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The effects of eastern red cedar (*Juniperus virginiana*) invasion and removal on a dry bluff prairie ecosystem

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Abstract Eastern red cedar (*Juniperus virginiana*) establishment increased dramatically in the tallgrass prairie biome of North America during the last 30 years. Since many of the remaining remnant prairies occur on steep, dry, and nutrient poor sites, threatened by the invasion of native and non-native woody species, it is important to understand how an invasive species such as eastern red cedar influences key environmental factors that may determine the future trajectory of these systems and whether abiotic and biotic components of the system are resilient following cedar removal. To address these issues we: (1) investigated the influence of eastern red cedar on micro-environmental factors; (2) evaluated how these micro-environmental factors responded to eastern red cedar removal; and (3) assessed the effect of eastern red cedar on herbaceous species germination and distribution. The invasion of eastern red cedar was associated with lower surface light availability and soil temperature, as seen in prior studies, but otherwise had effects distinct from those observed in prior studies. There was no effect of cedar on soil pH, and unlike prior studies, cedar patches had higher soil moisture compared to native C_4 prairie grass plots. Moreover, these effects had strong spatial signatures, with impacts of invasion on micro-environment and native vegetation differing dramatically with slope position and aspect. Three years after eastern red cedar was removed, micro-environmental factors and species composition became similar to the tree-free grass-dominated plots, indicating a significant capacity for recovery following possible cedar control. In a broader context, this study sheds light on the pathways and mechanisms driving the impacts of this biological invasion on dry, steep, nutrient poor systems and illustrates the capability of these systems to recover once the invading species is removed.

Keywords Biological invasion · *Juniperous virginiana* · Prairies

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Introduction

Woody vegetation has increased in abundance in the Great Plains and prairie-forest border region of the United States over the last century at the expense of relatively tree poor systems such as prairies and savannas (Bragg and Hulbert 1976; Hoch and Briggs

1998; Briggs et al. 2002b). Eastern red cedar (*Juniperus virginiana*, Carl Linnaeus), even though it is one of the most widely distributed conifers in the United States (Fowell 1965), while native, was historically not abundant in the prairie forest border region (Curtis 1959; Bragg and Hulbert 1976) because it is inhibited by fire. Eastern red cedar has increased dramatically in this region with the advent of fire suppression and decline of large ungulate populations (Bragg and Hulbert 1976; Onmsbee et al. 1976; Hoch and Briggs 1998; Briggs et al. 2002a). Schmidt and Leatherberry (1995) found that between the North Central Forest Inventory and Analysis (NCFIA) periods of 1962 and 1990 forest land cover increased by one million hectares in Illinois, Indiana, Iowa, and Missouri. A major component of this increase was eastern red cedar invasion into open grassland systems (Ferguson et al. 1968; Schmidt and Leatherberry 1995; Batek et al. 1999). Increases in fragmentation, suburbanization, and seed sources act as a positive feedback mechanism for this process by both increasing the invasion of eastern red cedar to the grassland community and decreasing land managers' ability to use fire as a management tool (Coppedge et al. 2001).

Disturbances such as fire may play a role in maintaining historical plant associations (Kota et al. 2007; During and Willems 1986). Eliminating this disturbance alters the ecological conditions on a site allowing for native and non-native species once absent or under-represented to invade and potentially dominate. Recently much discussion has centered on the terminology of invasion biology often distinguishing between native and non-native species invasions (Falk-Petersen et al. 2006). However, from the perspective of the conservation of a declining ecosystem, the impact of the invasion on ecosystem structure, composition, and function becomes the focus. As long as the dominance of one species, either native or non-native, is associated with loss of species richness the corresponding impact on community composition is similar (Meiners et al. 2001). Similar to other native and non-native invasive species Eastern red cedar invasion into the prairie system, even though it is native to the region, has multi-scale impacts including homogenization of community composition, altered species habitat, altered biogeochemical cycles and modification of disturbance regimes at a regional scale (Broadfoot 1951; Norris et al. 2001; Briggs et al. 2002a; Siemann and Rogers 2003; Reinhart et al. 2006). Large scale impacts such as these are characteristic of the threat to biodiversity that center around the biological invasions of non-native invasive species that has become the center of the biological invasion research currently (Blossey 1999) and therefore the invasion of a native species such as eastern red cedar poses a similar threat. The mechanism of invasion, impact of invasion, and the pathways that lead to system level impacts of eastern red cedar invasion are similar to those outlined for many non-native biological invasions (Siemann and Rogers 2003; Didham et al. 2005).

Previous studies provide useful information about the litter dynamics and canopy effects of eastern red cedar invasion in areas where it dominates flat to rolling and/or highly degraded sites. However, there is little information available on how eastern red cedar invasion affects steep, dry, nutrient-poor, intact prairie systems; and even less regarding the resilience of the system following removal of cedar. Of the remaining intact prairie or savannas nationwide, most occur in dry, nutrient-poor, shallow soils, and/or steep areas that were unsuitable for agricultural purposes. The effects of invasion may differ in these types of systems compared to flatter areas because of the effects of slope and of the existing soil properties. Directional effects, including those involving soil water, may be much more important on steep slope than flat ecosystems. It is critical to long-term maintenance and protection of the remaining prairie and savanna ecosystems to understand the effects of invasion on environmental conditions that may ameliorate or exacerbate the future success of eastern red cedar, and hypothetically move these systems into a new alternative stable state (Frelich and Reich 1999).

Biological invasions can alter environmental variables including sunlight and soil properties such as moisture, nitrogen, and Ph (Siemann and Rogers 2003; Batten et al. 2006; Reinhart et al. 2006). Prior studies illustrate that eastern red cedar cover characteristically results in increases in soil exchangeable Ca and decreases in soil moisture and soil temperature (Spurr 1940; Arend 1950; Broadfoot 1951; Vimmerstedt 1968). In these studies of abandoned fields, eastern red cedar decreased light penetration and hence soil temperature and decreased rain penetration leading to decreases in soil moisture. Soil calcium content generally increased as eastern red cedar became established (Spurr 1940; Broadfoot

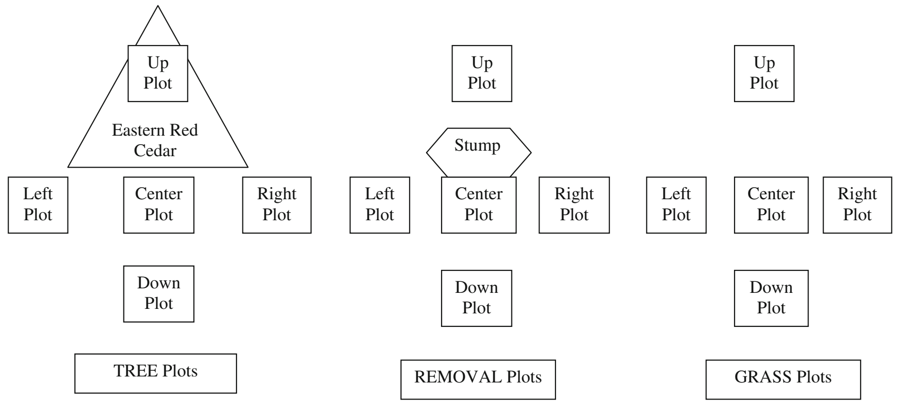

Fig. 1 Diagram outlining plot location based on slope position for each treatment (GRASS plots-areas within prairie without eastern red cedar, REMOVAL plots-areas where eastern red cedar tree was removed, and TREE plots-areas with eastern red cedar present). Slope positions include center of GRASS plots or stump (TREE and REMOVAL plots), *down slope*, *left slope*, *right slope*, and *up slope*

1951), presumably the result of the relatively (compared to pine and most oak species) high calcium content of the eastern red cedar litter (Arend 1950; Vimmerstedt 1968). Increased soil calcium and findings of higher excess-base levels (base content remaining after decomposition) could explain the increase in soil pH observed under eastern red cedar trees (Broadfoot and Pierre 1939). Additionally, eastern red cedar decomposition rate is slower than that of common prairie grasses potentially affecting fundamental ecosystem processes such as nitrogen cycling (Broadfoot 1951; Norris et al. 2001).

The current study was designed to explore how invasion of the native eastern red cedar affects the bluff prairie ecosystem by changing structure and species composition and thereby affecting light availability, nutrient cycling and other soil properties. We investigated the issues surrounding eastern red cedar invasion through a 3-year field study examining soil exchangeable base-cation concentrations, soil nutrient concentration and dynamics, and composition patterns under three different treatment conditions: (1) the presence of eastern red cedar trees (TREE plots), (2) the absence of eastern red cedar trees (GRASS plots), and (3) removal of existing eastern red cedar trees at the beginning of the experiment (REMOVAL plots). Due to the differences in topography between these bluff prairie systems and other systems examined in prior biological invasion research, treatments were further divided into five categories based on slope location or direction around the eastern red cedar trunks (up-slope, right-slope, left-slope, down-slope and center; (Fig. 1), leading to the following series of questions: How does eastern red cedar presence alter light availability, nutrient dynamics, soil moisture, soil temperature, and soil base cations and is the magnitude of these effects influenced by slope position around the tree (Fig. 1)? Once the eastern red cedar tree is removed, do environmental factors begin to approach those in areas unaffected when compared to areas where eastern red cedar remains? Do the effects of eastern red cedar on environmental factors such as light availability, soil moisture, and soil temperature affect ground layer plant species germination and distribution? Likely one of the most important portions of this study, from a conservation aspect, is the examination of how prairie systems respond once eastern red cedar is removed, helping to answer questions relevant to the recovery of this and other dry nutrient poor systems. This will also help distinguish aspects of eastern red cedar tree invasion that are simply due to the presence of the tree canopy from the possibly longer lasting aspects that are due to changes in soil properties and litter chemistry.

Methods

Study site and vegetation description

The research area consists of bluff prairie plant communities on extremely shallow soils that are N and water limited (Minnesota Department of Natural

Resources 2005). The taxonomic class of the soils on this site is loamy-skeletal, carbonatic, Entic Hapludolls of the Brodale series (United States Department of Agriculture Soil Conservation Service 1994). These soils are excessively drained very fine sandy loam with low available water capacity on south-southwest facing steep slopes (35–45%) (United States Department of Agriculture Soil Conservation Service 1994). The research sites lie within the Minnesota Department of Natural Resources (2005). Ecological Classification System Blufflland Subsection, of Minnesota in Goodhue (lat. 44.52°N, Long. 92.53°W and lat. 44.49°N, Long. 92.44°W) and Winona (lat. 44.18°N, Long. 91.99°W and lat. 44.19°N, Long. 91.99°W) counties. Average rainfall from May to August during the 3-year span of this study was 59.0 cm and average temperature was 19.3°C during the 3-year span (University of Minnesota Extension 2005).

Four bluff prairie sites were randomly selected from a list of bluff prairies with public ownership, south to southwest facing aspect, no current history of grazing (last 40 years), dominated by prairie species, and location at approximately 305 m elevation. Eastern red cedar stem density ranged from 56.7 to 63.1 stems/hectare, the average stand age was 40–35 years (Minnesota Department of Natural Resources 2008).

Experimental design

To determine the effects of eastern red cedar on the bluff prairie system, nine 4 m^2 plots on each of the four bluff prairie sites were selected: (1) three plots with eastern red cedar (TREE plots), (2) three plots where eastern red cedar was removed (cut) at the beginning of the experiment (REMOVAL plots), and (3) three plots showing no evidence of eastern red cedar presence (GRASS plots). All eastern red cedar trees were identified on each bluff and the TREE and REMOVAL treatments were randomly selected from these. GRASS plots were randomly located within areas unaffected by eastern red cedar presence. Trees were cut at the base of the trunk no more than 10 cm above the soil and removed. Soil remained undisturbed by this method of tree removal. Average age of trees sampled in TREE plots was 36.7 years and the average age of trees removed from REMOVAL plots was 38.67 years. Four 0.5 m × 0.5 m plots were established at the drip line of each TREE and REMOVAL plot (up slope, down slope, and one on either side of the tree) and similarly 1.5 m from the center of each GRASS plots and one plot was established at the trunk of TREE and REMOVAL plots and at the center of GRASS plots (Fig. 1). Environmental data were measured in each of these plots, including soil net N-mineralization, pH, exchangeable cations, carbon (C), and nitrogen (N); light availability at 2-m level and ground level; and bi-weekly soil moisture and temperature during the growing season.

Soil nutrients and other characteristics

Net N-mineralization and net nitrification were measured (2003, 3 years post cut) with semi-open in situ incubations using PVC plastic pipes (Reich et al. 2001). Measurements were taken at eight sampling points along each slope position transect, but >15 cm from treatment plots. Each pipe (2 cm diameter) was inserted into the soil to a depth of only 6 cm because of the extremely shallow soils. At each sampling point a pair of tubes were used, one removed on June 1 without incubation, and the second removed on June 30 after a 30-day incubation. All cores were processed using the analysis technique outlined by (Reich et al. 2001) and extracted using one molar KCL.

Samples were analyzed for NO_3^- and NH_4^+ colorimetrically on an Alpkem Rapid Flow Analyzer (Research Analytical Laboratory at the University of Minnesota. St Paul, Minnesota). Net N mineralization was defined as the difference between extracted N over the same 30-day incubation in the two cores.

To provide an average measurement of the ambient moisture supply, percent volumetric soil water content was recorded every other week during the growing season every year of the 3 year experiment using a HydroSense meter (Campbell Scientific, Australia Pty. Ltd) at the same eight sampling points where net N-mineralization and net nitrification were measured. The HydroSense meter measures the dielectric permeability of the soil. The probe was inserted into the soil surface ten times for each of the plots at an angle of approximately 20° to assure all plots were measured at the same depth (approximately 6 cm due to the shallow soils) and then averaged.

The Research Analytical Laboratory at the University of Minnesota (St. Paul, Minnesota) analyzed soil samples for pH, exchangeable cations, total C and N from separate cores. Soil pH was determined in deionized water ($5g_{soil}/5ml_{water}$) and exchangeable cations were determined using extraction with ammonium acetate ($3g_{soil}/30ml_{1\ M\ ammonium\ acetate}$) followed by ICP. Total N (300 mg sample) was determined using the Dumas method with a LECO FP-528 Nitrogen Analyzer. Due to the calcareous nature of the samples, total C was determined (5 g sample) using combustion where the evolution of CO_2 was measured by IR spectrum absorption and then inorganic carbon was measured by addition of phosphoric acid. Organic carbon was measured as the difference between total carbon and inorganic carbon.

Canopy

At the end of the 3 year experiment in July 2003 canopy openness was measured 2 m above ground surface and at ground surface in all plots using a Sunfleck Ceptometer Plant Canopy Analyzer (Decagon Devices Inc. Pullman, WA) measuring every 18 degrees over 360 degrees for each plot. Measurements were made at mid-day under conditions of full sunlight. Above and below canopy measurements were determined by moving the sensor into open conditions and then back under the canopy.

Species percent cover and germination

The absolute percent cover of extant vegetation in each plot was measured at the end of the 3-year experiment in June 2003 using a 0.5 m $\times$ 0.5 m square. For each species percent cover was estimated to the nearest 1%. Indicator species were recorded and placed into one of four categories (Curtis 1959; Gleason and Cronquist 1991; Minnesota Department of Natural Resources 2005), based on species typically found in: (1) prairie systems (native species including woody plants, grasses and forbs), (2) forested systems (native species), and (3) non-native species. The percent bare-ground was also recorded. Exposure of bare-ground is important in the bluff prairie system due to the susceptibility of the area to soil loss from runoff; hence bare-ground is included in the categories. The eastern red cedar cover was measured in the tree plots through canopy measurements.

Statistical analysis

The site, treatment, and slope position effects were analyzed using categorical variables. Plot level environmental factors were analyzed using a full factorial ANOVA to test for differences between site, treatments (GRASS, REMOVAL, and TREE), slope positions (center, down, left, right and up), and treatment $\times$ slope position interactions. Tukey's HSD (Honestly Significant Difference) test was used to further explore differences in slope position. Net N-mineralization and net nitrification were analyzed in relation to plot level environmental factors such as soil moisture, soil temperature, exchangeable base-cations, total soil carbon, soil C/N, and soil N.

The effect of the environmental factors measured on species germination and distribution was analyzed using *F*-tests based on linear regression. Species composition was analyzed in relation to all environmental factors using similar multiple linear regression. Factors were examined for collinearity and those that are, were dropped. To examine the relationship among the remaining variables a backward stepwise multiple-linear regression with partial *F* values was used (Weisberg 1985).

Results

Statistical analysis indicated that site was not significant and there were no interactions between site and treatments (GRASS, REMOVAL, and TREE) or slope location (up-slope, left-slope, right-slope, down-slope, and center), thus all further results analyzing treatments and slope location are reported as averages across all four sites. Slope position was analyzed using all five positions (up-slope, left-slope, right-slope, down-slope, and center) indicating no significant differences between left, right, and center slope. The data was re-analyzed using only up, down, and center slope locations and the results were similar to the analysis of all five slope positions. Therefore results are presented for the up, down, and center slope positions.

The effect of eastern red cedar presence and removal on environmental factors

Influence of tree canopy

Soil moisture was significantly higher ($P \leq 0.001$) and soil temperature and light availability ($P \leq 0.001$) were significantly lower in the TREE

Table 1 Plot level environmental factors (average weekly soil moisture as % volumetric water content and temperature at 6 cm depth, net N-mineralization, net nitrification, Calcium (Ca), total Carbon (C), light availability in full sunlight at 2-m level above the ground and ground level, and soil pH) showing significant differences for GRASS, REMOVAL (eastern red cedar removed), and TREE (eastern red cedar present) plots, significant main effects and interactions

Treatment						
Environmental factors	GRASS	REMOVAL	TREE	Treatment effects $P > F$	Position effects $P > F$	Interactions $P > F$
Calcium (mg/kg soil)	3,558 ± 214[b]	3,743 ± 210[ab]	4,038 ± 199[a]	NS	NS	NS
Moisture % volumetric water content	12 ± 1.2[b]	10 ± 1.1[c]	16 ± 1.5[a]	0.0001	0.0001	0.0001
Temperature (°C)	19.2 ± .6[a]	19.4 ± .6[a]	17.2 ± .9[b]	0.0001	0.0001	0.0001
Carbon (mg/kg soil)	7.37 ± .16[a]	6.95 ± .13[b]	6.99 ± .14[ab]	0.009	0.0001	NS
Net-N-mineralization (mg N m^{-2} day^{-1})	11.0 ± 1.67[a]	8.8 ± 1.9[a]	−9.1 ± 1.96[b]	0.0001	NS	NS
Net-nitrification (mg NO^{-3} m^{-2} day^{-1})	4.63 ± .96[a]	7.06 ± .91[a]	−1.36 ± .69[b]	0.0001	0.02	NS
Light-par-2 m	696.3 ± 16.16[a]	705.23 ± 18.10[a]	2,476.26 ± 25.07[b]	0.0001	0.0001	0.0001
Light-par-ground level	412.8 ± 17.2[b]	648.3 ± 17.64[a]	142.43 ± 17.88[c]	0.0001	NS	0.0013
pH	7.2 ± .16[a]	7.3 ± .2[a]	7.3 ± .17[a]	NS	NS	NS

Least square means (±SE) and analyses of variance probabilities ($P > F$) of the main effect of treatment (GRASS, REMOVAL, and TREE). For each environmental factor not sharing letters [following least square means (±SE)] were significantly different ($P \leq 0.05$)

plots than in GRASS plots and REMOVAL plots (Table 1). Soil moisture, soil temperature, and light penetration showed significant differences according to position and there were significant treatment × position interactions for these variables (Table 1). Slope position was a significant factor in the TREE plots but not in the GRASS plots for several of the environmental factors measured. The Tukey's HSD analysis indicated that the down slope position was consistently different showing higher soil temperature, light, and nitrification levels and lower soil moisture than the up-slope and center-slope positions (Table 2).

Biogeochemical consequences

Soil exchangeable base cations including potassium, calcium, and sodium were higher in TREE than in GRASS plots ranging from 10% higher in the case of calcium to more than 100% higher in the case of sodium. Soil total C content was approximately 14% higher in GRASS plots than in TREE plots, but organic C was 13% higher in TREE than GRASS plots. Net N-mineralization and net-nitrification were lower beneath trees than in the GRASS plots. In the plots where eastern red cedar was removed (REMOVAL plots) exchangeable base cations, net N-mineralization, and net nitrification were not significantly different than GRASS plots. Eastern red cedar presence did not influence the soil pH in this study (Table 1).

In addition to examining slope position in the TREE plots and GRASS plots separately, the relationship between slope position in the TREE plots and GRASS plots was examined for those factors that indicated significant interactions (Table 1). The down slope position of the TREE plots was not significantly different than any slope position in GRASS plots for soil moisture, soil temperature, and net-nitrification measurements.

The effect of eastern red cedar on plant composition and distribution

The TREE plots showed much lower prairie species cover but higher percent cover of woodland species, bare-ground, and non-native species than GRASS plots ($P \leq 0.001$), and the REMOVAL plots showed percent cover measurements between the two treatments trending closer to the GRASS plots than the TREE plots (Fig. 2). The only species composition metric in REMOVAL plots that was not significantly

Table 2 TREE plot level environmental factors (exchangeable Calcium (Ca), average weekly soil moisture as volumetric water content and temperature, total Carbon (C), net N-mineralization, net nitrification, and light availability in full sunlight at 2-m level above the ground and ground level) showing significant differences based on slope position (center, down, and up) in TREE plots

Slope position	Exchangeable Ca ($P > F$ 0.025)	Moisture % volumetric ($P > F$ 0.0001)	Temperature(°C) ($P > F$ 0.0001)	Total C (mg/kg soil) ($P > F$ 0.0001)	Net-N mineralization (mgN m^{-2} day^{-1}) ($P > F$ 0.05)	Net-nitrification (mg NO^3 m^{-2} day^{-1}) ($P > F$ 0.0003)	Light-2 m par ($P > F$ 0.0001)	Light-ground level par ($P > F$ 0.0001)
Center	4,403 ± 337^a	18 ± 1.2^a	16.7 ± $.5^b$	6.55 ± $.16^b$	−16.85 ± 5.58^b	−4.17 ± 1.18^b	129.5 ± 12.03^c	83.5 ± 8.9^c
Down	3,915 ± 268^b	11 ± 1^b	19.3 ± $.9^a$	6.69 ± $.20^b$	−0.76 ± 3.05^a	3.07 ± 1.08^a	559.83 ± 31.13^a	217 ± 7.5^a
Up	3,795 ± 274^b	18 ± 1^a	16.7 ± $.6^b$	7.73 ± $.11^a$	−11.51 ± 4.61^{ab}	−2.98 ± 1.36^b	141 ± 6.77^b	127.5 ± 12.37^{bc}

Least square means (±SE) and analysis of variance probabilities ($P > F$) of the main effects of site and site × position (up, down, and up) interactions were not significant. For each environmental factor, slope positions not sharing letters (following least square means (±SE)) were significantly different ($P \le 0.05$)

different than in GRASS plots was the woodland species percent cover.

Backward stepwise regression indicated that ground-light and soil moisture were important factors in the analysis of the percent cover of prairie species. This analysis indicated that as light availability at ground level increased and soil moisture decreased, the mean percent cover of prairie species increased. These factors explained 62% of the variance in prairie species percent cover. In contrast to prairie species, the percent cover of woodland and non-native species increased significantly with increasing soil moisture.

Similar to environmental factors, the species composition in the TREE plots showed significant differences based on slope position (Fig. 3). These differences followed a relatively uniform pattern based on plot position on the slope relative to the eastern red cedar tree. The down slope position showed significantly higher mean percent cover of prairie species (Tukey's HSD, $P = 0.0002$, down-slope 41% vs. center 4%) while the up-slope position was significantly higher in mean percent cover of non-native species ($P = 0.0001$, up-slope = 30% vs. down-slope 4%; Fig. 3) than any of the other slope positions. The down-slope position showed the highest level of ground light and lowest soil moisture associated with an increase in prairie species and a decrease in non-native species (Table 2; Fig. 3).

Discussion

Ecologists recognize that the invasion of new and dominant species into open grassland and woodland systems over the last century has been accompanied by changes in ecosystem properties and species composition (Gehring and Bragg 1992; Hoch and Briggs 1998, Funk and Vitousek 2007; Knight et al. 2007). These impacts are similar to the invasion of non-native invasive species such as buckthorn into open woodland systems across the upper Midwest (Knight et al. 2007). However, most such studies were performed in areas with little topographic variation or on abandoned agricultural fields, and much less is known of woody plant invasion in steep intact prairie systems, especially in dry, nutrient poor, shallow soils that are unsuitable for agricultural purposes. Additionally, to our knowledge there is no information in print on how the affected areas

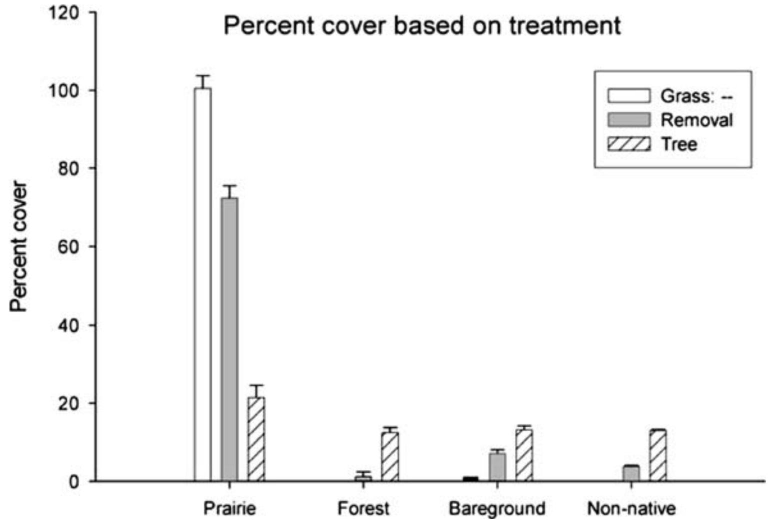

Fig. 2 Mean percent cover (±SE *bars*) of species categories (prairie, woodland, bare-ground, non-native) for GRASS, REMOVAL (eastern red cedar removed), and TREE (eastern red cedar present) plots

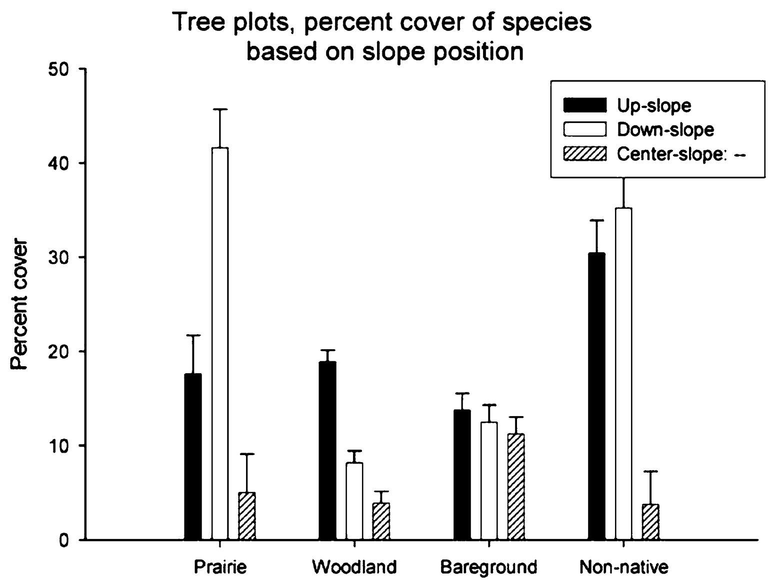

Fig. 3 Mean percent cover (±SE bars) of species metric (prairie, woodland, bareground, non-native) for TREE (eastern red cedar present) plots based on slope position (*Center*, *Up*, and *Down*)

respond once the invader is removed. The results of this study suggest that eastern red cedar invasion affects steep slope systems in a complex manner resulting from interactions with steep topography and slope aspect, and that the native ecosystem has a strong capacity for relatively rapid recovery once cedar is removed. Furthermore these results provided needed information on the links between the impacts of species invasion on community structure and ecosystem process (Levine et al. 2003). This information can help further our understanding of the general impacts of large scale native or non-native species invasion in to dry nutrient poor systems and help establish restoration and management priorities.

The effect of eastern red cedar presence and removal on environmental factors

Many of the environmental variables measured were significantly different under eastern red cedar trees (Table 1). This is similar in some ways and different in others compared to prior studies that found that eastern red cedar affects the litter dynamics and light environment of areas surrounding the tree (Engle et al. 1987; Gehring and Bragg 1992) thus resulting in changes in soil properties (Spurr 1940; Engle et al. 1987; Meiners and Gorchov 1998).

Studies have shown that this increase in canopy cover with eastern red cedar can divert rain infiltration and result in lower soil moisture surrounding eastern red cedar trees (Smith and Stubbendieck 1990). Contrary to prior research, the current study indicates higher soil moisture under eastern red cedar trees (Table 1). This increase in soil moisture is likely caused by the runoff from the upper portion of the slope that allows moisture to reach the soil surface under the eastern red cedar trees. The resulting soil moisture may be retained longer under the eastern red cedar due to reduced evaporation associated with the lower light availability and/or due to differences in "forest" floor roughness, infiltration, and structure resulting from cedar litter, root and shed branch characteristics. This suggests that conclusions about cedar effects based on studies in flat landscapes may not always be useful in hilly terrain.

Soil moisture, soil temperature, and light penetration were altered primarily by the presence of the eastern red cedar canopy; however, other environmental factors were altered by the biogeochemical impacts of the eastern red cedar or a combination of canopy and biogeochemical impacts. The transfer of Ca and other base cations from eastern red cedar litter to soil shown in previous studies is the best explanation for the increase in soil base-cations and pH in the soils surrounding eastern red cedar (Broadfoot and Pierre 1939; Spurr 1940; Bard 1952). However, the results of the current study showed no significant change in Ca and no change in pH under eastern red cedar likely due to the initial high levels of base cations in this system (Table 1).

Several studies have highlighted the role of species composition in nutrient turnover rates in related ecosystems (Wedin and Tilman 1990; Norris et al. 2001; Reich et al. 2001; Funk and Vitousek 2007; Knight et al. 2007). The results of our study are, however, contrary to some prior nearby research that indicates higher N-mineralization under trees and shrubs compared to adjacent grasslands (Zak et al. 1986; Reich et al. 2001). This likely involves the evergreen conifer characteristics of eastern red cedar (including low litter N concentrations, Norris et al. 2001) whereas these other nearby studies have focused on deciduous woody angiosperms with higher litter N levels. The differences in net N-mineralization and net nitrification measurements recorded between treatments (GRASS, REMOVAL, and TREE plots) are likely caused by a combination of changes in micro-environment (loss of understory vegetation and runoff), litter quality (decrease in the fraction of C_4 grasses and increase in eastern red cedar litter), and other plant inputs resulting from changes in species composition.

Slope position around eastern red cedar tree

Because of the steep topography of these prairies, slope position around the tree likely influences the impact eastern red cedar has on the environmental factors measured at a specific area. The difference between tree and non-tree plots in factors such as soil base-cations is enhanced down-slope perhaps because of the mobility of these base-cations in runoff as it moves down the slope. Once it reaches the down-slope position the runoff may slow and infiltrate into the soil due to increases in understory percent cover, concentrating more of the base-cations released from the eastern red cedar litter in the down-slope area. However, other factors such as light availability, soil moisture, soil temperature, and net N-mineralization that are affected by eastern red cedar presence were not significantly different between the down-slope position of TREE plots and the GRASS plots. The irradiance in the down slope position plots is presumably less affected, and the up slope position more affected, by the canopy of the eastern red cedar tree due to the angle of the sun as it hits the slope with south and southwest facing aspects. This shadow effect is the result of the dense and low canopy of eastern red cedar and the sun's angle relative to the tree. This study indicates that the magnitude of the effect of the eastern red cedar presence on the bluff prairie system is altered by the slope position around the tree through a combination of light availability due to canopy cover and slope aspect, and possibly runoff due to slope steepness or differential root water uptake based on slope position. These results emphasize the impact of invasion from a micro-scale, slope position, to a larger local scale, prairie composition, and potentially a regional scale as outlined by Pauchard and Shea (2006).

Eastern red cedar removal

Removal of eastern red cedar trees allowed us to verify that cedar was affecting the environmental factors measured and to assess how quickly these factors recovered to levels measured in the grass patches. All variables measured were affected by the removal of eastern red cedar, increasing or decreasing in the direction of those recorded in the GRASS plots (Table 1). These findings give considerable support to (Q_1), since many of the soil properties that continued to differ significantly from those found in GRASS plots should recover with time. The results of the removal experiment also provide insight into how this system will respond to restoration efforts. The resilience of dry prairie and oak savanna systems have been noted by other studies (Collada and Haney 1998; Leach and Givnish 1998) examining the potential to restore oak savanna systems noting a legacy response of the seed bank in dry sandy soils once invasive woody vegetation is removed. Bates et al. (2000) found a similar increase in understory response with the removal of western juniper (*Juniperous occidentalis*) in the sagebrush steppe of southeastern Oregon. Ansley and Rasmussen (2005) indicated that herbaceous vegetation recovery took at least 3 years once eastern red cedar was removed from dense (>40% bare-ground) stands highlighting the importance of early restoration efforts.

The effect of eastern red cedar on plant composition and distribution

The presence of eastern red cedar enhanced soil moisture and reduced soil temperature, light availability, and net N-mineralization and net nitrification (Table 1). How do these changes affect plant composition and distribution within the bluff prairie system? The presence of eastern red cedar was associated with higher percent cover of non-natives, woodland species, and bare-ground, and lower prairie species percent cover. These findings are supported by previous studies that have shown that the presence of eastern red cedar reduces understory percent cover in grassland systems by as much as 83% (Bard 1952; Gehring and Bragg 1992; Engle et al. 1987; Smith and Stubbendieck 1990).

This study suggests that prairie species percent cover decreases in the presence of eastern red cedar likely due to the trees' effect on soil moisture and light availability in conjunction with competition whereas woodland and non-native species percent cover increases in the presence of eastern red cedar due to the trees' influence on soil moisture (Table 1; Fig. 2). The down slope position of the TREE plots had higher percent cover of prairie species likely because of elevated light availability in the down slope position caused by the slope and southern aspect of these prairies. In contrast, the higher non-native percent cover (mainly buckthorn and honeysuckle) in the up-slope position was likely attributed to the higher soil moistures measured in the up-slope positions (Table 2). This may indicate that non-native woody species are limited by soil moisture conditions in other areas of the bluff prairie system which follows the hypothesis (Johnston 1986) that invasion of species into a community may be the result of removal of a barrier that has previously excluded the species (i.e., low soil moisture).

These results provide insight into the role of eastern red cedar in the facilitation of changes in species composition of the bluff prairie system (Table 1). Eastern red cedar is often the first tree species to become established in grassland systems, likely attributable to seed distribution by birds and its ability to grow in low moisture environments (Bazzaz 1968; Livingston 1972; Bragg and Hulbert 1976). Some researchers have conjectured that eastern red cedar may facilitate the establishment of other tree and shrub species through alterations in soil temperature (Broadfoot and Pierre 1939; Bard 1952; Bazzaz 1968). Siemann and Rogers (2003) discuss the changes in light and nitrogen that result after *Sapium sebiferum* and the native *Celtis laevigata* invade grasslands in the southern US as the mechanism involved in facilitating further tree invasions. The interplay between eastern red cedar, slope position and aspect, and soil moisture in the bluff prairie system may result in higher non-native species invasion compared to other grassland systems due to the likely facilitative effects of increased moisture on non-native species percent cover mainly *Ramnus cathartica* (buckthorn). Facilitation of one invasive species by another due to increasing supply of a limiting resource, increasing habitat complexity, or providing an escape from competitors has been noted in both native and non-native species invasions (Jordan and Larson 2008; Reinhart et al. 2006; Rodriguez 2006).

Summary

In conclusion, this study demonstrated that eastern red cedar presence affects the bluff prairie system through changes in light availability, soil properties, and nutrient dynamics. Slope position played a significant role in the patterns observed. In some ways the bluff prairie system seems to function similarly to other grassland systems where woody vegetation invasion has been shown to influence compositional and some environmental factors. However, important differences found in the bluffland region and other karst areas across the country, such as the steep slopes and the limestone and dolomite geology, override some of these previously noted effects of the eastern red cedar invasion. The steep slope alters the invasion pattern of non-native and woodland species and environmental factors such as soil moisture, temperature, light penetration, and prairie composition in the down slope position. The limestone and dolomite geology of the system may result in high baseline calcium and other base cations buffering the effect of eastern red cedar invasion on the pH of the soil. These results clarify some of the pathways or mechanisms that underlie the impacts of species invasion on this dry nutrient poor system (Levine et al. 2003). Also unique to this study and others conducted on dry sandy soils was the finding that once eastern red cedar is removed, the area affected by the tree approaches measurements found in the grass areas. While these results indicate that the bluff prairie system is affected by the invasion of eastern red cedar they also suggest that if restoration efforts are undertaken the interaction between the steep slope and the eastern red cedar may provide resilience to these systems allowing more time before an alternative stable state is reached (Frelich and Reich 1999). This ability for the system to recover provides the potential for an effective and efficient restoration. However, as restoration efforts occur, the interaction between the steep slope and the eastern red cedar must be considered carefully so that issues such as runoff, erosion, and the differential effects, depending on slope position, of the eastern red cedar can be addressed.

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