

Plant Community Response Following Removal of *Juniperus virginiana* from Tallgrass Prairie: Testing for Restoration Limitations

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Abstract

Woody plant encroachment in natural grasslands is a widely documented global phenomenon that alters ecosystem dynamics by altering historic vegetation composition and suppressing herbaceous productivity. Abundant woody plants often suppress native plants sufficiently to establish successional thresholds difficult to reverse without species augmentation. Juniper (*Juniperus virginiana* L.) is expanding in North American tallgrass prairie, but it is currently unknown if encroachment creates successional restrictions that limit restoration potential. We selected 16 50×50-m sites with juniper canopy cover ranging from zero to approximately 75% in tallgrass prairie near Stillwater, Oklahoma, USA. Juniper trees were removed from 7 of the sites along the gradient of juniper canopy cover. Canopy cover of plant species and herbaceous plant productivity were estimated at each site 1 year before and 1, 2, and 5 years after tree removal. Before trees were removed, plant species richness and productivity declined as juniper canopy cover increased, and plant community composition dissimilarity of reference sites increased as juniper canopy cover increased. These relationships remained consistent on all non-removal sites throughout the study. The first year after juniper removal, species richness increased on all removal sites compared to intact sites and productivity on removal sites increased two years after removal. Plant community dissimilarity between reference sites and juniper removal sites remained relatively high (30–60%) the first two years after tree removal on all removal sites, but dissimilarity was about 22% 5 years after juniper removal. Within 5 years, removal sites were comparable to reference plant communities. Grassland restoration frequently requires species manipulation and additional seeding, particularly when overcoming successional limitations. Juniper encroachment into tallgrass prairie alters plant community species composition and productivity. However, in our study, juniper associated succession limitations were not apparent, and complete autogenic restoration was achieved within 5 years without seeding or species manipulation.

Key Words: autogenic succession, grassland restoration, novel ecosystems, successional trajectory, thresholds, woody encroachment

INTRODUCTION

Ecologists have long attempted to describe and forecast temporal and spatial patterns of structure and composition in ecosystems that have somewhat predictable patterns of disturbance (e.g., fire return intervals) but less predictable patterns of recovery following disturbance. Many predictions about plant communities have been generated with the use of relatively simplistic equilibrium-based models (Dyksterhuis 1949) that assume deterministic and linear plant succession (Westoby et al. 1989; Laycock 1991; Beisner et al. 2003). Equilibrium-based ecosystem dynamics describe communities as self-regulated by predictable, internal, density-dependent, and negative feedback mechanisms centered on constant domains of attraction (Wu and Loucks 1995). Although these stable-state models provide important conceptual frameworks for comparing landscapes postdisturbance, they do not account for environmental stresses and ecosystem disturbances that are not within the historic range of variability (Seastedt et al.

2008). With more complete information on current disturbance regimes and other ecosystem processes, alternative predictive models have been constructed that account for stochastic and often nonreversible changes in ecosystem successional trajectories (Westoby et al. 1989; Laycock 1991; Beisner et al. 2003). This non-equilibrium-based approach reduced the focus on continuous and reversible vegetation dynamics characteristic of stable states, and emphasized discontinuous and nonreversible processes that result in ecological thresholds and alternative states. In these novel landscapes, autogenic succession following disturbance can be limited by thresholds that prevent recovery (Hobbs and Cramer 2008).

Ecological thresholds represent boundaries in space and time between any and all stable states in which several potentially interacting primary processes are irreversibly changed (Stringham et al. 2003). Thresholds can develop when exotic species invade landscapes and alter historical disturbance regimes or biogeochemical cycles, creating positive feedback mechanisms that perpetually drive the system toward altered states (Wu and Loucks 1995; Beisner et al. 2003). Invasive plants frequently dominate landscapes sufficiently to establish species-loss thresholds in which the remaining species richness is insufficient to re-form the historic community. As a result, landscapes

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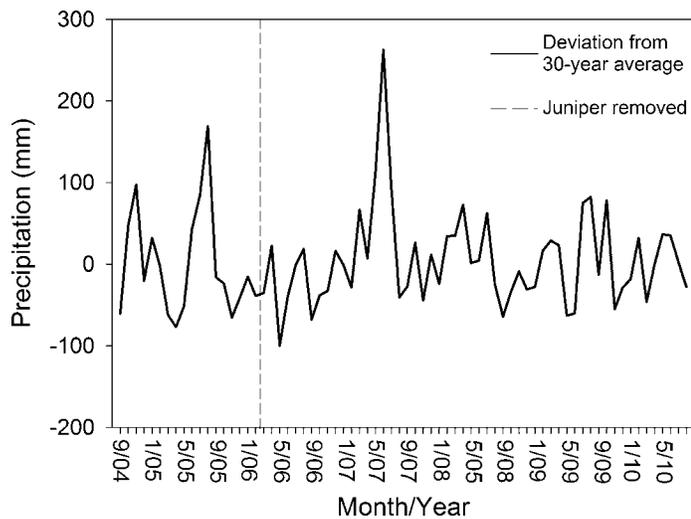


Figure 1. Precipitation received for each month within the study period (September 2004–August 2010) in relation to the 30-yr average near Stillwater, OK. The dashed vertical line indicates when juniper was removed from the treatment locations. Field conditions were dry several months before juniper removal and much of the first year after juniper removal, but precipitation was above average in the second spring after juniper removal.

remain largely depauperate and centered on alternative domains of attraction (Kirkman et al. 2004; Briske et al. 2006).

Woody plant encroachment is a widely documented global phenomenon in which native trees and shrubs increase in abundance and extent, often as a result of altered disturbance regimes such as fire suppression and herbivory (Archer 1994; Maher et al. 2010). Once established, native woody species can alter biotic and abiotic ecosystem so that woody establishment is further promoted and historic native herbaceous species composition and abundance are suppressed (Archer 1994; Van Auken 2000; Grant et al. 2004; Price and Morgan 2008; Limb et al. 2010a). Abundant woody plants often suppress native plant communities sufficiently to represent restoration limitations difficult to overcome without species augmentation (i.e., seeding) (Archer et al. 1995; Bestelmeyer et al. 2011; Briske et al. 2006; Eldridge et al. 2011).

Across North America, juniper (*Juniperus* spp.) is expanding rapidly, likely in response to altered grazing and fire regimes, but increased atmospheric CO₂, nitrogen deposition, and climate change may also contribute (Archer et al. 1995; Miller and Rose 1999; Briggs et al. 2002). North American prairies can respond rapidly to changing environmental conditions different from those from which prairies developed, particularly when remnant communities remain intact (Milchunas et al. 1990, 1998; Limb et al. 2010b). However, plant community dynamics and ecosystem resilience become increasingly altered with increased juniper canopy cover (Limb et al. 2010a). Juniper encroachment can create conditions of uneven resource distribution with nutrient-rich and -depleted zones developing under the canopy and within the interspaces (Ridolfi and D'Odorico 2008). Further, underneath the crowns of individual juniper trees, total solar radiation is reduced and light quality altered by filtering specific wavelengths (Scholes and Archer 1997; Siemann and Rogers 2003). Change in litter composition and depth alter soil moisture and nitrogen availability, which

suppresses seed germination and herbaceous seedling establishment, ultimately influencing the understory plant community (Gehring and Bragg 1992; Fuhlendorf et al. 1997; Yager and Smeins 1999; van Els et al. 2010). When juniper invades grasslands, plant composition can shift from C₄-dominated midgrasses and tall grasses to C₃-dominated midgrasses, short grasses, and sedges and abundant shrub species directly under individual trees (Gehring and Bragg 1992; Fuhlendorf et al. 1997; Briggs et al. 2002). At the stand level, juniper encroachment decreased herbaceous species richness as much as 80% and reduced herbaceous biomass as much as 99% compared to open grassland (Briggs et al. 2002; Limb et al. 2010a).

The tallgrass prairie of North America is one of the most endangered ecosystems globally, with a mere fraction of its pre-European settlement expanse intact (Samson and Knopf 1994). Efforts to restore tallgrass prairie are widespread throughout the region, particularly on abandoned old-fields where cultivation has all but eliminated native species and the associated seed banks, thereby retarding natural succession (Cook et al. 2005; Foster et al. 2007). Therefore, most successful restoration efforts do not rely exclusively on existing seed banks, but instead augment autogenic succession with native seed mixes. Similar to old fields, soil seed banks of native herbaceous plants are greatly reduced as juniper canopy cover increases on encroached grassland sites (Bakker et al. 1996; D'Souza and Barnes 2008). Furthermore, suppression of herbaceous plant communities is related to juniper canopy cover (Limb et al. 2010a). Together, these relationships suggest that thresholds limiting restoration of historic tallgrass prairie potential may align with canopy-cover gradients.

Despite the volume of ecological research on juniper encroachment, we are aware of only one study (Alford et al. 2012) that examined stand-level juniper removal to restore tallgrass prairie ecosystems. To address this important knowledge gap, we used site characteristics data from the Alford et al. (2012) study, which focused on small-mammal communities, combined with original detailed plant species composition and production data, to evaluate the plant community response to stand-level juniper removal along a gradient of increasing canopy cover. We used a modified before–after control-impact design (BACI; Stewart-Oaten et al. 1986) to examine successional trajectories of plant communities following removal. We predicted that temporal rates of recovery of the plant community would be proportional to the juniper canopy-cover gradient, with rapid response at low canopy cover and slower response at high canopy cover. We also predicted that restoration potential would be greatest at low levels of juniper encroachment. Furthermore, we predicted that restoration of tallgrass prairie would be impeded by high levels of juniper encroachment and that successional limitations would keep postremoval composition dissimilar to reference plant communities.

METHODS

This experiment was conducted on historic tallgrass prairie sites located approximately 18 km southwest of Stillwater, Oklahoma (lat 36°10'N long 97°5'W). The region has a

continental climate with an average of 204 frost-free days and 846 mm annual precipitation, 65% of which falls from May to October (Fig. 1). Grassland vegetation in the study area is characterized by little bluestem (*Schizachyrium scoparium* [Michx.] Nash), indiagrass (*Sorghastrum nutans* [L.] Nash), switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), *Carex* spp., and perennial forbs including ragweed (*Ambrosia psilostachya* DC.), *Helianthus* spp. *Lespedeza* spp. and *Solidago* spp.

We used 16 sites, described by Limb et al. (2010a) and Alford et al. (2012), located on the same ecological site with clay loam soils (US Department of Agriculture–Natural Resources Conservation Service [USDA-NRCS] 2006). All sites were moderately grazed year-long by free-roaming deer (*Odocoileus virginianus*) or with mixed-breed cattle at a stocking rate of 0.83 ha·AUM⁻¹. Sites represented a near-continual gradient of *Juniperus virginiana* canopy cover ranging between 0% (reference sites) and about 76%, as determined by aerial photographs and verified on the ground with densitometer at 50 points on each location. Sites were distributed over an area of approximately 10 000 ha, and tree age estimates indicated that initial encroachment occurred between 31 and 62 yr prior to the study, depending on the site location (Appendix 1; available on-line at <http://dx.doi.org/10.2111/REM-D-13-00147.s1>). A 50×50 m plot was established at each location, in 2005, with a 10-m buffer of similar vegetation around the perimeter. Within each plot, permanent grids were established with 16 evenly spaced sampling points where we measured herbaceous species composition and abundance within a 1×1 m frame at mid-summer. Plant species canopy cover and bare ground were estimated with the use of modified Daubenmire cover classes (0–1%, >1–5%, >5–25%, >25–50%, >50–75%, >75–95%, and >95–100%; Daubenmire 1959). The midpoint values for each class were used in analyses. A mean cover value was calculated for each species among the 16 sampling points to determine plot-level plant species abundance. Plant nomenclature follows the National Plant Database (USDA-NRCS 2011).

Visual obstruction was recorded within each location at 91 evenly spaced points with the use of the Robel pole technique (Robel et al. 1970). Herbaceous vegetation was clipped to ground height at 150 sampling points distributed among the 16 plots that encompassed a wide range of visual obstruction, and then oven dried to a constant weight. The Akaike's Information Criterion (AIC) model selection method (Akaike 1974; Burnham and Anderson 1998) was used to select the best model among linear, quadratic, and cubic options for the relationship between visual obstruction and herbaceous biomass (Higgins et al. 2005; Limb et al. 2007). The model selected was

$$y = 11.56 \cdot R + 13.97,$$

where y is herbaceous biomass (g·m⁻¹), and R is the observed visual obstruction. This relationship was subsequently used to estimate standing herbaceous biomass at each of the 16 sites and to determine the relationship between standing herbaceous biomass and juniper canopy cover.

We removed *J. virginiana* from 7 of the 16 sites in late winter 2006 and established a gradient of canopy removal between 15% and 75%. Trees were clipped at ground level with the use of a skid-steer-mounted hydraulic shear and removed from the

sites with minimal soil disturbance (Alford et al. 2012). Among the 16 sites, 2 sites with no juniper cover (reference sites, $n=2$) established at treatment controls. Species composition and herbaceous biomass were measured on all 16 sites at midsummer in 2006, 2007, and 2010 (one, two, and five growing seasons after juniper removal, respectively; hereafter referred to as 1, 2, and 5 yr posttreatment). Within each site, vegetation sampling locations and technique were the same pre- and posttreatment.

Plant community dissimilarity with the use of species cover data was determined between reference sites and intact juniper sites, and between reference sites and juniper-removed sites, in PC-ORD 6.0 with the use of the relative Srensen distance, which is presented as percent dissimilarity (McCune and Grace 2002). All univariate data were analyzed with the IBM-SPSS Statistics software package (Version 19; IBM Corp.). We compared species richness, relative species richness, and community dissimilarity of intact-juniper ($n=7$) and juniper-removed ($n=7$) sites with regression lines fit with the polynomial functions of juniper cover. One of the two reference sites was randomly assigned to the intact juniper sites and the other assigned to the juniper-removal sites for data analysis purposes. A significant regression slope indicated that a relationship existed between the response variable (species richness, community dissimilarity, and herbaceous biomass) and the level of juniper canopy cover (intact or removed). We used the AIC method to select the best model among linear, quadratic or cubic model options (Akaike 1974; Burnham and Anderson 1998).

Species composition data from sites for 2006, 2007, and 2010 were analyzed with nonmetric multidimensional scaling (NMS) in PC-ORD 6.0. Limb et al. 2010a indicated that specific species assemblages were not related to the level of juniper encroachment. Therefore, we analyzed the two reference and seven restored sites separate from the intact sites. We used the relative Srensen distance measure in PC-ORD autopilot mode, which conducts 250 runs with real data and 250 runs with randomized data. In the autopilot mode, PC-ORD selects the best-fit solution (lowest stress) in a possible one–six dimension solution (McCune and Grace 2002). Additional axes are selected if the resulting solution decreases the overall stress by 5 or more out of a possible 100. A Monte Carlo test comparing the real data to the randomized data was used to determine significance (McCune and Grace 2002).

RESULTS

Pretreatment species richness declined linearly along the increasing juniper canopy gradient from 36 and 37 species at the two reference sites to 13 and 15 species respectively at the two 76% canopy cover sites (Fig. 2), a 62% loss in species richness. The large decline in species richness from reference sites to nearly closed canopy stands remained consistent throughout the duration of the study (1-yr post, 2-yr post, and 5-yr post juniper removal) on intact juniper stands (Fig. 2). However, the first year following juniper removal, species richness increased at removal sites compared to intact sites, but species richness still declined along the pretreatment juniper

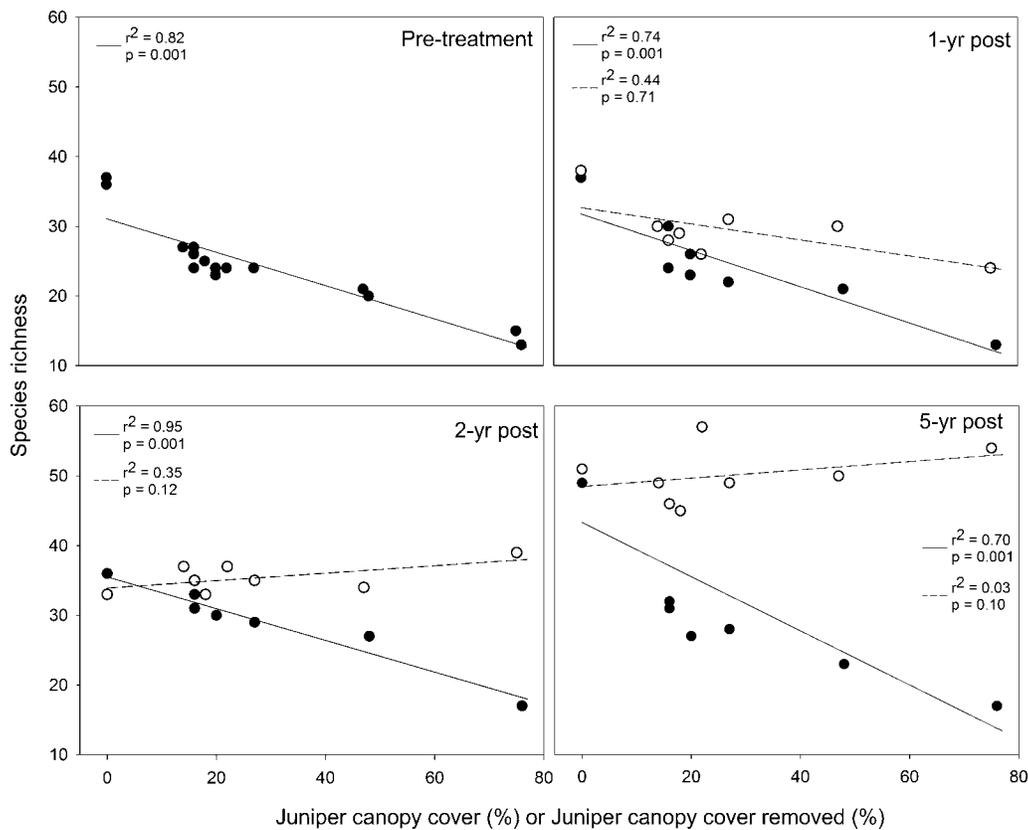


Figure 2. Plant species richness at tallgrass prairie sites along a gradient of *Juniperus virginiana* encroachment and two reference locations near Stillwater, OK, before and 1, 2, and 5 yr after juniper removal. Solid circles and lines represent intact sites, and open circles with dashed gray lines represent sites with juniper cover removed. One reference location randomly assigned to each treatment group for the duration of the study (pretreatment $y = -0.244x + 32.1$; 1-yr post, removed not significant, intact $y = -0.264x + 31.8$; 2-yr post, removed $y = 0.054x + 33.9$, intact $y = -0.23x + 35.5$; 5-yr post, removed not significant, intact $y = -0.328x + 38.4$).

canopy cover gradient. Species richness continued to increase on removal sites the second year following removal. However, sites that were formerly the most encroached with juniper showed the greatest increase in species richness such that all removal plots had similar species richness to the reference sites by 2-yr post treatment. This relationship persisted through the fifth year posttreatment with no relationship between species richness and pretreatment juniper canopy cover.

Plant community dissimilarity between the two reference sites was 0.21 for the preremoval year and ranged between 0.15 and 0.19 for the duration of the study (Fig. 3). The mean dissimilarity between the reference sites and juniper-encroached sites at the beginning of the study increased linearly along the canopy gradient to a maximum of 0.85 and 0.89 at the two 76% canopy cover sites, respectively. This positive linear trend of dissimilarity continued for the duration of the study on the intact juniper sites. The first year following treatment, plant community dissimilarity between the removal and reference sites continued to increase linearly with percent juniper canopy cover removed. However, the overall dissimilarity between reference and treatment sites decreased on all removal sites and continued a modest decline the second year following removal. Dissimilarity remained substantially higher than the two reference sites on all removed juniper sites until the fifth year following the removal, when the mean dissimilarity was 0.22 for all reference sites and juniper removal sites.

Plant community composition was strongly influenced by removal of juniper cover. NMS ordination of composition data for the removal and reference sites pretreatment and in the first, second, and fifth year posttreatment resulted in a significant three-dimensional solution with a final stress of 11.5. The reference sites remained fairly stationary along axis 1 for all years (Fig. 4). Successional trends were best represented along axis 1 in the two-axis biplot, displaying a strong temporal gradient represented by time since removal of juniper. Herbaceous plant species in each of the three sampling years after juniper removal represented a shift from early-seral annual species associated with strong positive scores in 2006, midseral species associated by near-zero scores in 2007, and predominantly late-seral perennial species associated with strong negative scores in 2010 (Table 1). The distribution of site scores along axis 1 is more variable pretreatment and declines with each of the three sampling periods after juniper removal (variance = 0.55, 0.41, 0.27, and 0.06, respectively) and is centered near the reference sites by the fifth year posttreatment (Fig. 4). Species composition on intact sites did fluctuate among years, but did not follow the same successional trends as the removed sites and was not consistent among sites between years.

Estimated herbaceous biomass had a strong negative linear relationship with juniper canopy cover, decreasing approximately 70% at the two 76% juniper canopy sites compared to

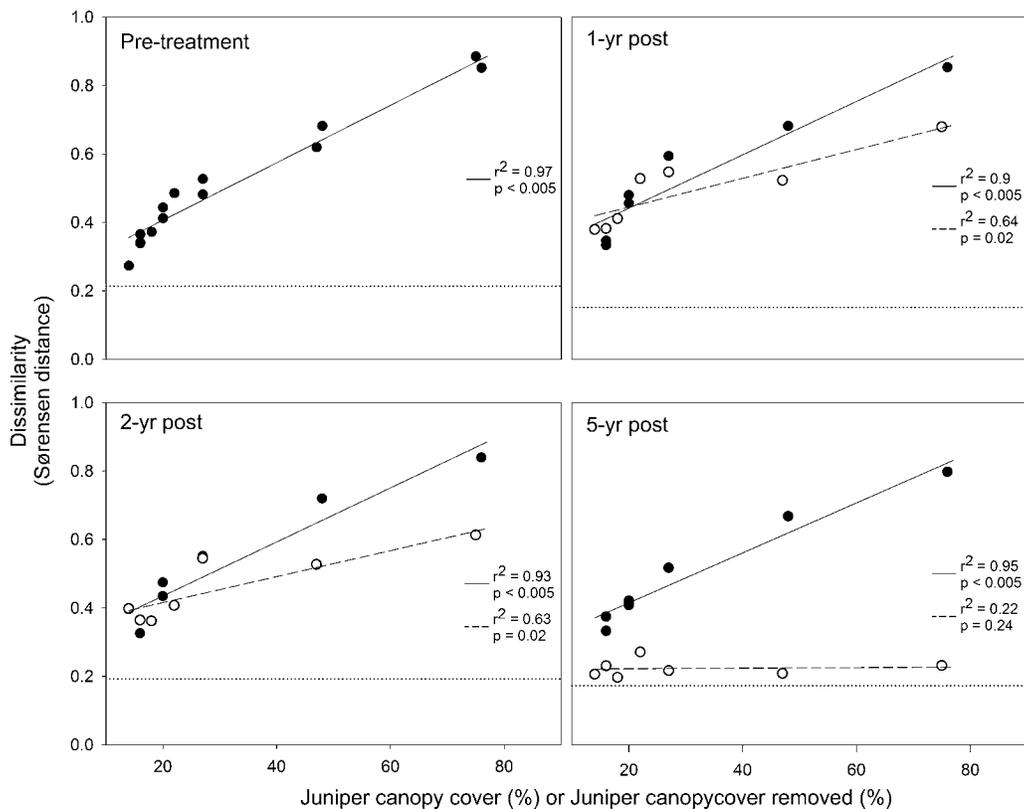


Figure 3. Plant community dissimilarity between reference locations and intact or removed locations along a gradient of *Juniperus virginiana* canopy cover at sites near Stillwater, OK before and 1, 2, and 5 yr after tree removal. Solid circles and lines represent intact sites and open circles with dashed gray lines represent sites with juniper cover removed. One reference location randomly assigned to each treatment group for the duration of the study. The dotted black line represents the dissimilarity between the two reference tallgrass prairie sites (pretreatment $y=0.009x+0.227$; 1-yr post, removed $y=0.007x+0.24$, intact $y=0.009x+0.24$; 2-yr post, removed $y=0.006x+0.23$, intact $y=0.009x+0.27$; 5-yr post, removed not significant, intact $y=0.008x+0.24$).

the reference sites (Fig. 5). This negative relationship remained relatively constant throughout the study at the intact sites with slight variations in biomass between years. Biomass on removed sites was slightly higher than on the intact sites the first year following removal, but a strong negative relationship between biomass and pretreatment canopy cover persisted on sites where juniper was removed. The second year posttreatment, herbaceous biomass on juniper removal sites equaled that of reference sites and persisted into the fifth year posttreatment.

DISCUSSION

Juniper encroachment into grasslands is a rapid and widespread phenomenon that is coupled with large changes in plant community composition and productivity, contributing to tallgrass prairie deterioration (Bragg and Hulbert 1976; Engle et al. 1987; Limb et al. 2010a). In tallgrass prairie encroached by juniper, we followed plant-community dynamics on sites cleared of juniper cover and sites remaining intact to test for thresholds indicating limited restoration potential. In our study, juniper-encroached sites returned to historic composition and productivity within 5 yr of tree removal, regardless of previous juniper canopy cover, indicating that a restoration threshold was not crossed.

Threshold establishment is largely classified into two broad mechanisms in which ecosystem change can be associated initially with biotic constraints followed by abiotic constraints (Whisenant 1999; Beisner et al. 2003; Hobbs et al. 2006; Hobbs and Cramer 2008). Further, Briske et al. (2006) outlined a sequential progression of triggers and subsequent thresholds that characterize the series of changes that can occur in an ecosystem from the original predisturbance state. Structural alterations of species composition and distribution, often facilitated by the presence of invasive species and deviations from historic disturbance regimes, represent the initial state of threshold development (Illius and O'Connor 1999; Briggs et al. 2005). Structural threshold establishment often facilitates declines in species richness, particularly at high levels of woody encroachment. In our study, juniper encroachment upwards of 80% canopy did not result in a species-loss threshold, as removal of juniper returned species diversity to reference levels within 2 yr.

The species-loss threshold is often crossed when exotic and invasive species become established in the system. Frequently, alterations to historic disturbance regimes maintain the plant community in a perpetual species-poor and early successional state (Davies and Svejcar 2008; Davies et al. 2011). In our study, sites with juniper removal were dominated by early-seral plant species the first year following treatment, particularly on sites with substantial woody cover. However, these species that

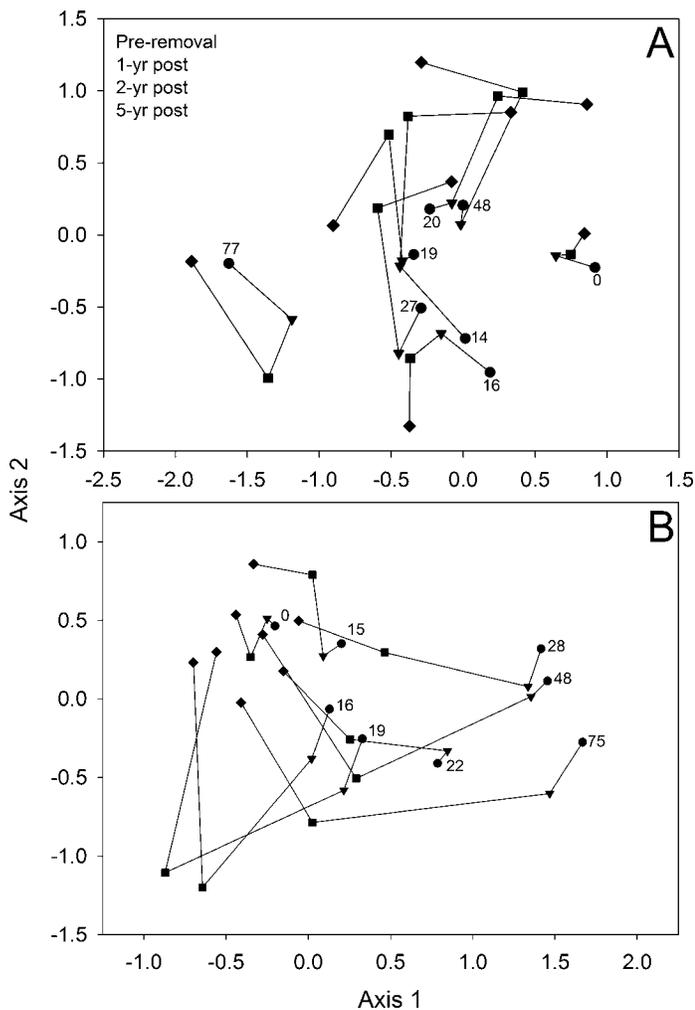


Figure 4. A biplot of nonmetric multidimensional scaling (NMS) axis 1 and axis 2 site scores for sites along a gradient of **A**, intact *Juniperus virginiana* canopy cover and **B**, previous *J. virginiana* canopy cover preremoval and 1, 2, and 5 yr after tree removal from tallgrass prairie near Stillwater, OK. Solid lines track individual treatment locations. Inset numbers indicate the intact or previous canopy cover, respectively.

initially recolonized the restored sites were not exotic, but rather, they are common to the tallgrass prairie region and common to sites with recent disturbance. Climatic variability, particularly dry years during restoration, often limits establishment of nonnative species and wet years are necessary for native species colonization (Bakker et al. 2003; MacDougall et al. 2008). In our study, the drought year immediately preceding and following juniper removal likely inhibited germination and establishment of nonnative species. Likewise, the unseasonably mesic conditions the second and fourth year following tree removal provided the necessary climatic window for native species to respond to removal of juniper competition. The colonization by native early-seral species may have facilitated the historic successional trajectory toward a predominantly native community dominated by mid- and late-seral species 5 yr post-juniper removal.

The biological integrity of ecosystems converted by woody encroachment is often compromised, either by an influx of

Table 1. Nonmetric multidimensional scaling (NMS) axis 1 species scores, life span, and seral stage for species representative of 1 yr before and 1, 2, and 5 yr after juniper removal at tallgrass prairie sites near Stillwater, OK. Life span abbreviations: A indicates annual; P, perennial. Seral stage abbreviations: E indicates early seral; M, midseral; L, late seral. Plant life span and seral stages as in Tyrl et al. (2002).

Species	NMS species scores Axis 1	Plant species descriptions	
		Life span	Seral stage
<i>Euphorbia marginata</i>	1.64	A	E
<i>Panicum capillare</i>	0.95	A	E
<i>Digitaria cognata</i>	0.70	P	E/M
<i>Solanum rostratum</i>	0.63	A	E
<i>Helianthus annuus</i>	0.23	A	E
<i>Diodia teres</i>	-0.12	A	E
<i>Achillea millefolium</i>	-0.14	P	M/L
<i>Schizachyrium scoparium</i>	-0.22	P	M/L
<i>Desmodium sessilifolium</i>	-0.27	P	M/L
<i>Sorghastrum nutans</i>	-0.30	P	M/L
<i>Andropogon gerardii</i>	-0.37	P	L
<i>Salvia azurea</i>	-0.43	P	L
<i>Panicum virgatum</i>	-0.55	P	L
<i>Oxalis violacea</i>	-0.60	P	L
<i>Bouteloua curtipendula</i>	-0.76	P	M/L

exotic species or by becoming species impoverished. Species losses are often due to abiotic factors, such as reduced light and soil nutrient limitations. If such conditions persist long enough, propagule additions are required to restore the lost species effectively (Foster and Gross 1997; Kirkman et al. 2004). In old-field restorations where historic vegetation is all but eliminated, native grassland species establishment was restricted to locations deliberately seeded (Bakker et al. 2003). Juniper encroachment into tallgrass prairie substantially reduces stand species richness, particularly under the crowns of individual trees. However, suppression of the native plant community is not uniformly distributed throughout the juniper stand, leaving intact islands of historic species where overstory canopy gaps allow unrestricted light and precipitation to reach the understory community (Limb et al. 2010a). We speculate that these remnant populations are capable of rapid vegetative expansion into the recently cleared areas, and likely limit the establishment of seed-dependent exotic grasses and forbs. Additionally, the viable soil seed bank in juniper-encroached grasslands remains largely intact for at least 40 yr after conversion to woodlands (D'Souza and Barnes 2008). Plant establishment from the seed bank likely enabled the rapid recovery of species richness, particularly for forb species. In contrast, juniper encroachment in arid western North American landscapes accelerated between 1850 and 1900, with stand age being more than double the 62 yr in our study (Miller et al. 2005). It is likely that opportunities for restoration relying on autogenic succession in tallgrass prairie would decline if juniper persists longer than native bank can remain viable.

The addition of woody vegetation into grassland environments shifts annual net primary production (ANPP) from largely herbaceous biomass to woody production (Norris et al. 2001). In our study, biomass declined nearly 70% under closed-

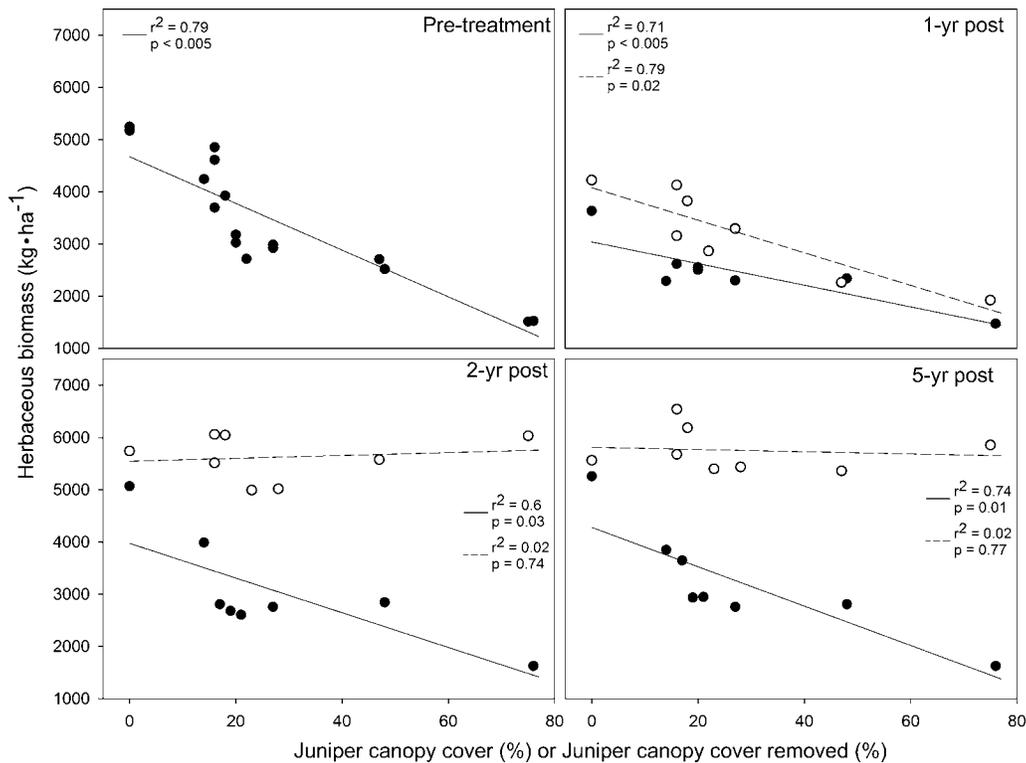


Figure 5. Herbaceous biomass at sites along a gradient of *Juniper virginiana* encroachment and two historic tallgrass prairie reference locations near Stillwater, OK, before and 1, 2, and 5 yr after juniper removal. Open circles with gray dashed lines represent sites with juniper cover removed and closed circles with solid black lines represent sites with intact juniper canopy cover. One reference site was randomly assigned to each treatment group for the duration of the study (pretreatment $y = -45.724x + 4690.0$; 1-yr post, removed $y = -32.137x + 4097.1$, intact $y = -21.003x + 3043.8$; 2-yr post, removed not significant, intact $y = -33.728x + 3983.6$; 5-yr post, removed not significant, intact $y = -38.224x + 4289.5$).

canopy juniper stands. However, there was complete recovery of herbaceous productivity within 2 yr at all levels of juniper encroachment. Directly under the crown of isolated trees, herbaceous ANPP is decreased by as much as 99% (Engle et al. 1987; Briggs et al. 2002). However, upon removal of the juniper canopy, light is no longer limiting and species present within the stands could fully express themselves. This response is in contrast to juniper encroachment in xeric ecosystems, where soil water can be a substantial limiting environmental factor (Bates et al. 2000; Miller et al. 2000). In these systems, juniper has a large zone of influence extending well beyond the drip line (Arnold 1964; Short et al. 1977), and complete recovery was not realized 10 yr after *Juniperus occidentalis* removal (Miller et al. 2005).

The particular life-history strategy of the target woody species, such as resprouting or nonresprouting, can strongly influence recovery of historic grassland species following removal (Archer 1994). *J. virginiana* is nonresprouting and, once removed from the system, does not continue to limit plant establishment and growth. Resprouting species, such as *Prosopis glandulosa*, *Juniperus deppeana*, and *Juniperus pinchotii*, are capable of basal sprouting in as few as 7 d following top removal and near 100% survival without repeated cutting (Scifres and Hahn 1971). The persistence of these woody species provides a mechanism for continued interspecific competition for soil nutrients and light (Lett and

Knapp 2005; Ansley et al. 2006; Bried and Hecht 2011), both of which were often limiting for the historical plant community.

MANAGEMENT IMPLICATIONS

Our study suggests that, at least in some circumstances, restoration of tallgrass prairie with even high levels of juniper encroachment may be achieved simply by removing the juniper. Landscape fragmentation, property ownership, and urbanization often limit the feasibility of fire as a restoration mechanism. Mechanical tree removal is an acceptable alternative to enhance grassland plant and animal community richness and productivity on encroached landscapes (Bates et al. 2000; Ansley et al. 2006; Alford et al. 2012) although restored floral assemblages do not always resemble the historic communities (Bestlemeyer et al. 2004). The full recovery of our sites within 5 yr of tree removal attests to the resilient nature of the tallgrass prairie. Frequently, a first strategy for grassland restoration is to add seed mixtures to offset depleted soil seed pools and propagule limitations. Although this strategy may be useful in certain situations where soils are eroded (Manjoro et al. 2012) or historic seed pools removed, autogenic succession remains a viable option for managing altered landscapes in grassland ecosystems and should be a first option for restoration.

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