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# Drivers of 30 years of ionomic change on a North American tallgrass prairie

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## Funding information

Division of Environmental Biology,  
 Grant/Award Numbers: 105393900,  
 105446600

**Handling Editor:** William C. Wetzel

## Abstract

Plant ionomes—the suite of chemical elements making up plant tissue—constrain plant performance and the nutrition of consumers. The possible mechanisms driving Nutrient Dilution—the globally distributed decline of essential element density (parts per million [ppm]) in plant tissue—are rarely evaluated together. Toward a remedy, we explored a 30+ year record of 17 elements in the grasses, forbs, and woody plants across three burn frequencies on Konza, a North American tallgrass prairie. About one quarter of ionomic variation arose among Konza's three plant functional groups, which differed in ppm and its regulation over three decades. Nutrient-poor grass biomass increased steadily with CO<sub>2</sub>, encroaching woody plant biomass accelerated over the same period, and nutrient-rich forb biomass decreased. Each functional group revealed its own pattern of nutrient dilution across the ionome, where it was more widespread in grasses (12/17 elements) than forbs (5/17) or woody plants (2/17). Competition with other functional groups regularly depleted the ionome ppm of grasses (9 elements) and forb and woody plants (4 elements). Unexpectedly, nutrient densities often increased in response to higher CO<sub>2</sub> (especially in forbs), suggesting photosynthate was invested in nutrient harvest. Fire suppression had fewer, and more idiosyncratic effects. In an era of herbivore declines, grass-feeding herbivores in this tallgrass prairie are experiencing more abundant but lower quality food. Forb feeders, in contrast, must search for less abundant but sometimes enriched food.

## KEY WORDS

aerosol deposition, animal declines, biogeochemistry, fire, food webs, global change, grassland

## INTRODUCTION

Ecological abundance, niches, and distributions are fundamentally constrained by Earth's abiotic template of temperature, moisture, and biogeochemistry (Dunson & Travis, 1991; Smith et al., 2019). This template is changing in the Anthropocene (Kaspari & Welti, 2024; Vitousek, 1994). Earth's grasslands—given their ubiquity

(ca. 40% of the terrestrial surface, Hoekstra et al., 2005) and high rates of conversion for agriculture—are a critical arena of such ecological change (Belovsky & Slade, 1995; Kaspari et al., 2021; Welti et al., 2020).

Ecological ionomics explores the causes and consequences of the variation in availability and distribution of life's essential chemical elements (Fagan et al., 2002; Kaspari & Powers, 2016; Sterner & Elser, 2002). At the

base of food webs, plant ionomics provide insights into a plant's functional niche (Kaspari et al., 2021; Sardans & Peñuelas, 2015). Ionomics also provides a template for the structure and function of consumer food webs (Clay et al., 2017; Kaspari & Welti, 2022; Prather et al., 2020; Welti et al., 2020; Welti & Kaspari, 2021).

In an era of widespread consumer declines, plant ionomes are also key predictors of the abundance of herbivores—consumers that must build an enriched ionome from an impoverished food supply (Kaspari, 2021). Herbivore abundance is sensitive to shortfalls, not only in macronutrients like N (Fagan et al., 2002; White, 1993) and P (Elser et al., 1996; Jeyasingh et al., 2020) but also in electrolytes like Na and catalytic metals like Cu, Fe, and Co, some of which are not even essential to the plants they consume (Orians & Milewski, 2007; Prather et al., 2020). Decreases in plant elemental densities—Nutrient Dilution—is a global phenomenon with high potential to drive declines in herbivores and the food webs they connect (Atwood et al., 2020; Filipiak & Filipiak, 2022; Welti & Kaspari, 2024).

## What drives ionomic variation in time and space?

To link plant ionomes to consumer food supplies (Figure 1) we first recognize that herbivores sample an ecosystem's ionomic variation (measured in parts per million [ppm]) bite by bite (Kaspari, 2021). As plants grow—harvesting local nutrients and manufacturing carbohydrates (made of C, H, and O, henceforth CHO)s—the balance of structural CHOs to other elements in plant tissues can decline by simple laws of mass balance: Nutrient Dilution by Growth (Marschner, 1995). For example, in temperate climates, tender spring foliage is often temporarily nutrient-dense (Jones & Hanson, 1985; Kaspari & Welti, 2022) before it accumulates stems and their structural CHOs (La Pierre et al., 2011), decreasing ppm of non-CHO elements on a per plant and per area basis.

Anything that promotes plant CHO biomass—for example, high rainfall or optimal temperatures (Hogan et al., 2024; La Pierre et al., 2016)—can decrease the ppm of plant elements when years of high productivity foster “green deserts” (Welti & Kaspari, 2024). This includes increases in CO<sub>2</sub>, which—observationally and experimentally—have been linked to the global increase in plant biomass in the last century (the Carbon Fertilization Effect, Campbell et al., 2017; Loladze, 2014; Luo et al., 2004; Wang et al., 2020). Likewise, any ecological driver reducing a plot's

biomass to a low turf system—including fire (Thapa et al., 2022) and grazing (Ozment et al., 2021)—has the potential to reverse Nutrient Dilution.

Nutrient Dilution also arises through declines in available nutrients. Declines in ionomic availability can arise through waning deposition (Kühn et al., 2025), leaching (Wardle et al., 2004), and drought (Kaspari et al., 2021; Marschner, 1995). Increases in CO<sub>2</sub> have also been posited to decrease nutrient ppm independent of biomass by enhancing photosynthetic efficiency (Gojon et al., 2023) and by feeding soil microbes with plant carbon exudates which boosts microbial biomass, locks up more nutrients, and makes them unavailable to plants (Shahzad & Rouached, 2022). Inter- and intraspecific competition can also drive Nutrient Dilution by reducing per capita nutrient availability (Schimel et al., 1991). Finally, fire, by immolating aboveground biomass (and the nutrients therein) can return nutrients to the soil as ash, or volatilize lighter atoms like C and N, while returning more massive atoms—like K, P, and S—to the soil (Connell et al., 2020; Hough, 1981). Thus, the effect of fire on community ionomics may be subtle (changing both biomass and nutrient availability), and element specific.

Here we explore the distribution of the concentrations of 17 elements in plant tissue across a 30+ year period on a southern mesic North American grassland, Konza Prairie. C4-dominated grasslands like Konza may be responsible for up to 23% of Earth's terrestrial GPP (Still et al., 2003). We quantify the two key determinants of plant elemental ppm—change in nutrient inputs via deposition and soil levels—and changing biomass of three functional groups—grasses, forbs, and woody plants. We evaluate mechanistic models of Nutrient Dilution (Figure 1) that predict annual changes in elemental ppm with changes in plant biomass, nutrient availability, fire, and competition.

## METHODS

Konza Prairie (henceforth Konza) is a National Science Foundation (NSF) Long-Term Ecological Research (LTER) site consisting of 3487 ha of predominantly unplowed, native tallgrass prairie in northeastern Kansas, USA. Konza operates landscape-scale two-way factorial experiments in which watersheds are subjected to different treatments of fire frequency and are ungrazed or grazed by bison or cattle. This work took place on three ungrazed Konza watersheds, consisting of 1-, 4-, and 20-year fire frequency treatments (watershed codes: 1D, 4B, and 20B, respectively).

## Abiotic data

Soil chemistry and pH were sampled every ~5 years across the three watersheds between 1982 and 2020 (Blair, 2023b). Temperature, precipitation volume, and precipitation chemistry (pH, N, Mg, S, Ca, K, Na) are collected at the Konza headquarters meteorological station

(Blair, 2023a) and stored by the Climate and Hydrology Database Project with support from NSF LTER, the USGS, and the USDA Forest Service (<https://climhy.lternet.edu/>). Annual CO<sub>2</sub> ppm was recorded from the Mauna Loa Observatory (Thoning et al., 2025).

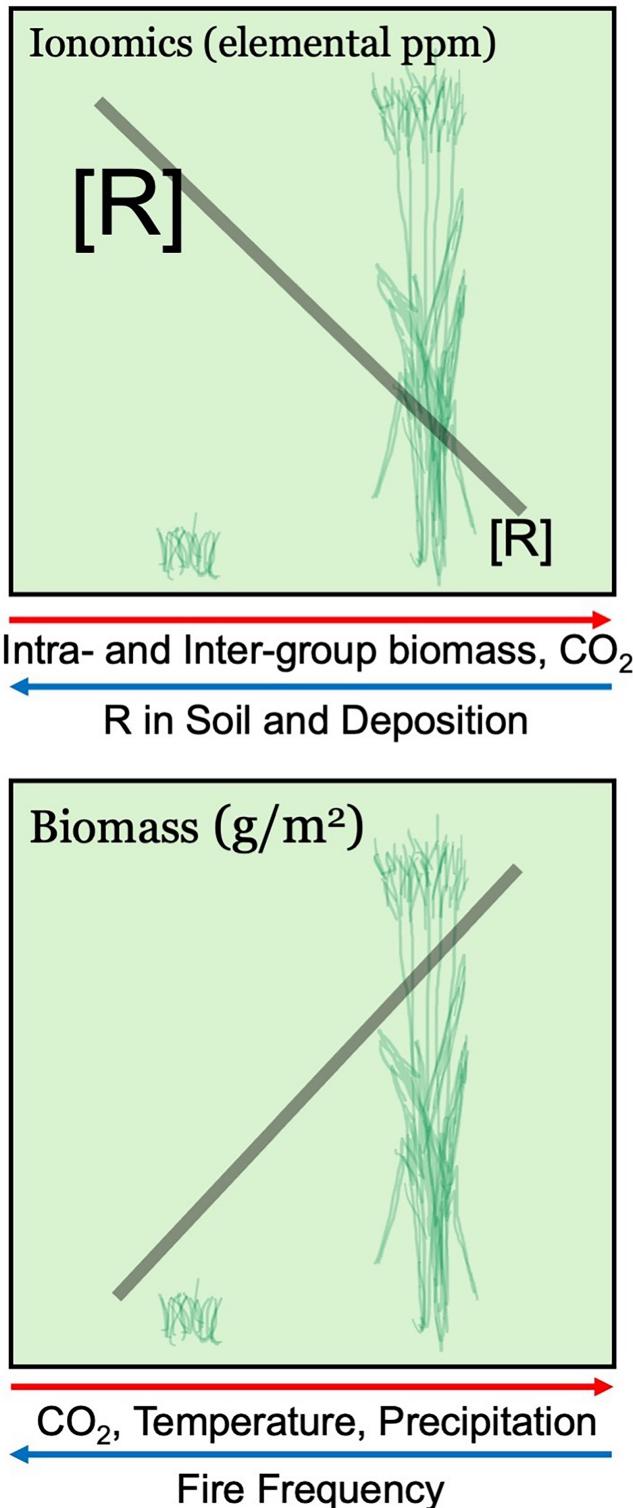
## Plant biomass and chemistry

Plant biomass on the three Konza ungrazed watersheds was collected annually at the end of the growing season (peak biomass, typically September or October) and was available over a 32-year period from 1985 to 2016 (Blair & Nippert, 2025). Live grasses, forbs, woody plants, and the previous year's dead vegetation are clipped from 0.1 m<sup>2</sup> quadrats in 20 plots/watershed/year in a random stratified design (i.e., no plots were resampled across years), dried, and weighed. Dried samples of live grass, forb, and woody biomass were averaged annually for each watershed. These samples were pooled, and a dried subsample was preserved for chemical analysis.

We obtained samples from the nine combinations of functional group/watershed from 1984 to 2016, dependent on availability (Grass: 1D  $n = 31$  years, 4B  $n = 30$ , 20B  $n = 25$ ; Forbs: 1D  $n = 27$ , 4B  $n = 28$ , 20B  $n = 25$ ; Woody: 1D  $n = 3$ , 4B  $n = 24$ , 20B  $n = 23$ ). End-of-season elemental composition of (non-woody) tissues from grass, forb, and woody plants from each watershed was analyzed using combustion analysis for percent N (Dumas Method, McClements et al., 2021), and using hot-plate digestion, and inductively coupled plasma atomic emission spectroscopy (ICP-AES) for concentrations of metals (ppm) at the Cornell Nutrient Analysis Laboratory (<https://cnal.cals.cornell.edu/>).

## Quantifying ionomic responses

Unlike the abiotic drivers of temperature and moisture, ionomics explores the ecological consequences of



**FIGURE 1** Hypotheses linking the environmental drivers of plant biomass (grams per meter squared) and the concentration of element R (parts per million) in the plant ionome. Biomass is constrained by the building blocks of carbohydrates and removed by fire. Enhanced biomass drives Nutrient Dilution via the accumulation of carbohydrates, as does competition with other species/functional groups; elevated CO<sub>2</sub> can additionally enhance nutrient dilution via its effects on photosynthetic efficiency and microbial competition and can be alleviated by enhancing sources of R in the soil or through aerial deposition. The effect of fire on the ionome depends on its effect on these latter two drivers. Images created by Michael Kaspari.

organisms investing in the acquisition of the 20+ essential elements for which shortfalls can lead to pathology (Frausto da Silva & Williams, 2001; Kaspari, 2021). We group elements into metabolic functional groups (Kaspari, 2021; Kaspari & Powers, 2016; Peñuelas et al., 2019). We use five such groups, which going forward we refer to as macro, electrolyte, membrane, catalyst, and animal. **Macro**-nutrients (C, N, P, and S) are four elements that are the widespread, common “nucleotides, proteins, and skeletons” (Peñuelas et al., 2019; Sterner & Elser, 2002). **Electrolytes** (K and Na) are two elements that govern water balance and the flow of water and nutrients through the vascular tissue (Kaspari & Welti, 2022; Wakeel et al., 2011). **Membrane** integrity (B and Ca) elements promote the synthesis, maintenance, and function of plant plasma membranes and cell walls (Marschner, 1995; Sharma, 2006). **Catalyst** (Mg, Fe, Zn, Mn, Cu, and Ni) elements include seven metals key to enzyme structure and function (Kaspari, 2021; Peñuelas et al., 2019). **Animal** essential (Cr, Co) elements are required for animal, but not plant, metabolism (Frausto da Silva & Williams, 2001).

General Linear Models, including least squares linear regressions, ANCOVA, and multiple regression, were used to test hypotheses regarding temporal and spatial dynamics of plant ionomes and their drivers on Konza. All analyses were run in the program SAS using the functions Proc Reg and Proc GLM (Proc GLM, SAS Institute, 2013). As this was a seasonal environment, reset by winter annually, we used annual measures as replicates. Abiotic and atmospheric dynamics were evaluated over a 30+ year time series using linear regression. Dynamics of soil chemistry (measured every 5 years) and functional group biomass (measured annually) were evaluated in an ANCOVA contrasting the effects of year and burn treatment.

To explore drivers of plant biomass for each functional group, we used linear regression to simultaneously test the effects of CO<sub>2</sub>, burn frequency, annual precipitation, and mean annual temperature. Variance Inflation Factors for this analysis ranged from 1 to 1.2 (Appendix S1: Table S1).

To explore patterns in plant ionomics, we analyzed changes in each of the 17 elements and tallied their responses. We first used a two-way ANOVA to partition variance attributable to functional group and fire treatment. We used a linear regression to test for Nutrient Dilution by Growth for each element in each of the three functional groups. All elemental concentrations were log<sub>10</sub> transformed prior to analysis. We next expanded this regression analysis to contrast the effects of intergroup biomass, CO<sub>2</sub>, and years since the last fire. Variance Inflation Factors for this analysis ranged from 1.1 to 2.3 (Appendix S1: Table S1).

## RESULTS

Over a 32-year period, the biogeochemistry of the atmosphere, soils, and three functional groups of plants has changed on the Konza tallgrass prairie.

### Decadal changes in the abiotic template

Since 1982, atmospheric CO<sub>2</sub> and temperature have increased by +60 ppm and c.a. 1°C (Appendix S1: Figure S1). CO<sub>2</sub> increases over this period are near linear with year (least square means regression  $r^2 = 0.99$ , Appendix S1: Table S2). Annual temperature, while more variable ( $r^2 = 0.17$ ) has increased about 1°C over this period, while precipitation shows no linear trend ( $r^2 = 0.01$ ). The pH of precipitation, with one conspicuous outlier, increased from c.a. 5 to 6.

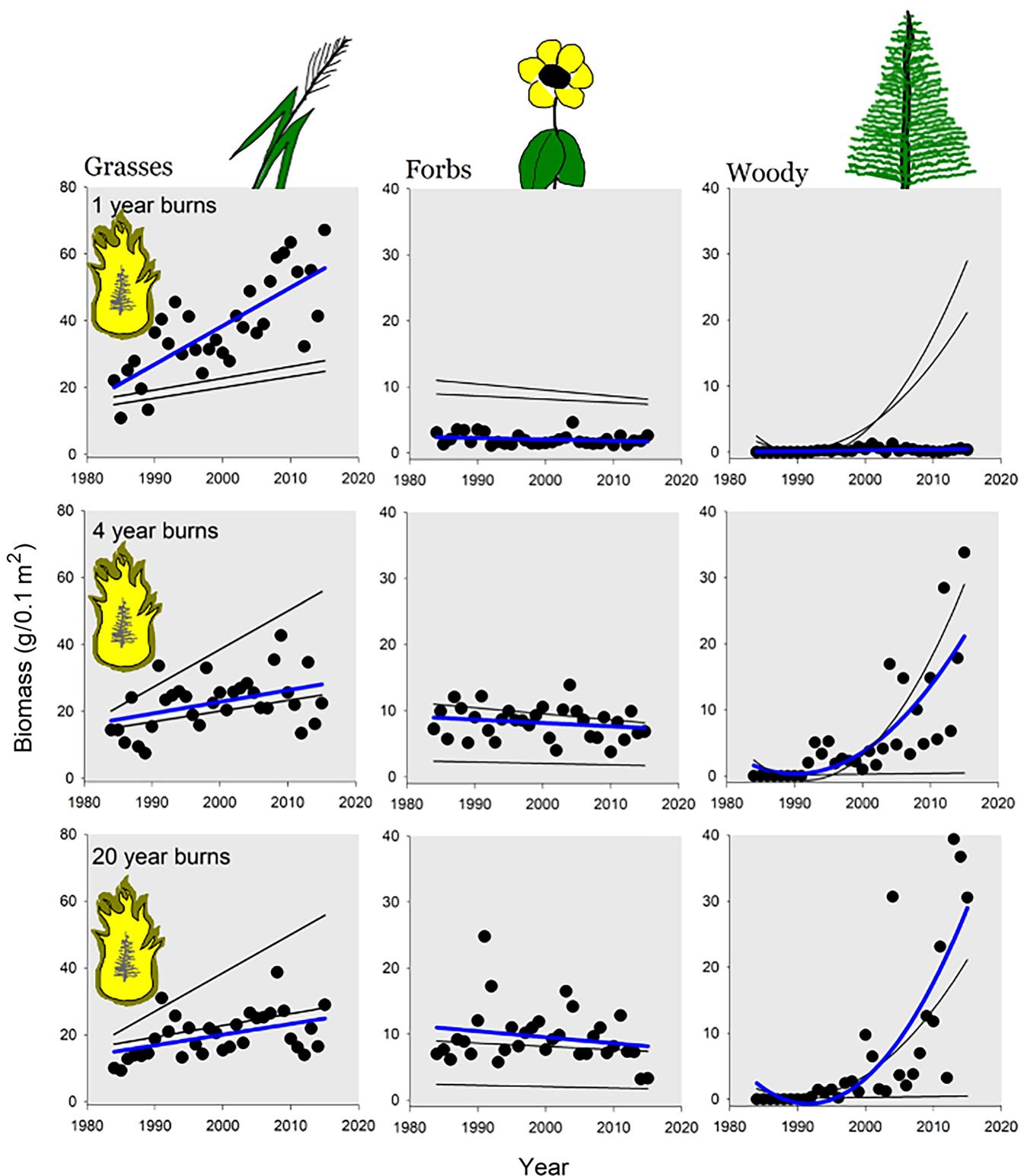
Atmospheric deposition showed decadal trends in two of six measured elements (Appendix S1: Table S2, Figure S1). Sulfur (as SO<sub>4</sub>) almost halved over 30+ years, from 12 to 6 mg year<sup>-1</sup> ( $r^2 = 0.49$ ). Calcium ions increased by c.a. 1 mg year<sup>-1</sup> ( $r^2 = 0.25$ ). All other elements (Mg, K, Na, N) showed no clear change in their atmospheric deposition over the 35 years ( $r^2$ 's  $\leq 0.10$ ).

Soil chemistry and pH—sampled every ~5 years—generally showed no linear trends over 30 years nor differed with burn frequency, while the macronutrient nitrogen and electrolyte potassium both varied with burn frequency (Appendix S1: Figure S2, Table S3). Soil nitrogen was ca 13% higher on the watershed burned every 20 years and lowest on annual burns. Soil potassium was highest on 4-year burns, and lowest on 20-year burns. Nitrogen was the only soil element to increase over the sampling interval from a ~15% increase on the annual burn watershed, to 50% on the 20-year burn.

### Konza is accumulating more grass and woody plants and losing forbs

Over a 32-year period starting in 1984, the biomass of three plant functional groups on the Konza prairie trended in often opposite directions as CO<sub>2</sub> increased (Figure 2, Appendix S1: Figure S3, Table S4). Consistent with CO<sub>2</sub> as a driver increasing plant biomass, grasses consistently increased by up to four-fold over time across the three burn frequencies. Woody biomass accelerated after being largely absent pre-1990 and was better fit with a quadratic model. In contrast, forb biomass incrementally declined over the same period.

Plant biomass also varied among the 1, 4, and 20 year burn frequencies (Figure 2; Appendix S1: Table S4).



**FIGURE 2** Thirty-five years of plant biomass (grams per a tenth of a meter square) on a North American tall grass prairie. Columns represent three functional groups—grasses, forbs, and woody plants. Rows represent watersheds that are burned every 1, 4, and 20 years. Each functional group column shows three least square regressions: The one in blue for the scatterplot represented, the thin black lines depicting the other watersheds for comparison. Linear regressions are fit to grass and forb data; quadratic regression for woody plants. Note biomass y-axis for grass is 2× the magnitude of forbs and woody plants. Images created by Michael Kaspari.

Consistent with fire as a suppressor of aboveground biomass, both forbs and woody plants were less abundant on annual burns. Grasses, the functional group with the most belowground meristem, showed the opposite pattern with aboveground dry biomass dominating on annual burns, at 26 times higher than forbs and 191 times higher than woody plants.

Interannual variation in precipitation and temperature contributed little to variation in biomass in forbs and woody plants (Appendix S1: Table S4). Grass biomass increased, all else being equal, in wetter years.

In sum, on three representative watersheds ungrazed by bison or cattle, Konza plant functional biomass has become grassier and woodier over time, with fewer forbs, while frequent burning favored grasses. Although the explanatory power of the models is roughly similar ( $R^2$ 's between 0.35 and 0.45), burn frequency accounted for the most variation in forb and grass biomass, while woody plant biomass was shaped roughly equally by  $\text{CO}_2$  and burn frequency.

## Functional groups are a chief source of ionomic variation

To identify drivers of plant chemistry—the ppm of 17 elements in plant tissues, grouped by their metabolic function—we examined the effects of burn frequency, functional group, and their interaction (Appendix S1: Table S5). Our ability to account for variation varied greatly among the elements. At one end of the spectrum, models accounted for two-thirds of the variation in the membrane elements Ca and B, and the electrolyte K. At the other end, virtually no variation in the electrolyte Na and the animal element Cr was accounted for by fire frequency or plant functional group.

Across the 17 elements, functional group accounted for an average of ~25% of their variation, including most of the variation in 12 of 17 elements, and co-majority for 3 more (Appendix S1: Figures S4 and S5, Table S5). Grasses had the lowest tissue ppm of elements—or shared that status—with every element but Mo. Forbs, in contrast, had the highest ppm of elements—or shared that status—in 12 elements, while woody plants had the highest concentrations of C, Mn, and Cr. Nearly across the board, an herbivore would have a higher rate of element ingestion consuming forbs instead of grasses. Relative to functional group effects, ionomes were largely consistent across the three burn frequencies (~3.5% of ionome variation, on average). Interactions (i.e., the ionomes of functional groups depended on burn frequencies) were strongest for Mo and Mn, but overall accounted for only ~8% of variation

in plant elemental ppm. Given these results, we next focus on the rules governing the ionomes of the three functional groups.

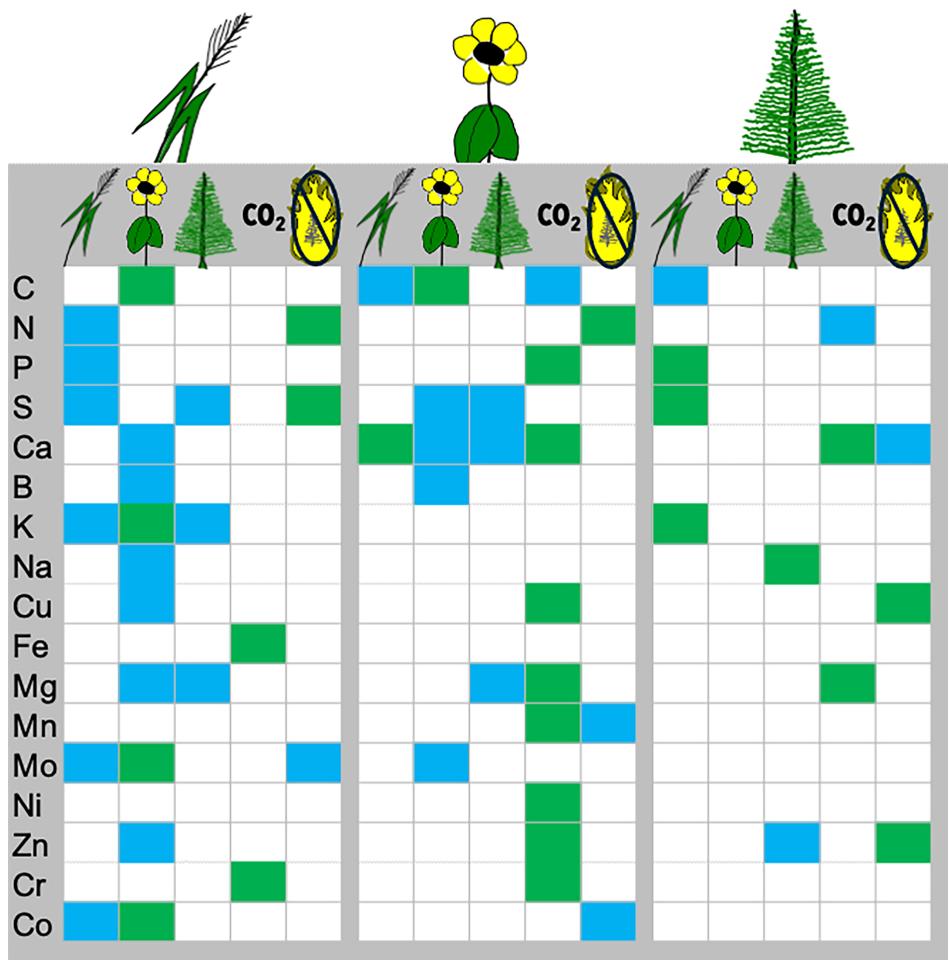
## Nutrient dilution and enrichment in the three functional groups

We next test hypotheses for ionomic variation (Figure 1) in each of the functional groups (Figure 3 Appendix S1: Tables S6–S8, Figures S6–S8). Depending on the data availability of each functional group, we used up to 35 years of biomass data across up to 3 watersheds with different fire frequencies.

Among the grasses—the most nutrient-poor of the functional groups and dominating in total biomass—an average 30% of ionomic variation was linked to biomass,  $\text{CO}_2$  levels, and years since the last burn (Figure 3, Appendix S1: Table S6, Figure S6). Grasses were most likely to experience Nutrient Dilution in this analysis (12 of 17 elements, including three of the macronutrients (N, P, S), all membrane (Ca, B) and electrolyte (K, Na) elements, four catalysts (Cu, Mg, Mo, Zn), and one animal element (Co)). Elemental ppm declined with increased grass biomass (6 elements), and/or forb or woody biomass (8 elements). Unexpectedly, the residual (i.e., non-biomass-related) effects of increasing  $\text{CO}_2$  were associated with increases in ppm of Fe and Cr. Grass N and S ppm increased as time since the last burn lengthened. In contrast, Mo ppm was highest in the annually burned watershed, which also supported the highest grass biomass (Figure 2).

Among the forbs, an average 25% of ionomic variation was linked to plant biomass,  $\text{CO}_2$  levels, and years since the watershed last burned (Figure 3, Appendix S1: Table S7, Figure S7). Nutrient Dilution emerged for 6 elements from macro (C, S), all membrane (Ca, B) and two catalysts (Mg, and Mo): 4 were diluted with increases in forb biomass, 3 with woody biomass and 1 with grass biomass. As in the grasses, the residual (i.e., non-biomass-related) effects of increasing  $\text{CO}_2$ , rather than suppress forb elemental concentrations, was associated with increases in the ppm of 8 elements (P, Ca, five catalysts Cu, Mg, Mn, Ni, Zn, and the animal essential Cr).

Woody plants were rare in the early years of sampling, and their ionomic patterns were less well accounted for (average  $R^2 = 0.19$ , Figure 3, Appendix S1: Table S8, Figure S8). Compared to forbs and grasses, only the catalyst Zn showed Nutrient Dilution, while woody plants had less C in areas and times of high grass biomass. N ppm, by contrast, was diluted by increases in  $\text{CO}_2$ , suggesting a non-biomass driver of Nutrient



**FIGURE 3** A heat map summary of hypotheses tests for five drivers of plant tissue concentration (ppm) of 17 elements from a North American tallgrass prairie (see Appendix S1: Figures S6–S8, Tables S6–S8). From left to right at the top, results are summarized for grasses, forbs, and woody plants. Drivers for each—as determined by least squares regression—from left to right, are the biomass of grasses, forbs, and woody plants, CO<sub>2</sub> levels, and the number of years since the plot had last burned. For each element, a blue square represents a decrease associated with that driver (e.g., grass N declines with grass biomass: nutrient dilution). A green square represents an increase (e.g., grass N increases with increasing time between fires). Elements are arranged vertically and grouped by function. From the top, Carbon, Nitrogen, Phosphorus, and Sulfur are macronutrients; Calcium and Boron enhance cell membrane integrity; Potassium and Sodium are electrolytes; Copper, Iron, Magnesium, Manganese, Molybdenum, Nickel and Zinc are catalytic metals, and Chromium and Cobalt are metals essential to animals but not plants. Images created by Michael Kaspari.

Dilution. Surprisingly, woody tissue in high grass biomass plots increased in the macros P, S, and electrolyte K concentrations, while in plots with high woody biomass Na increased, and higher CO<sub>2</sub> was associated with increased Ca and Mg. Time since the last burn had no effects on woody plant N, but decreased ppm of the membrane element Ca, and increased ppm of the catalysts Cu and Zn.

To further examine the role of nutrient availability, we used annual deposition data on Konza available for six elements (the macronutrients N and S, the membrane Ca, the electrolytes K and Na, and the catalyst elements Mg, Appendix S1: Figure S1). When these 30+ years of data were added as additional drivers to

the above GLMs, none accounted for further variation of the tissue ppm for any of the three plant functional groups (Appendix S1: Table S9).

## DISCUSSION

Over the past 30 years, the changing abiotic drivers of the Konza tallgrass prairie—especially fire and increasing CO<sub>2</sub>—are contributing to linear increases in above-ground biomass of grasses, less dramatic decreases in forbs, and an acceleration of woody plant biomass. These biomass changes drive plant Nutrient Dilution, especially in the already nutrient-poor grasses where

two-thirds of essential elements—those whose shortfall causes pathology—have declined over this period. At the same time—and unexpectedly—rising CO<sub>2</sub> was often associated with enhanced nutrient levels (>50% of essential elements in forbs). Experimentally, the abiotic “consumer” fire further drove ionomic change on Konza, with frequent fires favoring nutrient-poor grasses. The emerging picture is of a grassland richer in plant biomass but more impoverished in a variety of elements essential and limiting to the diet of consumers, a future in which specialists on herbaceous forbs find fewer plants to feed upon and grass feeders face widespread Nutrient Dilution.

## Konza LTER provides a decadal picture of climate change

Ecological observatories like Konza LTER document the multivariate changes of Earth’s Anthropocene, from those shared by most global ecosystems, like increasing CO<sub>2</sub> and temperatures, to the more site-specific. We briefly focus on two such local changes—in soil N and aerosol deposition.

Soil nitrogen—an essential element that is often limiting in terrestrial plants and herbivores—has increased up to 13% at Konza over the past nearly four decades. Moreover, one possible cause—increasing atmospheric nitrogen deposition—is not evident on Konza where values have decreased since c.a. 2000 (Appendix S1: Figure S1). Bison and cattle grazing and their resulting N-rich urine and feces increase soil nitrogen cycling on other Konza watersheds (Anguiano et al., 2024). It is conceivable that nutrients from these excreta are dispersed across watersheds over time. Soil microbes, limited by labile carbon, can also benefit from increased carbon exudates in a +CO<sub>2</sub> world, in turn locking up more total soil N as microbial biomass (Luo et al., 2004) and driving Nutrient Dilution among competing plants (Kaspary & Welti, 2024).

Aerosol deposition of sulfur decreased and Ca (as well as pH) increased over the same time period on Konza, a pattern repeated across five sites in Ohio (Grider et al., 2023). Sulfur declines (and at least part of the trend in pH) have been documented worldwide due to regulation of emissions (Benish et al., 2022). In Ohio (Grider et al., 2023) increases in Ca were attributed to Ca dust from traffic on gravel roads. Combined, changes suggest a Konza soil pH that is more amenable to cation exchange and plant nutrition (Marschner, 1995). Whether this may buffer Nutrient Dilution by enhancing uptake is an interesting working hypothesis.

## Functional group ionomics and biomass change

Functional groups—and the suite of traits they represent—are all built from the same 20+ essential elements but frequently in different proportions (González et al., 2018; Peñuelas et al., 2019). Konza’s grasses, forbs, and woody plants differed in their ionomics, their biomass dynamics and ultimately, the way that nutrient dilution was expressed in the last three decades. The three functional groups responded to increases in CO<sub>2</sub>, with fire favoring the accumulation of grasses (with their often-protected underground meristems). Wet years favored only grass biomass. Notably, temperature failed to account for variation in biomass, perhaps because plants in inland, mesic ecosystems like Konza are most likely to show acclimation in temperature optima (Wang et al., 2024). Overall, c.a. one-third of the combined watershed and annual variation in biomass was accounted for by just two or three drivers.

These ionomic differences may help account for the partial failure of an early prediction from global change theory—the promotion of C3 versus C4 plants under enhanced CO<sub>2</sub> (Reich et al., 2018)—with implications for woody encroachment (Ratajczak et al., 2012) and global carbon storage (Wang et al., 2020). Instead, this C4-dominated grassland revealed strong increases in grass (mainly C4) and woody biomass (C3) over three decades and a 20% increase in CO<sub>2</sub>.

Why are C3 forbs declining relative to C4 grasses and woody plants? Our working hypothesis is that grasses have two functional traits which combine to give them an advantage. First, the low-ppm ionome of grasses shows the ionomic profile of high Nutrient Use Efficiency (González et al., 2010; Tilman, 1988; Vitousek, 1982). In this view, grass ionomes are depleted because they do not invest much in building the enzymes and transporters dedicated to resource harvest, instead investing in building CHO-rich stems to raise leaves above the canopy, enhancing their ability to compete for light (Schimel et al., 1991). As a result, grasses benefit passively—achieving more nutrients from the soil for less investment in harvest—when higher soil nutrients make them easier to access (Kaspary et al., 2021).

Forbs often must spend more time under the shade of grass and tree canopies (Poorter et al., 2019). We suggest that on Konza, forbs diverge from grasses by investing in active, energetically costly nutrient harvest in roots in order to build nutrient-rich shade-tolerant leaves (Kaspary et al. in review). In this way, Konza’s increasing soil nitrogen may be fostering the growth of high NUE grasses (Tilman, 1988) just as, in a meta-analysis, nitrogen fertilization enhanced grass aboveground biomass by

79% but had no effect on forbs (You et al., 2017). In short, we posit that grasses and forbs coexist by attaining similar photosynthetic capacities, the former by reaching high light environments, the latter by making each photon do more work via element-rich leaves (Mu & Chen, 2021).

A second grass trait enhances this effect—the ability of grasses to harvest episodic rainfall. Recall that precipitation boosted grass biomass on Konza, but not that of forbs or woody plants. In the above meta-analysis high rainfall years also boosted the biomass promotion of grasses but not forbs (You et al., 2017). Grasses invest in shallow roots, giving them first access to rainfall (Eggemeyer et al., 2009). In contrast, encroaching woody plants—with deeper roots capable of reaching the water table—are less affected by short-term moisture fluctuations (O’Keefe et al., 2022). Rainfall promotes biomass through two of the three elements in CHOs. It also enhances local uptake of nutrients via mass flow (Marschner, 1995). If widespread, tradeoffs in the way functional groups access water, nutrients, and light may be promoting the “grassification” of prairies, especially when burning and grazing are curtailed.

## Nutrient dilution (and enrichment) on a changing prairie

The ionome dynamics on Konza has implications for positive and negative interactions between functional groups. Increases in functional group biomass drove Nutrient Dilution in 13 of the 17 elements over 30+ years (Figure 3, Appendix S1: Figures S6–S8). It was found for all four macro elements (including carbon), both membrane and electrolyte elements, four of seven catalysts, and one animal-essential element. Moreover, each functional group revealed its own ionomic pattern, with elements in grasses most commonly exhibiting nutrient dilution. The biomass of co-occurring functional groups also regularly drove down the elemental ppm of ionomes, especially for grasses. This implicates competitive soil nutrient depletion as a separate mechanism for Nutrient Dilution, in contrast to the accumulation of an individual’s CHO-rich biomass (i.e., Nutrient Dilution by Growth).

To our surprise, nutrient enrichment effects were also widespread. Some responses are consistent with the mechanism of nutrient dilution by growth (e.g., in plots with high forb biomass, carbon made up a larger part of the grass, suggesting grasses were building taller plants, Figure 3). At the same time, high biomass years for forbs promote higher tissue ppm of carbon, potassium, molybdenum, and cobalt. How do these potential ionomic subsidies between groups work? Consider molybdenum, a

key metal in nitrogen fixation (Frausto da Silva & Williams, 2001). In years of high forb biomass on Konza, detritus from nitrogen-fixing forbs like *Baptisia* and *Amorpha* may leach molybdenum into the soil to be passively absorbed by grasses (Kaspari et al., 2021). An alternate hypothesis is that higher intergroup competition demands increased investment in nutrients as a counter-measure (Kaspari et al. in review). Experimental litter transplants would efficiently address the first hypothesis, while combinations of fertilization and plant density manipulations would address the second.

In contrast, we found no evidence for nutrient deposition effects from aerosols. Only the availability of C, H, O (via CO<sub>2</sub> and precipitation) and perhaps soil nitrogen (see previous section) drove ionomic change in our analysis.

Finally, our most unexpected result was how CO<sub>2</sub>—ceteris paribus—frequently *promoted* higher ionomic ppm. In forbs, 8 elements (phosphorus, calcium, copper, magnesium, manganese, sodium, zinc, and chromium) increased with levels of CO<sub>2</sub>. Such increases in CO<sub>2</sub> were associated with nutrient enhancement of only two elements in grasses (iron and chromium) and woody plants (copper and magnesium). For the nutrient-rich forb, increasing CO<sub>2</sub> may be providing the metabolic fuel needed to further enhance its enriched ionome.

## Consumers will find more nutrient-poor grass and less nutrient-rich forbs

Evidence accumulates for the widespread decline of plant consumers (Atwood et al., 2020; Kaspari & Welti, 2024; Welti & Kaspari, 2024). These populations of detritivores and herbivores are limited by the nutrient density and availability of macro and micronutrients in plant tissues (Prather et al., 2020). For the grasshoppers, a group that consumes as much foliage on Konza as the ungulates (Jonas & Joern, 2007), declines in grass ionomic ppm are associated with 2% declines per annum in population density (Welti et al., 2020). This is likely due at least in part to slowing maturation rates (Kaspari et al., 2022) and the need to consume more food but for lower returns in fecundity (Robinson et al., 2012; Stiling & Cornelissen, 2007).

Our results suggest that herbivores in the elevated CO<sub>2</sub> Anthropocene will encounter grasslands with more CHOs, abundant but less nutritious grass, and reduced access to high-nutrient forbs. If consumers equate “more elements” with “more nutrients,” then the declining ionomic ppm of grasses and declining abundance of forbs predict further declines in both grass and forb feeders, and an accumulation of the latter on unburned watersheds. If, in addition, consumers specialize on host

plants—a trait especially common among forb-feeders (Rosenthal & Janzen, 1979)—this has the potential to magnify declines in (highly edible) forb abundance if forbs become nutritious islands in a grassy nutritional desert. As forbs already represent the most diverse and least abundant component of grasslands (Bråthen et al., 2021), their declines should ramify through the prairie food web.

## Caveats and future directions

This study benefits from Konza LTER’s long-term datasets for soil, atmospheric, and plant chemistry. The unique data that come from ecosystem scale experiments also come with unique constraints. For example, Konza’s 30+ year annual samples of plant biomass and chemistry come from three watersheds 59–135 ha in size, each sampled by four transects arrayed from ridge to valley, 50–200 m apart (Ratajczak, 2023). As each watershed has its unique, experimental burn history, our domain of inference regarding the impact of burns on biomass and ionomics is similarly constrained. Moreover, while time is a highly precise and accurate proxy for CO<sub>2</sub>—which has been experimentally linked with Nutrient Dilution via FACE experiments (Loladze, 2014)—other changes with time not documented here may contribute to the variety of CO<sub>2</sub> effects. Similarly, the ubiquitous effects of functional group biomass on nutrient density (Figure 3)—can be further explored with field experiments. The effects of targeted plant removals on competitor ionomes are of particular interest.

All three of our watersheds excluded large ungulate grazers (in this system, bison, and cattle). Bison, in particular, are historical drivers of forb abundance and diversity (Bråthen et al., 2021; Ratajczak et al., 2022) preferring grasses over forbs and woody plants (Knapp et al., 1999). Grazers increase nitrogen availability for plants on Konza via deposition of feces and urine (Anguiano et al., 2024). Ungulates (and their microbiomes) have distinctive effects on plant chemistry: plant ionomes across 54 grasslands were richer in metals associated with bacteria in sites grazed by cattle (Kaspari et al., 2021). How grazer diet selection and excreta interact with burning and functional group effects on the ionome is a question of high priority.

Finally, we highlight two directions for future work. By provisionally organizing essential elements by metabolic function Figure 3, suggests several patterns in the ecological regulation of plant ionomes across functional groups. For example, the catalytic metals (often classified as “micronutrients,” Kaspari, 2021) are diluted in grasses as forb biomass increases, are enhanced in forbs as CO<sub>2</sub> increases, and fail to vary much in the woody plants. As

these metals are key to the function of enzymes and transporters (Frausto da Silva & Williams, 2001), our results suggest the role of competition with forbs in decreasing a key element of grass performance, and that of CO<sub>2</sub> enrichment in promoting a key ionomic niche of forbs. Likewise, while grasses and woody plants—that rely on reaching the canopy—adjust electrolytes to competition with the other functional groups, these responses are absent in lower stature forbs. Finally, the nutrient dilution of Ca and B—two critical elements in the structural integrity of cell membranes and walls—is apparent in grasses and forbs but not in woody plants whose structural integrity relies more on lignins. The reader may see more working hypotheses in our data.

Herbivores are also a major player shaping grasslands (Anguiano et al., 2024; Jonas & Joern, 2007; Knapp et al., 1999; McNaughton, 1984; Ratajczak et al., 2022; Rosenthal & Janzen, 1979). A second, functional direction would explore the ionomics of herbivory. For example, grasses are defended by silicon (Orians & Milewski, 2007; Vogel, 2008). Unfortunately, due to lab error, Si was left out of our ionomic analyses. Similarly, some chemical defenses in forbs are based on nitrogen (e.g., alkaloids) and elevated levels of ionomes could be linked to enhanced defense investment (Rosenthal & Janzen, 1979). Additionally, key compounds such as essential amino acids, lipids, and non-structural carbohydrates can be limiting to herbivores but cannot be assessed by elemental analyses alone (Behmer, 2009). Understanding how herbivory varies across the ionomic gradients and functional group abundance will provide clues as to the relationships between plant ionomes and edibility (Welti & Kaspari, 2021).

## Long-term monitoring is our window into a changing Earth

The outdoor laboratory of Konza LTER provides a myriad of insights into long-term shifts in biogeochemistry and grassland ecosystems. Here, we identify an increase in grass biomass over three decades that paralleled declines in grass tissue concentrations of key elements used to build food webs. Forbs also exhibited some evidence of nutrient dilution by Growth during periods of high biomass but weakly declined in their biomass over time in these ungrazed sites. Finally, woody plants greatly expanded when burned infrequently, with evidence of CO<sub>2</sub> driven declines in their nitrogen concentrations. Across functional groups, these changes suggest increasingly challenging conditions for nutrition-limited herbivores. Considering the strong effects of human activities on biogeochemical rates (Schlesinger et al.,

2011), further governed by ongoing changes in regulatory legislation (Kanter et al., 2020) and the high potential for effects of changing nutrient availability on biotic systems (Wetzel et al., 2016) long-term monitoring endeavors such as NSF's LTER program are paramount.

## ACKNOWLEDGMENTS

We are grateful to the ecologists of Konza Prairie and other scientists who take on the challenge of long-term monitoring. This project was funded by NSF DEB 105393900 for the field portion and DEB 105446600 for the analysis and writing portion of this project.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Plant ionomics data (Kaspari, 2025) are available in the Open Science Framework repository at <https://doi.org/10.17605/OSF.IO/GZX3N>. Additional data are available in the Environmental Data Initiative (EDI) Data Portal as follows: Blair (2023a), <https://doi.org/10.6073/pasta/295644787ee8a1c00edd6f48dde75c4e>; Blair (2023b), <https://doi.org/10.6073/pasta/73fb69230e21d5a2647a1bd86beba595>; Blair and Nippert (2025) <https://doi.org/10.6073/pasta/38206ea12b42bbd77ad97e1c0747353d>; Ratajczak (2023), <https://doi.org/10.6073/pasta/128eabc592716cc9805dece31e70515>.

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## SUPPORTING INFORMATION

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

**How to cite this article:** Kaspari, Michael, and Ellen A. R. Welti. 2025. "Drivers of 30 years of Ionomic Change on a North American Tallgrass Prairie." *Ecology* 106(11): e70266. <https://doi.org/10.1002/ecy.70266>