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OPINION PAPER

Juniper (*Juniperus virginiana*) encroachment into grassland results in increased trace-element inputs

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Abstract

Background and aims Woody plant encroachment poses a significant threat to grasslands globally, and in the southcentral USA, juniper (*Juniperus virginiana*) is rapidly taking over large areas of grasslands. Despite ongoing research, the reasons behind the rapid encroachment of juniper species in Oklahoma remain elusive. We hypothesized that the interaction between juniper canopy, aeolian, and wet-deposition processes lead to a modification in trace-element inputs through stemflow and throughfall. This, in turn, plays a crucial role in determining the success of juniper encroachment.

Methods We measured the influx of trace-elements in stemflow and throughfall beneath juniper canopies of different sizes, contrasting the results with those obtained under ambient precipitation.

Results Our research unveiled a significant influence of the juniper canopy on trace-element inputs via stemflow and throughfall. Specifically, there was a significant increase in manganese, boron, and chlorine inputs, coupled with a decrease in copper inputs. Additionally, there was an increase in most cations and sulfate.

Results Our results indicate that juniper encroachment alters the profile of trace-element, cation, and anion inputs beneath their canopies. Increased levels of manganese and reduction of copper inputs into the ecosystem may enhance the juniper growth, creating a positive feedback mechanism that could contribute to the success of juniper and other woody encroachers.

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Introduction

Globally, grassland area has decreased with 70% of historic grasslands converted to pastures or farmland (Foley et al. 2011). Most remaining grasslands have been encroached upon by woody species (Anadón et al. 2014), which may result in a transition to woody-dominated systems. Woody plant encroachment in the southern Great Plains, particularly by juniper species (e.g., eastern redcedar (*Juniperus virginiana*) and mesquite species (e.g., honey mesquite [*Prosopis glandulosa*]), have significant impacts on the region's ecosystems and human activities. Grassland loss can substantially reduce the abundance and diversity of grassland-dependent birds, such as lesser prairie chickens (*Tympanuchus pallidicinctus*), and small mammals (Coppedge et al. 2001; Fuhlendorf et al. 2002; Horncastle et al. 2005). Grassland and savanna conversion into woodlands or shrublands can lead to increased water use and reduced water availability for other plant species and humans (Huxman et al. 2005; Zou et al. 2018; Zhong et al. 2020). Furthermore, woody plant encroachment can reduce rangeland productivity, limit livestock and deer forage availability (McKinney et al. 2023), and increase costs of management and control efforts (Anadón et al. 2014; Simonsen et al. 2015).

Juniper has been able to rapidly encroach into grasslands (Wang et al. 2018) where other woody species such as oak (*Quercus* spp.) have not. In the southcentral Great Plains, eastern redcedar is typically the sole encroacher (Briggs et al. 2002). Many studies have attributed eastern redcedar's success to anthropogenically induced disturbances such as fire exclusion and grazing regimes (Blewett et al. 1986; Holthuijzen and Sharik 1985; Horncastle et al. 2004). Others have suggested that species-specific attributes such as drought resistance and abundant seed dispersal may drive eastern redcedar encroachment (Blewett et al. 1986; Eggemeyer et al. 2006; Volder et al. 2010). Additionally, juniper trees are evergreen, retaining foliage throughout the year, which is a stark contrast to the deciduous nature of many native woody species in the southern Great Plains (*personal observation*). Juniper trees, especially in open grasslands, often exhibit a high leaf area index (2.5–12.7) that efficiently captures aeolian nutrients through dry deposition (Hicks and Dugas 1998). Despite this observation, there is a critical research gap as no study has systematically quantified the trace-element, cation, and anion influx in stemflow and throughfall beneath juniper canopies or the potential role of altered nutrient input in influencing the juniper establishment in grasslands.

In arid and semi-arid landscapes, trees influence nutrient influx to the soil via the interaction of canopy, aeolian processes (Field et al. 2012), and wet-deposition processes. For example, precipitation carrying nutrients in the form of dust travels through the canopy and/or dust is collected by the emergent tree canopies and subsequently washed into the soil through stemflow and throughfall. The "islands of fertility" effect (Garcia-Moya and McKell, 1970) has been well established in arid and semi-arid regions, i.e., shrubs and trees growing in deserts or grasslands increase macronutrients under themselves. Recent work found that in addition to the increase in macronutrients via the "islands of fertility" effect, trees and shrubs can alter trace-element influx. For example, some trace-elements (Cu and B) increased under shrubs and trees, while another trace-element (Fe) was higher in grasslands (Woods et al. 2022). Furthermore, trees and shrubs can increase the amount of cations (Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}), which may ultimately increase soil exchangeable cations (Ward et al. 2018; Woods et al. 2022). Many soil exchangeable cations and anions are elements (e.g., Ca^{2+}, Mg^{2+}, K^{+}, NO_3^{-}, etc.) that are tree "macronutrients" (Brady and Weil 2008). Thus, increasing these cations and anions under woody species may increase woody encroachment rates when these nutrients are limiting in the rest of the ecosystem, as nutrient limitations constrain primary production (Menge et al. 2009).

Relatively recent work hypothesized that the difference in trace-elements or micronutrients input with precipitation may drive woody encroachment success. Mills et al. (2017) showed that the Cu: Mn ratio was the single best predictor of woody encroachment into grasslands after manipulating soil micronutrient availability (via fertilization) of the grassland's soils. Specifically, Mills et al. (2017) showed that a decrease in the Cu: Mn ratio was associated with woody plant

Table 1 Average aboveground morphological characteristics of the 15 eastern redcedar seedlings (*J. virginiana*) in this study

Tree size	Stem height (cm)	Diameter at root collar (cm)	Crown short axis (cm)	Crown long axis (cm)	Crown area (cm^2)
	Mean ± SD*	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Small	74 ± 16	1.6 ± 0.5	39 ± 7	45 ± 8	1415 ± 486
Medium	153 ± 34	3.8 ± 1.1	95 ± 36	102 ± 38	8476 ± 6498
Large	275 ± 39	8.0 ± 1.1	179 ± 44	186 ± 45	27,344 ± 12,085

*SD stands for standard deviation

encroachment. Across Oklahoma, Mn concentrations in soils decrease from east to west, whereas geographically Cu concentrations do not change (Carpenter, 1980). Eastern redcedar encroachment has occurred across the state of Oklahoma but has not been as rapid as in the east (Wang et al. 2018). Further work on plant growth limitation due to trace-elements has shown that B concentrations can also be very important for plant growth (Lannes et al. 2020; Mills et al. 2020, 2023), and prevention of tree encroachment into grasslands (Mills et al. 2020, 2023). Eastern redcedars may be able to alter the nutrient input profile with precipitation, as has been shown in other species (Ward et al. 2018; Woods et al. 2022), which may enhance eastern redcedars ability to encroach into the unencroached areas of Oklahoma.

For this study, our objective was to compare element inputs in stemflow and throughfall under encroaching eastern redcedar trees versus ambient precipitation. We hypothesized that: (1) due to stemflow and throughfall effects, trace-element deposition and pH would increase under trees relative to open (grassy) areas; and (2) copper (Cu) to manganese (Mn) ratio in throughfall and stemflow would be lower under trees; and (3) cation and anion deposition would increase under trees relative to open (grassy) areas.

Materials and methods

Study site

This study was conducted in a grassland approximately 10 ha in size near Lake McMurtry Service Road in Stillwater, OK USA (36°10'58''N, 97° 11'29''W). Mean annual precipitation at this location typically averages 850 mm with a mean annual potential evapotranspiration average of 1170 mm (Wine and Zou 2012). Herbaceous vegetation at this location was dominated by warm-season C_4 grasses including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Eastern redcedar encroachment into the grassland was in its early phase with canopy coverage less than 30% and tree heights ranging from less than 0.5 m to nearly 3 m.

We randomly selected 15 eastern redcedar trees close to the center of the grassland and divided them into three size classes: small (under 1 m in height), medium (1–2 m in height), and large (> 2 m in height) in spring 2016 (Table 1). For each tree, stemflow and throughfall collectors were installed. Stemflow collection followed the same methodology as in Zou et al. (2015). Briefly, a metal collar with plastic tubing was sealed to each tree. The attached plastic tube allowed collected precipitation to run out to the edge of the canopy for collection in a container prior to nutrient analysis. Throughfall collectors were water-resistant trays made of PVC pipes. Throughfall collector length was determined by the average diameter of the canopy of each size group. Collecting areas were 70, 236, and 480 cm^2 for small, medium, and large size groups, respectively. Tray lengths varied by canopy size. Tray collection lengths ranged from 20 cm, 40–100 cm, and 100–150 cm, for small, medium, and large size groups, respectively. For each tree, trays ran from the bole to the canopy edge and were anchored in a way that water could naturally flow into rain collectors via attached plastic tubing. Additionally, at random locations (> 3 m away from any tree canopy edge), five manual rain gauges were installed above the grassy canopy to quantify precipitation and collect water samples for open grassland. Rain gauges were 35 cm in height and 5 cm in radius

(Productive Alternatives, Inc., Fergus Falls, MN). From May 2016 to May 2017, 30 complete rainfall events for a total rainfall of 469.6 mm were observed and analyzed. Some other precipitation events were missed due to equipment failure and were therefore not reported here. Minimum rainfall amount in a single event was 1.1 mm, while the maximum was 72.7 mm. Rainfall events that were not fully collected or samples that took longer than 6 h to transport to the laboratory were excluded from the analysis.

Water sample analysis

Within several hours of each rain event, precipitation samples were collected and volume was determined at the study site. Prior to element testing, samples were combined into a composite sample based on tree class size (one sample each from small, medium, and large groupings) or open collector ($n = 1$). From the composite samples, 200 mL were transported to the laboratory for chemical analysis. Then water samples were filtered through 0.45 µm membranes. Element concentrations and pH analyses were performed by Oklahoma State University Soil, Water and Forage Analytical Laboratory (SWFAL). Sodium, K^+, Ca^{2+}, Mg^{2+}, B, Zn, Cu, Mn, Fe, and P were determined by inductively coupled plasma (ICP) spectrometers (Spectro-Ametek. Kleve, Germany), NO_3^-, Cl^-, SO_4^{2-}, and NH_4^+ by flow-injection auto-analyzer (Lachat, Milwaukee, WI), and HCO_3^- by titration. Annual means for different elements or compounds in the open and under trees can be found in Table S1. All analyses followed standard procedures with adequate quality control measures as described in Lipps et al. 2023.

Statistical analysis

Element data were scaled to a per-canopy area basis. Specifically, elemental input was calculated as shown:

$$\textit{Elemental input}\left(mg\ m^{-2}\right) = \frac{\textit{Throughfall volume}\ (L)\times\left(\frac{\textit{crown area}\left(m^2\right)-\textit{basal area}\left(m^2\right)}{\textit{tray area}\left(m^2\right)}\right)\times\textit{Throughfall element}\left(mgL^{-1}\right)+\textit{Stemflow volume}\ (\mathrm{L})\times\textit{Stemflow element}\left(mgL^{-1}\right)}{\textit{Canopy area}\left(m^2\right)}$$

Element input data were then summed for all sampling events (across 13 months). Changes in the annual input of a trace-element, cation, or anion were determined by calculating the ratio between the under-tree input and average ambient air input. To get average pH under trees, fractional inputs from stemflow and throughfall were divided by their respective canopy area and then summed.

Multiple trees within 3 different size classes (small, medium, and large) were combined to form experimental units ($n = 3$). Size was accounted for to ensure that any effects of canopy size and the related amounts of collected elements or nutrients were not simply due to tree size. One-sided student's t-tests of the three tree size classes against average ambient precipitation from open (grassy) areas ($n = 1$) were conducted. Values of 1 indicated no difference in the ratio of trace-elements input between grassy (open) areas and under trees. All statistical analyses were conducted in R 4.2.3 (R Core team 2023).

Results

Of the trace-elements examined, Cu was significantly reduced under trees (total elemental input) compared to ambient precipitation collected (trees/open areas = 0.65; $p = 0.007$) (mg m^{-2}/ mg m^{-2}), whereas Mn was significantly elevated under trees (ratio = 7.67; $p = 0.029$) (Fig. 1). Specifically, eastern redcedars increased the amount of Mn inputs by an average of ~8x the amount of annual input from ambient precipitation (Fig. 1b). Conversely, Cu under eastern redcedars was reduced to 65% of the average annual input received from ambient precipitation. Other significantly increased trace-elements were B and Cl ($p = 0.020$ and 0.048, respectively) (Fig. 1). Boron and Cl inputs were increased relative to grasses by 1.32x and 2.27x, respectively. Iron and Zn were not significantly different under trees relative to area under ambient precipitation ($p > 0.05$) (Fig. 1). Additionally, the Cu: Mn ratio

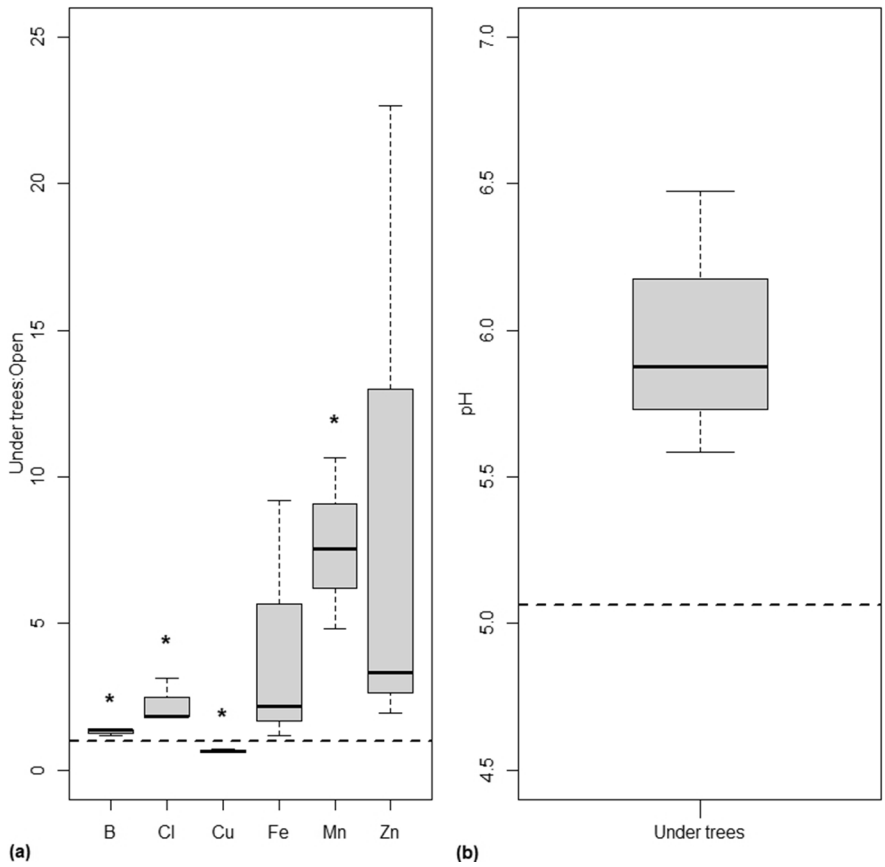


Fig. 1 Effect of trees on trace-element and pH annual inputs. **a** Box-and-whisker plots of annual ratios of trace-element inputs (Boron [B], Chlorine [Cl], Copper [Cu], Iron [Fe], Manganese [Mn], and Zinc [Zn]) inputs under trees versus ambient precipitation (mg m^{-2}/ mg m^{-2}). The boxplots with an (*) indicate significant differences ($p < 0.05$) under eastern redcedars. Values above 1 indicate that areas under trees had higher input of that element. Values below 1 indicate that ambient precipitation had higher input of that element. **b** Box-and-whisker plots of the pH of area scaled average stemflow and throughfall under trees. The dotted line indicates the pH value of areas ambient precipitation. A boxplot with an (*) indicates a significant difference ($p < 0.05$) under eastern redcedars in combined stemflow and throughfall pH

was significantly reduced under trees (0.15 ± 0.03 SE) relative to area under ambient precipitation (1.58) ($p < 0.001$). pH of the overall throughfall and stemflow under trees (5.98) was not significantly increased compared to ambient precipitation (5.59) ($p = 0.136$) (Fig. 1).

Most cations and half of the anions had elevated inputs under trees relative to ambient precipitation. Specifically: Ca^{2+}, K^{+}, Mg^{2+}, and Na^{+} were significantly elevated (tree/ambient precipitation = 2.22, 3.63, 2.39, and 2.06, respectively; $p = 0.018$, 0.014, 0.002, and 0.001, respectively) (Fig. 2a). Of the anions measured, only SO_4^{2-} was elevated under trees relative to ambient precipitation (tree/ambient precipitation = 3.33; $p = 0.003$) (Fig. 2b). NH_4^{+}, and NO_3^{-} were not significantly different under trees than in ambient precipitation ($p > 0.05$) (Fig. 2).

Discussion

Trace-element inputs

Our hypothesis that pH and trace-elements would increase under trees had mixed support, i.e., B, Cl, and Mn increased, Cu decreased, and Fe and Zn were not significantly altered. Conflicting evidence for Cu and Mn has been reported from other studies (Mills et al. 2016, 2017; Ward et al. 2018; Woods et al. 2022). Specifically, Cu was found to be higher in grasslands soil

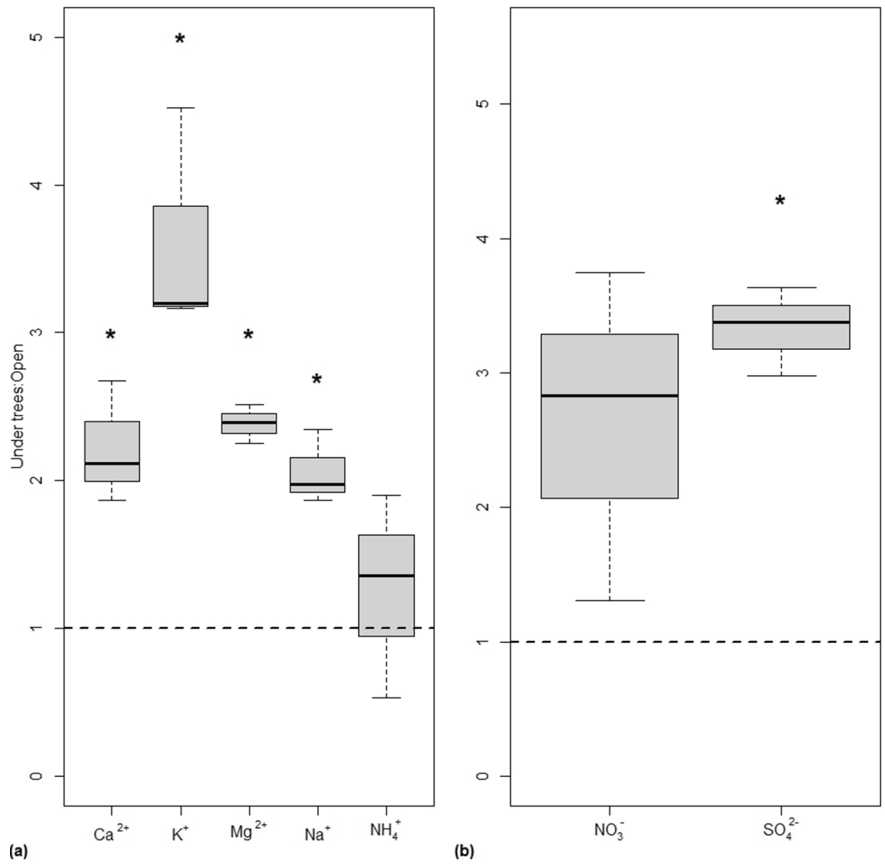


Fig. 2 Effect of trees on cation and anion nutrient annual inputs. **a** Box-and-whisker plots of ratios of annual cation (Sodium [Na^+], Potassium [K^+], Calcium [Ca^{2+}], Magnesium [Mg^{2+}], and Ammonium [NH_4^+]) inputs (mg m^{-2}/mg m^{-2}) under trees versus in ambient precipitation. The boxplots with an (*) indicate significant differences ($p < 0.05$) between the different cover types. See Fig. 1 for explanation as to which cover type has more input for the given element with relation to a ratio of 1. **b** Box-and-whisker plots of annual anion (Nitrate [NO_3^-] and Sulfate [SO_4^{2-}]) inputs in ambient precipitation versus under trees. Boxplots with an (*) indicate significant differences ($p < 0.05$) between the different cover types

by Mills et al. (2016), while Woods et al. (2022) and Mills et al. (2017) found higher Cu levels under forest canopy than grasslands. Manganese was found to be similar in the soils between grasslands and forests (Mills et al. 2016; Woods et al. 2022) or was higher under woody species (Mills et al. 2017; Ward et al. 2018). Our findings indicated that trees increase the B in the soil, as has been shown in some studies (Mills et al. 2017; Ward et al. 2018). Zinc, on the other hand, was generally shown to be the same in the soils under grasslands or woody species (Mills et al. 2016, 2017; Woods et al. 2022). Additionally, Fe has been shown to decrease in the soils under tree canopies relative to grasslands (Mills et al. 2012, 2016; Woods et al. 2022), but here we found no difference between ambient precipitation inputs and under tree inputs of either Zn or Fe. Most of these prior studies examined soils and not nutrient inputs via stemflow and throughfall. Therefore, it is likely that these studies were affected by plant uptake and rhizosphere processes (Jobbágy and Jackson 2004), while our measurements focused solely on trace-element inputs carried by precipitation. Additionally, these groups' measurements were taken from different geographical areas, which likely had different aerosol contents.

Cu: Mn ratio

We found evidence to support our hypothesis that Cu: Mn ratio in combined throughfall and stemflow would be lower under trees than in ambient precipitation. The ratios we found were substantially larger than those found in mesic Australia (0.018–0.029 under trees and grassland, respectively) (Mills et al. 2016), but our study was done in stemflow and throughfall and not soils. While we assume that greater inputs led to greater soil values for all the elements or compounds we found elevated or decreased, relating inputs to availability is the next step. Further examination at our location might show an even smaller ratio of Cu: Mn in Oklahoma soils, as trees need to use the Cu present in the soil, while simultaneously reducing the amount of Cu input to the soil via

precipitation. Further experimentation is necessary to confirm the stemflow and throughfall input effects in soils. Trees also need to use the Mn in the soil, but the effect will be much less, as the stemflow and throughfall substantially amplify the amount of Mn added to the soil relative to grasslands. Therefore, over time it is likely that the Cu: Mn ratio difference in the soil between cover types would grow larger. Our throughfall and stemflow differences in Cu and Mn indicate that differences in the Cu: Mn ratio previously found in soils is likely due to differences in inputs as well as root uptake of different vegetation types.

The prevailing explanations of eastern redcedar encroachment include increased grazing and lack of fire (van Auken 2000). However, an experiment within the South African savanna showed that the strongest predictor of woody encroachment was soil concentrations of Cu and Mn, as well as the ratio between them (Mills et al. 2017). Furthermore, in an experiment, Mills et al. (2017) showed that under certain Cu: Mn ratios, there was no woody encroachment at all. Mills et al. (2017) indicated from this experiment that woody encroachment may be limited by the trace-elements present in the soil of different grasslands. Unfortunately, this study has never been replicated, to our knowledge, so it is unclear if the drivers of this Cu: Mn gradient are maintaining the grassland areas over the woody encroached areas or if Cu: Mn ratio shifts due to woody encroachment itself.

Cation and anion inputs

For cation and anion inputs, we found that Ca^{2+}, K^+, Na^+, Mg^{2+}, and SO_4^{2-} were significantly increased, while NH_4^+ and NO_3^- were not significantly different under trees relative to ambient precipitation (Fig. 2). In soil studies, conflicting results have been shown for Ca^{2+}, Mg^{2+}, K^+, and Na^+ (Mills et al. 2012, 2016; Ward et al. 2018; Woods et al. 2022). Some studies found increased pH, NO_3^-, and S (Mills et al. 2012; Ward et al. 2018). NH_4^+ was lower on woody encroached sites in one study (Woods et al. 2022). In a stemflow study, pH, Cl, Ca^{2+}, Mg^{2+}, K^+, Na^+, and SO_4^{2-} were all significantly greater with one tree species relative to another, which suggests that the input of these elements into the soil via precipitation can be influenced by the tree species that make up the canopy (Levia et al. 2011).

Foliar leaching and uptake on stemflow and throughfall chemistry

One explanation for the differences between precipitation and under eastern redcedar canopies in elemental composition is accumulation of aerosols that are then washed down with rainfall. However, foliar leaching may also play a role. Leaching is a large factor contributing to chemical alteration of rainfall before water hits the ground (Leininger and Winner 1988). In addition to nutrients in dry deposits, more elements can be leached out of leaves through elements and compounds being pulled from intercellular spaces connected to translocation systems within plants (Tukey et al. 1961; Parker 1983). Furthermore, leaching can occur from most aboveground plant organs (Silva and Rodríguez 2001). Of the elements, Na^+ and Mn are most easily leached from foliage, with K^+ at a slightly lesser rate (Parker 1983). This may explain why we saw such significantly increased levels of Mn, Na^+, and K^+ in throughfall relative to precipitation (Figs. 1, 2, and 3). Furthermore, grass leaves likely had some effect on elemental input levels with precipitation into the soil, but we did not measure this effect.

We also measured a reduction of Cu in stemflow and throughfall. This could be due to foliar uptake, which is the reverse of foliar leaching (Parker 1983). Absorption of mineral nutrients through foliage is well documented in agricultural crops (Wittwer and Teubner 1959). Foliar application studies have shown that leaves can absorb most elements at differing rates (Bukovac and Wittwer 1957). However, phloem transport may limit the absorption rate of different elements (Bukovac and Wittwer 1957). Additionally, certain elements may be absorbed at significantly less rates depending upon soil conditions and transpiration rate of plants (Niu et al. 2021). Ammonium is commonly known to have a fast foliar uptake rate, so it typically has a negative leaching rate (Parker 1983). However, here we did not find that NH_4^+ concentration of throughfall was less than that of precipitation collected in open areas (Fig. 2). Unlike NH_4^+, Cu showed a reduction in inputs under trees relative to open areas. Copper was likely taken up by tree foliage, which would have decreased the concentration of Cu in throughfall. Additionally, in general, increased or decreased input under trees relative to ambient precipitation was somewhat consistent over time (Fig. 3). This suggests that phenological events were likely not the cause of shifts in trace-element inputs.

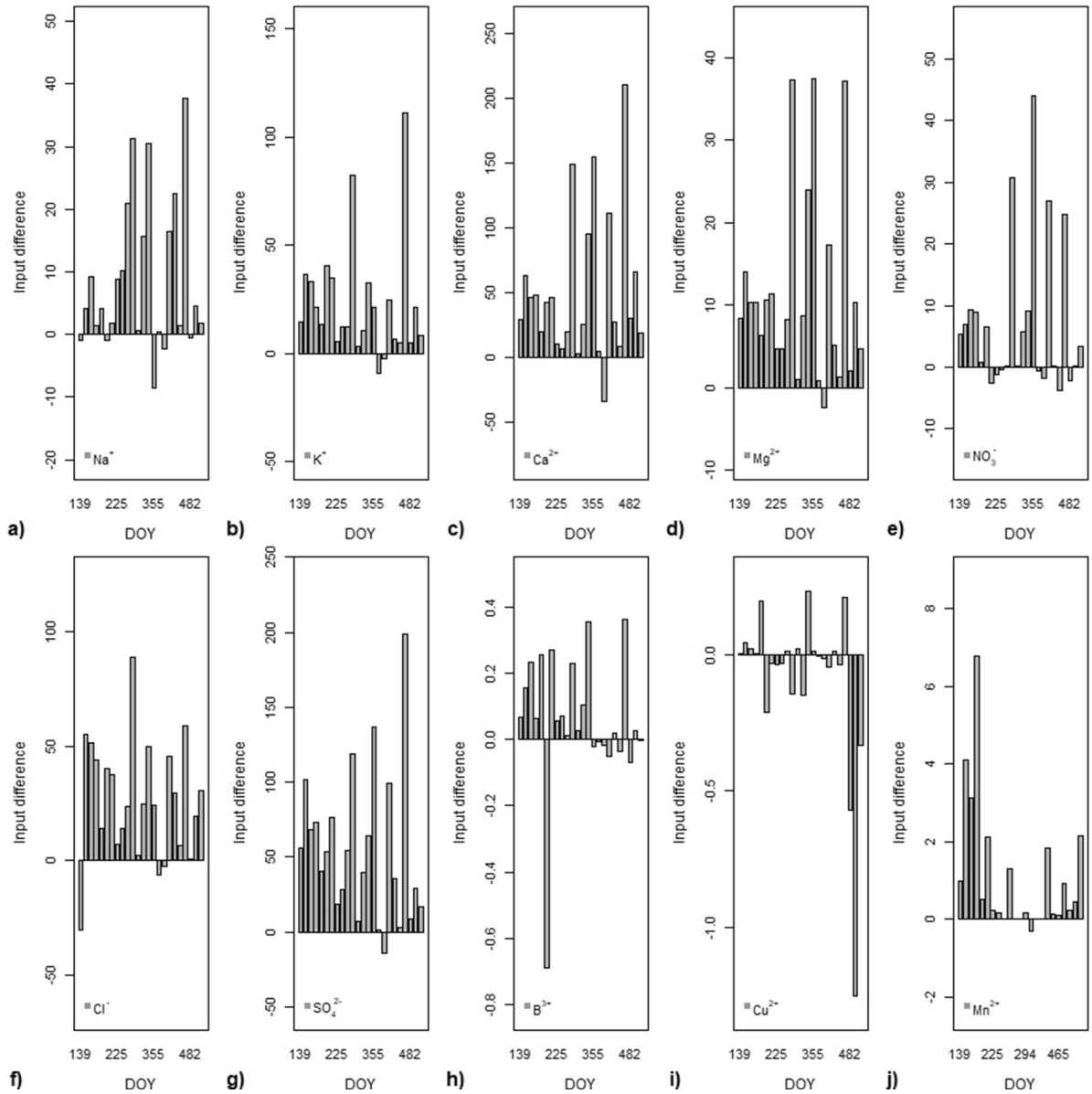


Fig. 3 Difference in input under trees for trace-elements, cations, and anions over 13 months. Gray bars represent the difference between the average under tree elemental input and ambient precipitation input (mg m^{-2}). Time is in day of year (DOY) for the period of collection. Only precipitation collection dates were displayed. When element concentrations in ambient precipitation and under trees were equivalent, the input difference was 0. Positive bars reflect more elemental input under trees than in ambient precipitation. Negative bars reflect more elemental input in ambient precipitation than under trees. Note that in each panel plots y-axis is scaled differently. Panels **a**) – **j**) represent Na^+, K^+, Ca^{2+}, Mg^{2+}, NO_3^-, Cl^-, SO_4^{2-}, B^{+3}, Cu^{+2}, and Mn^{+2}, respectively

Impact on Woody Encroachment in Oklahoma

Oklahoma has a clear geographic pattern of decreasing soil Mn, from east to west (Carpenter, 1980), as well as a decreasing gradient of eastern redcedar encroachment, from east to west (Wang et al. 2018). Agriculture may well have slowed eastern redcedar encroachment in western Oklahoma (Wang et al. 2018); however, if the reduction in eastern redcedar encroachment was due to a lower Mn concentration in soil, our work here suggests that

overtime woody plants will alter the soil trace-element input profile, which will likely enhance their capacity to encroach the west over time. Furthermore, some plants have been shown to accumulate Mn as a by-product of mobilizing phosphorus in soil (Lambers et al. 2015, 2021). This effect could be detrimental to grasses and other nearby plants if Mn were to continue to accumulate to toxic levels in soil. However, as rainfall increases from west to east (Wang et al. 2018), it is possible that the geographic distribution of Mn across Oklahoma is more related to precipitation than eastern redcedar encroachment. Inputs of manganese through rainfall are expected to exceed losses via leaching, particularly given the study showing relatively minimal leaching under areas dominated by eastern redcedar (Zou et al. 2014). Further experiments testing the viability of eastern redcedar establishment with reduced soil Mn concentrations would further elucidate the strength of this element on eastern redcedar encroachment.

Conclusions

Formation of eastern redcedar tree canopy in grassland shifts the trace-element, cation, and anion input profile. Specifically, eastern redcedars increased the amount of B, Cl, Mn, Ca^{2+}, K^{+}, Na^{+}, Mg^{2+}, and SO_4^{2-}, while decreasing Cu. This shift in the trace-element, cation, and anion input profile under trees may provide eastern redcedars with an advantage over nearby growing grasses. This may allow eastern redcedars to successfully encroach grasslands at a more rapid rate than other native woody species.

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Data Availability Data available upon request.

Declarations

Conflicts of interest There were no conflicts of interest.

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