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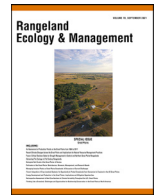
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# Rapid Re-encroachment by *Juniperus virginiana* After a Single Restoration Treatment<sup>☆</sup>

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## ABSTRACT

Grasslands across the world are transitioning to woody-dominated states with major consequences for ecosystem service provisioning. Managers have consequently turned to woody plant removal or “brush management” as a tool for grassland restoration. Yet the lifespan of brush management treatments depends on rates of re-encroachment, which are often unknown and seldom considered in restoration planning. In this study, we determine the rate of re-encroachment for *Juniperus virginiana* L. after 16 yr of fire-based restoration actions in the Loess Canyons Experimental Landscape in Nebraska. In this experimental landscape, reclamation fires are used to collapse *J. virginiana* woodlands and have been applied almost every yr since 2002 as part of a regional restoration initiative. We observed rapid rates of re-encroachment after fire-based restoration. Seedlings re-established within 1–2 yr and reached densities similar to unburned woodlands in 5–11 yr. Cover was low and stable 8–10 yr after restoration and then transitioned to a rapid growth phase as trees escaped the herbaceous layer. The tallest trees reached heights associated with the onset of seed production after 7–11 yr, marking a demographic transition in the re-encroachment process as restoration sites become sources of seed exposure. These results suggest that single restoration treatments are likely to be short-lived. A key implication is that follow-up *J. virginiana* treatments are needed to maintain restored grasslands at fairly regular intervals.

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## Introduction

Woody encroachment is the process in which grasslands transition to an alternative, woody-dominated state (Ratajczak et al. 2014; Wilcox et al. 2018). Woody transitions result in fundamental changes in the structure, function, and composition of grassland systems including reductions in herbaceous biomass and diversity, as well as altered nutrient cycles, hydrology, and carbon storage (Scholes and Archer 1997; Jackson et al. 2002; Huxman et al. 2005; Archer and Predick 2014). In response to these threats, managers have turned to woody plant removal, generally known as “brush management” in North and South America, as a restoration tool used to induce a shift back to a grass-dominated state.

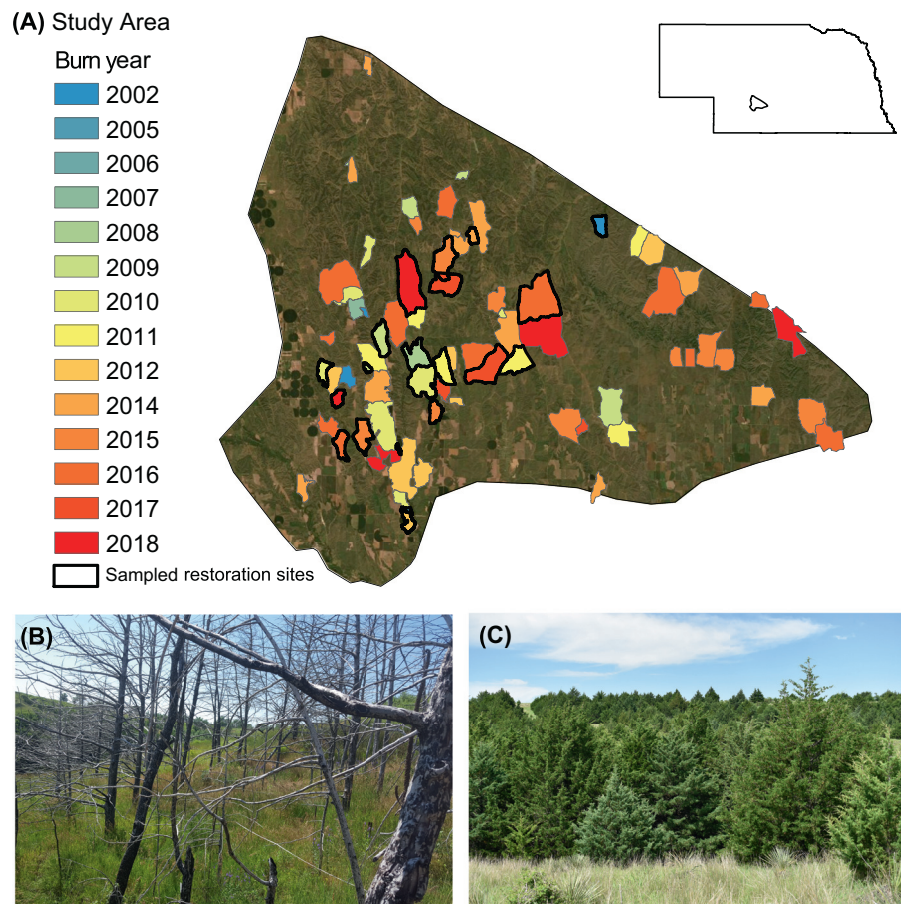
Indeed, various forms of brush management have proven to be effective in restoring herbaceous biomass and diversity (Archer et al. 2011). However, the lifespan of brush management treatments depends on rates of re-encroachment and recovery (Archer and Predick 2014). One of the biggest risks to sustaining costly brush management programs is if projects are short-lived. Yet rates of re-encroachment are currently unknown for some of the most common encroaching species (Archer et al. 2011), despite substantial investments in brush management.

Here, we implemented the first study to track *Juniperus virginiana* L. re-encroachment following restoration with high-severity fire. *J. virginiana* is a notorious encroaching species in the North American Great Plains and is driving a large-scale woodland transition associated with a suite of social-ecological consequences (Briggs et al. 2002; Twidwell et al. 2013b). As the impacts of *J. virginiana* encroachment become more apparent, some managers have turned to high-severity fire as a cost-effective restoration method at large scales. In this study, we use a regional restoration initiative to quantify rates of *J. virginiana* re-encroachment 16 yr following woodland collapse with high-severity fire. This study answers several questions concerning the re-encroachment

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**Figure 1.** A, Map of fire treatments (2002–2018) for the Loess Canyons Experimental Landscape in Nebraska, used to determine rates of re-encroachment by *Juniperus virginiana* following fire-based restoration. B and C, Example of a recently restored site compared with a recovered site 17 yr after initial restoration with fire, respectively.

process: 1) Does *J. virginiana* quickly recover following restoration or is a slow re-establishment process observed? 2) How long are seedlings present in the herbaceous layer before beginning a process of rapid growth in cover? and 3) when does *J. virginiana* reach heights associated with seed production?

## Methods

### Study system

This study was conducted in the Loess Canyons Experimental Landscape located in central Nebraska (Fig. 1). The Loess Canyons Experimental Landscape spans a 72 843-ha area and consists of private properties that are connected to form a large landowner coalition. Mixed-grass prairie is the dominant vegetation community with an average herbaceous plant height of 0.3 m (Fogarty, unpublished data). Dominant grass species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.). Before European settlement, the estimated fire return interval for this region was 6–10 yr (Guyette et al. 2012), which limited the distribution of *J. virginiana* to steep canyons where fire was rare. However, fire suppression has since allowed *J. virginiana* to encroach into previously uninhabitable grasslands, resulting in woodland expansion (Fogarty et al. 2020). Elevation ranges from 781 to 989 m above sea level. Mean annual precipitation is 550 mm, and mean annual temperature is 9.8°C (Arguez et al. 2012).

Prescribed burning has occurred almost every year in the Loess Canyons Experimental Landscape since 2002, with fires averaging 309 ha in size. Prescribed burns are conducted by prescribed burn associations to manage woody encroachment and restore grassland dominance (Fogarty et al. 2020; Bielski et al. 2021). On the basis of a landowner reconstruction of prescribed fire history, 84 fire treatments were implemented across 26 191 ha in the Loess Canyons Experimental Landscape from 2002 to 2018 (see Fig. 1). Prescribed fire treatments were typically implemented between early February and late April. All fire prescriptions targeted weather and fuel conditions to create fire intensities above juniper mortality thresholds (*sensu* Twidwell et al. 2013a). To promote this, localized tree cuttings were often used to manipulate the fuel structure and were stuffed under *J. virginiana*-dominated patches.

### Experimental design, sampling, and analysis

We used a space-for-time substitution to quantify rates of *J. virginiana* re-encroachment. Twenty-two restoration sites were selected for this study (see Fig. 1). Restoration at these sites consisted of a single fire treatment and did not include reseeding of herbaceous plants or postfire management of woody plants (Bielski et al. 2021). The selected sites spanned an array of time-since-fire history and ranged from 3 mo to 16 yr. Within each site, we sampled re-encroachment within a former *J. virginiana* woodland patch that collapsed as a result of the fire treatment. Collapsed *J. virginiana* patches were selected on the basis of the following criteria: 1) all patches were formerly a *J. virginiana* woodland patch (representative of unburned woodland sites; see later), at least 1 000 m<sup>2</sup>

in area; 2) all patches were located on canyon slopes (patches on canyon tops and bottoms were avoided to reduce variability across sampling locations); 3) all patches were collapsed (i.e., 100% tree mortality) as a result of fires surpassing critical surface fireline intensity thresholds necessary for juniper mortality (Twidwell et al. 2013a), and then 4) shifted back to a herbaceous-dominated state. These criteria were confirmed through a combination of remotely sensed imagery and field observations. We also selected three intact *J. virginiana* woodland patches to establish a reference point for unburned woodlands in the Loess Canyons Experimental Landscape.

A 30-m transect was established at the center of each sampled patch and oriented parallel to the canyon top and bottom to minimize differences among sites. Canopy cover of *J. virginiana* was measured along this transect using the line-intercept method. Density and tree height were measured in three 10 × 10 m plots centered along the 30-m transect. Density measures included all individuals rooted within plots. Seedlings obstructed by herbaceous vegetation and woody debris were located by closely searching the herbaceous vegetation layer within 1 m of ground level. Survey time was kept consistent across all sampled patches. Height was recorded for all trees using a telescoping measuring pole. All field sampling was conducted in July 2018.

We used a candidate set of four regression models to determine whether a linear, logarithmic ( $\ln[x+1]$ ), second-order, or third-order polynomial trend described the relationship between each response variable (density, percent cover, height, and maximum height) and time since fire-induced collapse. Cover and density response variables were log-transformed ( $\ln[y+1]$ ) to meet normality and heteroscedasticity assumptions. We used Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) to identify the top model (i.e., linear, logarithmic, or polynomial) based on the lowest  $\Delta AIC_c$  value and then used  $R^2$  as a measure of the top model's fit. To account for model uncertainty at longer times since fire, 95% confidence intervals were calculated based on the 2.5th and 97.5th percentile from a set of 1 000 refitted models using bootstrap samples (Toms and Lesperance 2003). All statistical analyses were conducted using R version 3.5.1 (R Core Development Team 2018).

## Results and Discussion

*J. virginiana* re-encroachment began almost immediately after initial restoration with fire. Seedlings established 1–2 yr after restoration and then increased in density following a logarithmic trend ( $y = \exp[0.4259 + 2.9675 \cdot \ln\{x+1\}] - 1$ ;  $R^2 = 0.66$ ) (Fig. 2A). Density recovered to levels within the range of unburned woodlands (633–1 267 trees ha<sup>-1</sup>) within 5–11 yr after restoration (based on bootstrapped 95% confidence intervals), although some individual sites recovered earlier (see Fig. 2A). Cover increased following a polynomial trend ( $y = \exp[0.064044 - 0.111451x + 0.023644x^2] - 1$ ;  $R^2 = 0.78$ ), in which cover was low and stable in the first 8–10 yr after restoration and then transitioned to a period of rapid growth as more trees escaped the herbaceous layer (see Fig. 2B). Mean and maximum tree height increased along polynomial ( $y = 0.018684 + 0.00518x + 0.005317x^2$ ;  $R^2 = 0.72$ ) and linear ( $y = -0.82801 + 0.28257x$ ;  $R^2 = 0.61$ ) trends, respectively (see Fig. 2C and 2D). Eight yr after restoration, mean tree height was 0.4 m (0.1 m > mean herbaceous plant height) and the tallest trees were 1.4 m. Beyond this point in the re-encroachment process, relatively incremental increases in mean tree height (0.1–0.2 m yr<sup>-1</sup>) corresponded to potentially large increases in cover (see Fig. 2). Between 7 and 11 yr after restoration, the tallest trees reached heights associated with the onset of seed production (1.5 m; Owensby et al. 1973), marking a demographic transition in the re-encroachment process as restored

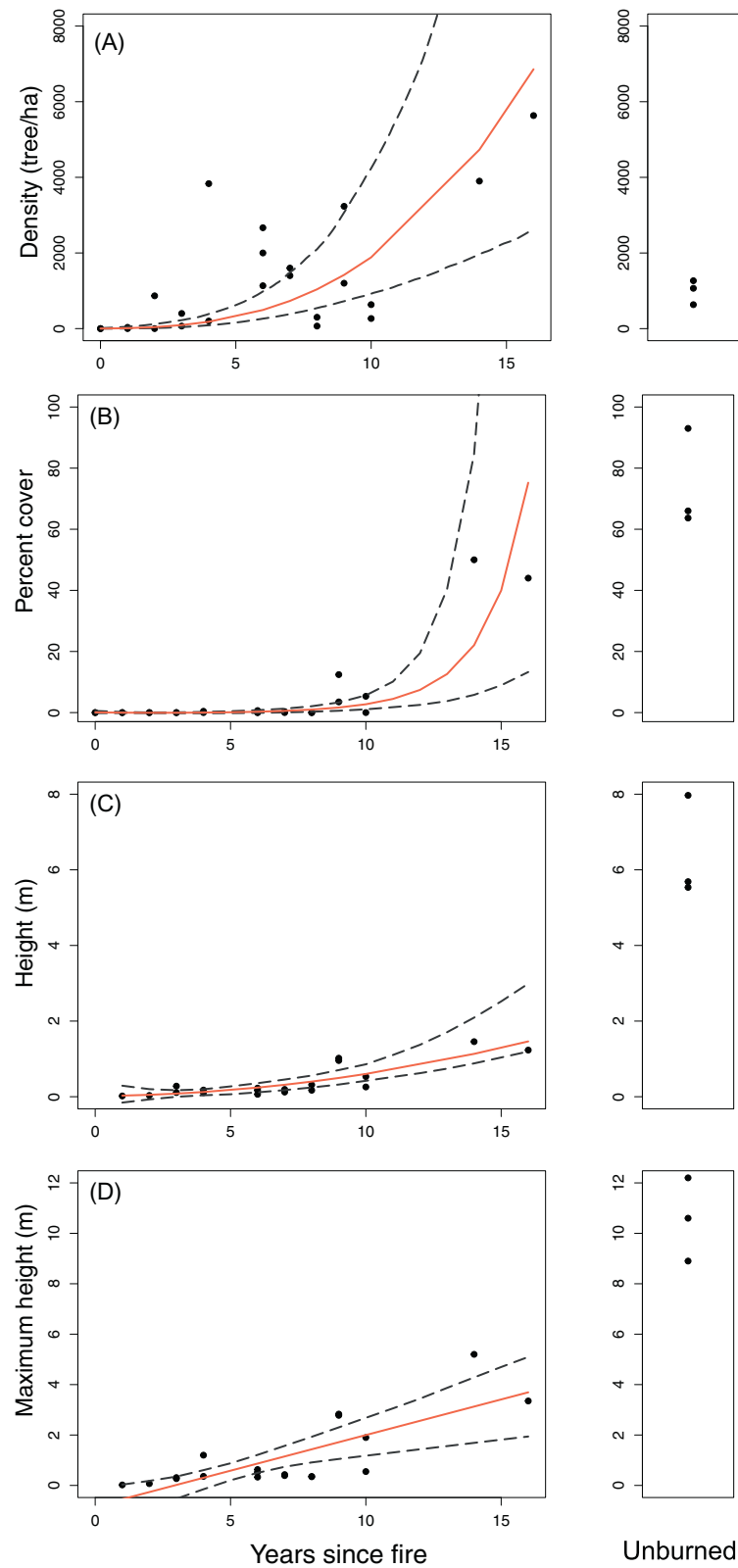
sites become seed sources and further contribute to encroachment. Fourteen yr or more after restoration, sites were dominated by dense stands of *J. virginiana* (3 900–5 633 trees ha<sup>-1</sup> with trees up to 5.2 m in height) and resembled a young woodland (see Fig. 1C).

Our results show two stages of re-encroachment after restoration; the first is an incipient stage characterized by seedling re-establishment, followed by a second stage of rapid growth and demographic transitions to mature (i.e., cone-producing) trees. This general pattern of nonlinear recovery is consistent with expectations based on patterns of initial encroachment and woodland transition (Briggs et al. 2002). Yet this study provides the first evidence of a rapid and nonlinear re-encroachment process for juniper. Results from previous studies of juniper removal in North America are consistent with the incipient stage of re-encroachment documented here (e.g., Bates et al. 2005; Ansley et al. 2006; Alexander et al. 2018). This is an important distinction between this study and others because the onset of a nonlinear increase in cover signals that the end of a treatment's lifespan is approaching. Indeed, the timing of a nonlinear increase in *J. virginiana* cover, ~10 yr after initial restoration, is associated with early declines in herbaceous biomass (Bielski et al. 2021). This suggests that single restoration treatments may be short-lived in the Great Plains due to rapid rates of re-encroachment, compared with other juniper-encroached systems in the Great Basin where treatment lifespans are estimated to range from 40 to 100 yr (Bates et al. 2005, 2006).

Multiple demographic stages, as well as the speed of demographic transitions, have potential to limit the rate of re-encroachment (Archer et al. 2017). In the Loess Canyons, multiple lines of evidence suggest that re-encroachment is limited by the speed of demographic transitions, rather than bottlenecks or traps associated with single demographic stages: 1) Seedlings quickly reestablished within 1–2 yr and 2) shortly thereafter reached densities similar to those of woodlands, suggesting that neither seed availability nor seedling establishment are limiting; 3) Tree size steadily increased, suggesting an absence of demographic traps limiting transitions to mature size classes; and 4) increases in cover were generally consistent with nonlinear growth patterns of individual tree canopies (Engle and Kulbeth 1992), suggesting tree growth rates as a primary limiting factor. We therefore expect our results to be generally applicable for similar grassland systems where re-encroachment is not limited by early demographic stages (e.g., seed availability or seedling reestablishment), with variance in the rate of re-encroachment based on tree growth rates and local differences in seedling density. For instance, density showed considerable variation among our sites, suggesting local differences in seed abundance and/or seedling establishment. We expect these differences to result in local variation in rates of re-encroachment, including the timing of nonlinear increases in cover. However, research is needed to explore how multiple demographic stages can limit re-encroachment and the potential management implications.

## Implications

Brush management is a widespread restoration practice in global rangelands, and our study contributes to a growing body of literature showing that restored lands are highly vulnerable to re-encroachment (reviewed by Archer et al. [2011]). A key implication is that sustaining restored grasslands will require follow-up management, consistent with historical fire return intervals, to promote feedbacks that limit woody plants and promote grasslands. Clearly, re-encroachment will influence what it takes to scale up conservation success and should be incorporated into future planning efforts.



**Figure 2.** A–D, Relationship among *Juniperus virginiana* density, percent cover, height, and maximum height and time since fire-induced woodland collapse in the Loess Canyons Experimental Landscape, Nebraska, respectively. Modeled fits are shown by solid lines and are bounded by 95% confidence intervals calculated using a bootstrap technique. Right panels provide a point of reference for unburned woodlands, reflecting longer time-since-fire trajectories.



## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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