the season (Figure 1b,c, Appendix S1: Table S1). Nutrient dilution by growth was common: tissue concentrations of universally essential common elements all declined 10- to 100-fold, accounting for 45% to 93% of seasonal variation (Figure 1d, Appendix S1: Table S1); 4 of 6 universally essential microelements (all but Mn and B) declined over the season, accounting for less (17%–53%) of the temporal variation (Figure 1e). Of the three animal-only essential elements, only one, Na, declined in plant tissue over the season (Figure 1f).

Invertebrate abundance, measured on central plots with a BugVac, grew increasingly variable from June through September (Figure 1a; Appendix S1: Table S1) and did not significantly vary with month for herbivorous insects ($R^2 = 0.0$).

Experimental responses of plant height and moisture

Plant height and moisture content responded synergistically to factorial fertilization with Na and K (Figure 2; Appendix S1: Table S2). Although there was a strong effect of time that was consistent across all three treatments ($p < 0.0001, \text{all } \text{trt} \times \text{time interactions NS}$), by themselves, Na and K fertilization generated modest to no effect on plant height (Figure 2, all $|\text{Cohen’s } d| < 1$). When combined, however, Na and K generated increases in plant height of ca. 1–2 SD above control plots (Na × K interaction: $p = 0.005$).

The moisture content of grasses increased with both Na and K fertilization by ca. 2% (Figure 2; Appendix S1: Table S2, +Na: $p = 0.001$, +K: $p < 0.0001$). Na and K combined additively (Na × K interaction: NS) with NaK treatments increasing moisture content by ca. 4%.

Experimental responses of grass ionomes

Na and K fertilization had differing effects on the Na and K ppm of sampled grasses (Figure 2; Appendix S1: Table S3). K ppm in grass tissue increased on +K plots from 0.5 to 1.3 SD (K and month effects: $p < 0.0001$); +Na plots had no such effect (Na and K × Na interaction: NS). Na ppm in grass tissue varied from suppressed relative to controls in June to enhancement in September (Figure 2, −0.88 to 1.05 SD), with no net effect ($p = 0.88$, Appendix S1: Table S3). +K plots strongly suppressed Na ppm in all months but July, a response ameliorated on +NaK plots (Na × K × time interaction: $p = 0.03$). In sum, +K plots were consistently richer in plant K and mostly poorer in Na, but +Na plots did not have similar effects on plant Na.

The macronutrients N and P responded differently to factorial Na K fertilization (Figure 2, Appendix S1: Table S3). +K plots enhanced N in plant tissue from June to August, N in plant tissue was up to 1.9 SD higher on +K plots ($p < 0.04$), and all three treatments showed N peaking at >1 SD in July with a negative effect at the end of the season (month effect: $p < 0.0001$). Treatment effects on P, in contrast, were not apparent, although P in tissue on treatment plots dipped below controls by ca. 1–2 SDs by September (month effect: $p < 0.0001$).

The entire grass ionomes (minus Na and K, Figure 2, Appendix S1: Table S4) behaved similarly across the three fertilization treatments (trt: $p = 0.75$, trt × month: $p = 0.76$) but varied conspicuously over the season (month: $p = 0.0001$). In June, 1 month after fertilization began, +K plots generated grass ionomes indistinguishable...
**FIGURE 2** Response of plant ionome, height, and water content, and invertebrate abundance to factorial Na and K fertilization (Cohen’s $d$, SD). Monthly fertilization began in May and continued through August ($n = 5$ per treatment and control). Gray regions represent decreases relative to controls (negative effect sizes), white regions represent increases (positive effect sizes). Bottom: all elements in the ionome except Na and K in response to fertilization (see Appendix S1: Figure S2 for identification), and the LSMean and SE of these effect sizes. Lower middle: effect sizes of two macronutrients, N and P and manipulated elements Na and K to factorial fertilization. Upper middle: effect sizes of plant height (measured by pasture meter) and water content. Top: effect sizes of arthropod number from central m² plot measured by BugVac.
from controls (Generalized Linear model LSmean of Cohen’s $d = 0.14$ SD, $p = 0.67$); +Na plots suppressed grass ionomes ($-0.67$ SD, $p = 0.04$) with +NaK plots intermediate ($-0.50$ SD, $p = 0.13$). In July, there was strong evidence for richer ionomes on treatment plots relative to controls (Cohen’s $d$’s for +K, +Na, +NaK > 0.77, $p > 0.02$). By August and September, all three treatments yielded ionomes that were indistinguishable from controls (Cohen’s $d$’s < 0.18, $p > 0.18$).

To look for patterns among elements, we identified strong effects of fertilization (defined by Cohen (1988) as $d > 1.0$ SD) across the 15 elements and 4 months (Figure 3). Adding an electrolyte was 2.2× more likely to strongly increase an element in grass tissue; 71% of those increases happened in June/July, while 88% of significant declines occurred in August/September. July was responsible for most of the increases and none of the decreases. Of the electrolyte treatments, those with K were most effective in changing the plant ionome, except in July. The majority of strong responses (discounting the elements Na and K added as treatments) included increases in Mn, Zn, and N/Cu, and decreases in (animal essential) Cr, and B (only in September).

### Experimental responses of invertebrates

Invertebrates on treatment plots generated alternating increases and decreases relative to controls (Figure 2, Appendix S1: Table S5, month effects: $p < 0.0001$) with a three-way interaction suggesting a dampening effect when Na and K were combined. +K plots progressed from abundances $+0.5$ SD above controls, to $-0.9$ SD below in July, back to $+0.53$ SD in August, and down to $-0.23$ SD below controls in September. +Na responses were similar but more extreme (+1.17 to $-1.4$ to $+0.98$ to $-1.11$ SD). A three-way interaction (Na × K × month: $p = 0.03$) suggested a flattening of the oscillation until a strong decline in September ($0.32$ to $-0.62$ to 0.13 to $-0.94$ SD).

### DISCUSSION

The food webs of temperate grasslands—among the most common biomes on Earth (Hoekstra et al., 2005)—have a seasonal ontogeny (Figure 1):

1. in spring, perennial plants produce new nutrient-rich growth;
2. as vegetation grows and matures, the plant tissue is depleted in nutrients and moisture;
3. after producing flowers and seeds, plants resorb essential elements (Vergutz et al., 2012).

In an inland tallgrass prairie, we show that electrolytes K and Na enhance seasonal patterns of growth, moisture, and the translocation of nutrients. Our results suggest that

| trt | month | K   | Na  | N   | P   | B   | Ca  | Cr  | Cu  | Fe  | Mg  | Mn  | Mo  | S   | Si  | Zn  | Increases | Decreases |
|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|-----------|
| K   | 6     | 1.1 | $0.3$ | 0.7 | $-0.1$ | $-0.6$ | $-0.8$ | 0.4 | 1.2 | 0.3 | $-0.6$ | 1.5 | $-0.1$ | $-0.1$ | $-0.3$ | 0.3 | 3          | 1          |
| K   | 7     | 1.0 | 0.3 | 1.9 | 0.2 | $-0.6$ | $-0.5$ | 0.1 | 1.2 | 1.0 | 0.4 | 1.3 | 0.7 | 2.6 | 0.7 | 0.9 | 6          | 0          |
| K   | 8     | 0.5 | $-0.9$ | 0.5 | $-0.8$ | $-0.4$ | $-1.2$ | $-0.1$ | 0.1 | $-0.3$ | $-0.7$ | 1.3 | $-1.6$ | 0.1 | $-1.0$ | 1.4 | 2          | 2          |
| K   | 9     | 1.3 | $-2.0$ | $-0.3$ | $-1.5$ | $-1.5$ | $-0.7$ | $-0.2$ | $-0.3$ | $-0.3$ | $-0.7$ | 2.4 | $-1.0$ | $-0.5$ | $-0.7$ | 1.5 | 3          | 4          |

| trt | month | K   | Na  | N   | P   | B   | Ca  | Cr  | Cu  | Fe  | Mg  | Mn  | Mo  | S   | Si  | Zn  | Increases | Decreases |
|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|-----------|
| Na  | 6     | 0.8 | $-0.9$ | 0.5 | $-0.3$ | $-0.6$ | $-1.5$ | 0.6 | $-0.1$ | $-0.4$ | 1.1 | $-0.7$ | $-0.1$ | $-0.1$ | 0.1 | 0          | 1          |
| Na  | 7     | 0.8 | 0.7 | 1.6 | 0.8 | 0.0 | 0.8 | 0.3 | 2.1 | 1.1 | 0.2 | 1.2 | 0.3 | 1.6 | 0.4 | 1.3 | 6          | 0          |
| Na  | 8     | $-0.1$ | $-0.2$ | 0.3 | $-0.3$ | 0.0 | $-1.1$ | $-1.2$ | 0.4 | $-1.5$ | 0.5 | 0.7 | $-0.6$ | 0.2 | $-0.2$ | 0.5 | 0          | 3          |
| Na  | 9     | $-0.1$ | $-1.1$ | $-0.5$ | $-0.8$ | $-1.8$ | $-0.1$ | $-0.4$ | $-0.2$ | $-0.5$ | 0.3 | 1.2 | $-0.4$ | $-0.3$ | $-0.9$ | 0.2 | 2          | 2          |

| trt | month | K   | Na  | N   | P   | B   | Ca  | Cr  | Cu  | Fe  | Mg  | Mn  | Mo  | S   | Si  | Zn  | Increases | Decreases |
|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|-----------|
| NaK | 6     | 2.0 | $-0.8$ | 1.2 | 0.9 | $-0.8$ | $-0.9$ | 0.7 | 1.3 | $-0.7$ | $-0.5$ | 2.7 | $-0.6$ | 0.3 | $-0.4$ | 0.3 | 3          | 0          |
| NaK | 7     | 1.1 | 0.0 | 1.9 | 0.3 | $-0.1$ | $-0.5$ | $-0.8$ | 1.1 | 1.1 | 1.1 | 1.6 | 0.3 | 1.0 | 0.3 | 1.4 | 0.8 | 1.2 | 9          | 0          |
| NaK | 8     | $-0.7$ | $-0.1$ | 0.6 | 0.1 | $-0.5$ | $-0.8$ | $-1.1$ | 0.7 | $-1.3$ | $-0.9$ | 1.3 | $-1.0$ | 0.3 | $-0.7$ | 1.3 | 1          | 2          |
| NaK | 9     | $-1.2$ | $-0.6$ | $-0.9$ | $-1.0$ | $-0.4$ | $-0.3$ | 0.0 | $-0.5$ | $-1.7$ | 1.4 | $-1.0$ | $-0.8$ | 0.0 | 0.1 | 0.3 | 3          | 2          |

**FIGURE 3** Summary of strong (Cohen’s $d > 1.0$) responses of elements in grass tissue to the factorial NaK fertilization over 4 months, with green shading increases and yellow shading decreases.
K—and to a surprising extent, Na—co-limit and empower grassland plants to tighten their nutrient economy—filling growing grasses with essential metabolites in June and July and sequestering them below-ground in August and September as the growing season concludes. These nutrients go on to generate nonlinear dynamics in invertebrate abundance, with abundance alternating between strong increases and decreases (particularly for Na) that are buffered when Na and K are added together. Electrolytes that are naturally supplemented as aerosols (NADP, 2007) and experimentally added here in levels simulating monthly visits by large grazers (Kaspari, 2021; Steinauer & Collins, 1995), co-limit and ramify through this tallgrass prairie food web.

Electrolytes facilitate nutrient translocation and plant growth

K is an essential plant electrolyte (with Na playing a substitute role, Kronzucker et al., 2013; Subbarao et al., 2003) but both contributed additively in promoting plant moisture, and synergistically in promoting plant height, especially early and late in the season (Figure 2). This increase in water availability—along with an up to 3× increase in CO₂ fixation found in +K supplements (Marschner, 1995)—was linked to the translocation of nutrients from below-ground and back again (Figures 2 and 3). This result points to the unique function of electrolytes to effectively move elements through the plant, just as N and P build cellular structures. While climate, nutrient standing stocks, and plant functional group have all been linked to variation in plant nutrient resorption (Vergutz et al., 2012) our experiment implicates electrolytes as key players in a plant’s nutrient economy.

A variety of elements beyond macronutrients like N responded to electrolyte fertilization. The most common increase in above-ground tissue was in manganese (Mn)—a catalyst of photosynthesis (Sharma, 2006c)—and with it copper (Cu) and zinc (Zn). Although all these metals have multiple catalytic roles (Frausto da Silva & Williams, 2001), one functional similarity is their role in superoxide dismutases that disable damaging free radicals produced by metabolic oxygen (Bowler et al., 1994). One possibility is that K and Na fertilization increased metabolic production of O₂ and hence the demand to neutralize free radicals. If true, then co-fertilization with K and either Mn or Cu + Zn (which are cofactors in the same dismutase) should yield more plant growth than adding K, Mn, Cu, or Zn alone. In one relevant study of 54 grasslands, increases in N and P—long known to limit plant biomass production (Elser et al., 2007; Fay et al., 2015)—generated increased demand for K, Mn, Cu, and Zn (Kaspari et al., 2021). This cascading effect of elemental demands has become the signature of ionomics and multiple element limitation (Fan et al., 2021; Kaspari & Powers, 2016; Salt et al., 2008).

Likewise, in seasonal environments that also regularly burn, electrolytes promote the importance task of resorbing key nutrients below ground (Vergutz et al., 2012). In the latter two summer months, we saw a shift on electrolyte supplemented plots toward the significant depletion of a variety of elements below those found on control plots: on +K plots Na, P, boron (B), and molybdenum (Mo) all strongly decreased in September, with September decreases of B found in all three treatments. As B plays a key role in cross-linking structural polysaccharides (Sharma, 2006a) it is a reasonable surmise that, at the end of the growing season, senescing grasses are recovering elements previously needed to produce erect plants.

Although this is not a paper on functional ionomics, field additions of K and Na do provide grist for this growing field (Peñuelas et al., 2019; Salt et al., 2008). Our larger take-home is that electrolytes, by ramping up plant growth early in the season, and nutrient resorption at the end of the season, point to how higher supplies of K—like those close to oceans (NADP, 2007; Sardans & Peñuelas, 2015) or on grazed grasslands and pastures (Jones & Hanson, 1985; Kaspari, 2020; Ozment et al., 2021)—increase plant nutrient use efficiency.

Grassland food webs have a seasonal structure of bottom up and top down control

Grasshopper biomass approaches that of bison on Konza prairie (Branson et al., 2006) and, due to their smaller size and higher per gram metabolism, prairie grasshoppers can consume more plant biomass than mammals (Belovsky & Slade, 2000). K and Na can limit both invertebrate abundance (Prather, Laws, et al. 2018; Welti et al., 2019) and development (Kaspari et al., 2022; Peterson, Welti & Kaspari, 2021; Snell-Rood et al., 2014). Here, we go beyond the snapshot sampling of invertebrates in response to fertilization—which has already yielded considerable insights on the role of N, P, and Na, on limiting invertebrate abundance (Lind et al., 2017; Prather, Laws, et al. 2018; Welti et al., 2019)—to explore the covariation of plant nutrients and consumer abundance over the season. The resulting cycle-like behavior of the Konza invertebrates in response to a press of Na and/or K (Figure 2) recalls similar behavior resulting from the destabilizing effects of eutrophication...
(Rosenzweig, 1971). Of particular note was the profound drop in invertebrate numbers—from an initial increase of 0.3 to 1.2 SD over controls to a decline in those same numbers of 0.6 to 1.2 SD the following month—as the above-ground ionomes of grasses reached their richest states. All of this occurred as control plots were experiencing strong Dilution by Growth (Figure 1; Ball et al., 2001; La Pierre et al., 2011; Marschner, 1995). We suggest two, complementary, hypotheses for the suppression of arthropod numbers when nutrient densities were at their peak:

1. **H1:** Elements are used by plants to form toxins: four elements >1 SD above controls on treatment plots—N, K, Cu, and S—are all key ingredients in plant defensive compounds, including N in hydrogen cyanide (Nicollier et al., 1983), K and Cu in antifungals (Marschner, 1995); and S in a variety of secondary metabolites linked to defense (Burow et al., 2008). One or all may be synthesized in surplus to defend rapidly growing plant tissue.

2. **H2:** Ecological stoichiometry (Sterner & Elser, 2002) and nutritional ecology (Simpson & Raubenheimer, 2001) both suggest that fertilization, by producing nutrient imbalances, can hinder consumer fitness. This can happen in at least two ways. First, the +1 SD increases in plant tissue K relative to Na (Figure 2) can lead to pathology given their tandem requirement in animal ATP-ases (Bonoan et al., 2017; Denton, 1982; Jones & Hanson, 1985). Second, the increase in N on +Na and +K plots may elevate the protein:CHO availability in the direction of protein toxicity, a common phenomenon when rapidly growing and metabolizing insects require ample quantities of CHOs (Behmer, 2009; Simpson et al., 2004).

Both H1 and H2 could be tested using cafeteria experiments, where consumers are allowed to choose among grasses harvested from Na K supplements over time.

**Caveats and next steps**

Our food-web approach to electrolyte availability is a first step toward understanding its influence on consumer abundance. However, large grazers like bison—both a natural source of the fertilizer and one of the consumers of the resulting plant biomass—also are major players on the prairie landscape (Hartnett et al., 1996; Knapp et al., 1999; Moran, 2014; Ozment et al., 2021; Steinauer & Collins, 1995). Bison create and revisit 50 m$^2$ grazing lawns (Knapp et al., 1999) where they crop plant biomass down to the low levels we find in May (Figure 1, with corresponding high nutrients). These nutrient-rich patches are then exploited by insect herbivores (Moran, 2014; Ozment et al., 2021). But bison are also highly mobile, moving ca. 50 m every 12 min (McMillan et al., 2021) and thus likely to leave smaller NaK deposits across a substantial part of the rest of the prairie. Many of our results—in particular the wide swings in above-ground nutrients enabled by a dose of electrolytes—seem to best apply to these latter fertilization events that create patches that are ungrazed/untrodden as well as taller, wetter, and more or less nutritious grass depending on the time of year. Indeed, here we give a biogeochemical spin to the growing literature on how bison shape the heterogeneity of grassland landscapes (Knapp et al., 1999; Ozment et al., 2021; Steinauer & Collins, 2001).

Ecological ionomics is a nascent field and this study—the first of its kind to simultaneously manipulate Na and K in a press experiment—is not unassailable. For example, our decision to reuse 7 × 7 m$^2$ plots fertilized in 2018 with the same Na doses in 2019 may have led to unanticipated legacy effects. This was not, however, evidenced by the May 2019 Na levels from plots fertilized the year before.

Our sources of plant chemistry also varied over the course of the experiment: clip plots in May (when plant height was low and plants undifferentiated), gave way to *Andropogon* in June, and *Sorghastrum* in July–September. When analyses using only the *Sorghastrum* data were performed on plant chemistry, water, and height (Appendix S1: Tables S1, S2a, S3a, S4a) most of our results were replicated on these sparser datasets. A key exception was the effect of K fertilization on plant Na and N, which disappeared, and thus may be driven by differences in the response of the co-dominant grasses *Andropogon* and *Sorghastrum*, lower statistical power, or both.

Finally, we assume that nutrients that increase then decrease in above-ground samples relative to controls are being transported to and from below-ground tissues. We did not excavate and analyze the biomass, moisture content, or elemental chemistry of roots. Such quantification is an important next step.

Electrolytes have thus far not constituted a subject of concerted study in food webs. With the Great Plains predicted to be warmer and wetter (Hajek & Knapp, 2022), the effect of increasing precipitation—beyond plant production and including the Na and K deposited with that rain—holds considerable interest.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Kaspari, 2022) are available in the Open Science Framework at https://doi.org/10.17605/OSF.IO/25WNB.

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REFERENCES


SUPPORTING INFORMATION

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

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