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Influence of resource availability on *Juniperus virginiana* expansion in a forest–prairie ecotone

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Abstract. Woody plant expansion into grasslands and savannas is a global concern. Rapid expansion of *Juniperus virginiana*, a tree native to North America, has profound ecological consequences. We used transplanted *J. virginiana* seedlings to investigate the role of resource availability on *J. virginiana* expansion following the removal of fire, the factor historically limiting range expansion of this fire-intolerant species. We evaluated *J. virginiana* seedling survival and seedling growth, two important phases in woody plant expansion, relative to two belowground resource factors, plant-available soil water (soil clay content, an index of plant-available soil water) and plant-available nitrogen (PAN), and an aboveground factor, photosynthetic active radiation (PAR). In three plant communities associated with an oak forest–tallgrass prairie ecotone, we transplanted 2-yr-old *J. virginiana* seedlings in a systematic grid design and measured *J. virginiana* seedling survival and growth 8, 20, and 30 months following the transplant. We also measured soil clay content, PAN, and PAR in 1-m^2 quadrats centered on each transplanted seedling. We employed path analysis at two spatial scales (144 and 2916 m^2) to compare the role of resource factors in seedling growth and survival. *Juniperus virginiana* seedling survival was about 10% greater in tallgrass prairie and upland oak forest than in the old field, and seedling growth in tallgrass prairie exceeded the two other communities by about a factor of five. Tallgrass prairie in our study area is clearly more vulnerable to expansion of *J. virginiana* than the other two plant communities. Survival and growth were controlled largely by available light (PAR) and secondarily by plant-available soil water, indexed by soil clay content. In all three vegetation types and at both fine and coarse scales, soil clay content also exerted an indirect effect, possibly by mitigating the influence of light. Results of this study suggest that soil distribution maps and associated ecological site designations might be useful for directing *J. virginiana* management in the oak forest–tallgrass prairie ecotone by identifying the potential hotspots of invasion.

Key words: cross timbers; eastern redcedar; invasion; seedlings; soil texture; tallgrass prairie; upland oak forest; woody plant expansion.

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Introduction

Woody plant expansion is a global phenomenon in grassland and savanna ecosystems (Archer 1994, Binggeli 1996). Drivers of woody plant expansion include domestic livestock grazing, fire suppression, and climate change (Archer 1989, Van Auken 2000, Volder et al. 2013). A synthesis of over two decades of research on woody plant expansion in the tallgrass prairie of

central North America illustrates the widespread expansion of woody plants in the absence of fire (Briggs et al. 2005). Not only does infrequent fire accelerate woody plant expansion, restoring historic fire regimes in this region may not reverse woody plant expansion (Briggs et al. 2005, Bond 2008). One such example of a rapidly expanding native woody species is *Juniperus virginiana* L. in North America (Schmidt and Leatherberry 1995, Hoch et al. 2002, DeSantis et al. 2010). Expansion of *J. virginiana* is of ecological concern because it changes the plant and animal community composition (Gehring and Bragg 1992, Coppedge et al. 2001, Horncastle et al. 2005, Alford et al. 2012, Powers and Larsen 2014), reduces grassland productivity (Engle et al. 1987, Smith and Stubbendieck 1990), alters hydrology (Zou et al. 2013, Starks et al. 2014), and alters biogeochemistry (Norris et al. 2001, 2007, McKinley and Blair 2008).

Plant community attributes, such as species composition or diversity, have been hypothesized to regulate invasibility of plant communities (Elton 1958, Richardson and Pyšek 2008), a function largely of niche overlap, which is clearly an important contributor to invasion resistance (Hooper and Dukes 2010). However, plant species richness and diversity may not regulate *J. virginiana* expansion in the Southern Great Plains (Ganguli et al. 2008*b*). Alternatively, resource availability, the amount of unused resources in plant communities, has been suggested as the most important factor in determining invasibility (Davis et al. 2000, Davis and Pelsor 2001). In this view, there may be no relationship between the diversity of a plant community and its invasibility (Davis et al. 2000). Rather, the availability of limiting resources predicts competition intensity within the resident plant community such that competition intensity decreases as unused resources increase (Davis et al. 1998, 2000, Tognetti and Chanetou 2015). Within a plant community, resource availability can change as a result of disturbance that increases resource levels directly or alters resource use by resident vegetation and by biogeochemical processes that increase resource availability (Tilman 1985, Davis et al. 2000, Seastedt and Pyšek 2011). A species can expand into or invade new communities by acquiring more of a limiting resource (Davis and Pelsor 2001), by using limiting resources more efficiently (Funk and Vitousek 2007), by tolerating lower resource levels (Gurevitch 1986), or by enduring harsher conditions than resident species. Plant community diversity and resource competition can interact to influence the community invasion through niche preemption, whereby higher levels of diversity can increase the resource competition and thereby decrease the invasion (Mallon et al. 2015).

Plant–soil interactions and resulting plant community dynamics are hypothesized to be driven by limiting resources that vary along a precipitation gradient (Lauenroth and Coffin 1992, Burke et al. 1998). Areas of low precipitation characterized by arid to semiarid grassland plant communities are postulated to be dominated by belowground constraints and where water is the most limiting resource (Noy-Meir 1973, Lauenroth et al. 1978). In contrast, areas of high precipitation characterized by mesic forests are postulated to be dominated by aboveground constraints and where light is the most limiting resource (Kaelke et al. 2001, Lin et al. 2002, Green et al. 2004). In areas of intermediate precipitation, such as subhumid to humid grasslands, this hypothesis suggests that plant community dynamics are characterized by indeterminate limiting resource factors, commonly water, nitrogen, and light that are spatially and temporarily variable (Lauenroth and Coffin 1992, Seastedt and Knapp 1993, Burke et al. 1998).

We do not understand completely the role of resource limitation in *J. virginiana* expansion in North America. *J. virginiana* expansion was limited historically by fire (Schmidt and Leatherberry 1995, Hoch et al. 2002). In the absence of fire, soil water (Davis et al. 1998, 1999), light (Nicotra et al. 1999, Lin et al. 2002), and soil nutrient availability (Kaelke et al. 2001) might limit woody plant expansion. Plant-available soil moisture on a site is determined by the interaction between precipitation, topography, potential evapotranspiration, vegetation, and soil properties, particularly soil texture (Tolk 2003). Given similar precipitation regimes and topography, soil texture largely controls plant-available soil water because of infiltration and water retention properties of soil texture. Water infiltrates rapidly into sandy soils, but water also drains rapidly from the large pores in sandy soils. In contrast, water infiltrates slowly into clayey soils where water is held against gravity in small pores among small clay

particles and by the larger matrix force exerted by the comparative larger surface area provided by small clay particles. Therefore, even though clayey soils can hold more water than sandy or loamy soils, more of the water in clayey soils is bound tightly to the soil particle and unavailable for plant use. Therefore, in the semiarid to subhumid climates characteristic of the Great Plains, woody plants might be expected to encroach more aggressively on soils with neither extreme in soil texture (i.e., neither sand nor clay) because of more plant-available soil water.

Our objective was to determine the role of resource availability on *J. virginiana* expansion, particularly the role of abiotic factors light, soil nitrogen, and soil water on success of *J. virginiana* establishment and growth in a subhumid oak forest–tallgrass prairie ecotone. We transplanted *J. virginiana* seedlings into three plant communities to evaluate *J. virginiana* seedling survival and seedling growth, two important phases in woody plant expansion. We examined the survival and growth relative to direct and indirect effects of three resources, assessed using two belowground factors, potential plant-available soil water (indexed by soil texture through soil clay content) and plant-available nitrogen (PAN, indexed by extractable soil ammonium and nitrate), and an aboveground factor, photosynthetic active radiation (PAR).

Methods

Site description

We conducted our study from 2001 to 2003 in north-central Oklahoma (36°03′ N, 97°12′ W) within the Cross Timbers, a mosaic of upland oak forest, savanna, and tallgrass prairie encompassing about 4.8 million hectares from southeastern Kansas to north-central Texas (Hoagland et al. 1999). The cross timbers is in a transition zone in which upland oak forest occupying sandstone-derived soils and tallgrass prairie occupying soils derived from shale and limestone (Dyksterhuis 1948, Hoagland et al. 1999).

To evaluate the relationship between *J. virginiana* seedling survival and growth and resource availability, we established study sites in three plant communities—old field, tallgrass prairie, and upland oak forest. These plant communities are experiencing encroachment by *J. virginiana* throughout the region (Engle et al. 2008). According to a report on land-use history of an adjacent research location with the same ownership and management history (Ewing et al. 1984), the area was homesteaded between 1895 and 1905. The old field resulted from cultivation, which was accompanied by soil erosion that ceased by 1937 when the U.S. government purchased the land (Ewing et al. 1984). The government constructed shallow terraces in the cultivated field, which was allowed to naturally revegetate as an old field. The upland oak forest and tallgrass prairie were largely undisturbed (Ewing et al. 1984). Domestic cattle grazed the research site at varying rates before the study, and light stocking of cattle was practiced in the decade before the study. We excluded livestock during the study. Average annual precipitation in this area is 831 mm, mostly falling from April through October, and the average frost-free growing period is 203 d (National Oceanic and Atmospheric Administration 1999). Water-year (October 1–September 30) precipitation for the three years spanning the study period averaged 744 mm, about 10% drier than average.

The tallgrass prairie and old-field sites are comprised of fine to fine-loamy soils (Renfrow-Coyle-Grainola Association) derived from weathered shale, limestone, and sandstone under prairie vegetation (Henley et al. 1987). The dominant herbaceous species on the tallgrass prairie site were *Schizachyrium scoparium* (Michx.) Nash, *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, and *Ambrosia psilostachya* DC (nomenclature follows the PLANTS database [USDA, NRCS 2016]). The dominant plants on the old field were *S. scoparium*, *Aristida purpurascens* Poir., *S. nutans*, and *A. psilostachya*. The upland oak forest sites are comprised of loamy to fine-loamy soils (Stephenville-Darnell Association) derived from weathered sandstone under oak (Henley et al. 1987). Dominant species on this site included *Quercus stellata* Wangenh. and *Q. marilandica* Münchh. See Ganguli et al. (2008*b*) for additional description of plant community composition.

Experimental design

We investigated *J. virginiana* expansion through a transplant experiment in which 2-yr-old bare-root *J. virginiana* seedlings (obtained from

Goldsby, Oklahoma, USA) were transplanted in a systematic grid design (180 × 180 m) within each plant community from 20 March to 27 March 2001. Tree planting bars (Jim-Gem) 10 cm wide, 30 cm long, and 2.5 cm thick were used to plant the seedlings by hand to minimize disturbance effects, and the ground was locally compacted by foot to close the hole and eliminate air pockets. By systematically planting established seedlings, we intended to control for germination effects and the clumped dispersal of *J. virginiana* by birds and mammals (Holthuijzen et al. 1987). In each grid, we transplanted 900 seedlings so that each seedling was 6 m distant from each neighbor seedling. We established permanent 1 × 1 m plots around each seedling for subsequent soil measurements.

We used this spatial design to investigate the effect of scale (i.e., increasing grain size) on the relationship between resource availability and *J. virginiana* seedling survival and seedling growth. Spatial dependence of ecological processes can occur in large landscape investigations (Godfray and Lawton 2001, Fuhlendorf et al. 2002) as well as small plot investigations (Purves and Law 2002). Therefore, we selected two spatial scales to investigate the effects of scale on the relationship between resource availability and *J. virginiana* seedling survival and seedling growth. We used ArcView GIS software v.3.3 (ESRI, Redlands, California, USA) with the Moving Windows Statistics v.1.1a extension to aggregate groups of 4 and 81 adjacent samples into single data units (Isaaks and Srivastava 1989) corresponding to areas of 144 and 2916 m^2 to reflect the area of influence of an individual tree or small group of trees and a stand of trees, respectively (Table 1).

Field methods

We measured crown height and stem diameter at the time of transplanting, and we measured crown height, stem diameter, and survival of seedlings at 8, 20, and 30 months following transplanting. Height of seedlings was measured as the standing height of the tallest leader, and seedling diameter was measured with digital calipers approximately 1 cm above the soil surface in two opposing directions. Seedlings were counted as dead if they did not appear to contain chlorophyll or if seedlings were removed (i.e., by herbivores or by animal excavation) from the transplant location. Average crown height and stem diameter of seedlings at the time of transplant were 255 mm and 5 mm, respectively. We combined seedling crown height and diameter into an index of seedling size (seedling size = seedling crown height × seedling stem area) from which we calculated the percentage growth or the percentage change in seedling size, ([final seedling size − initial seedling size]/initial seedling size) × 100, so that we could assess seedling performance using a single response variable. The index of seedling size is equivalent to calculating stem volume of seedlings, a commonly used response variable in forestry investigations (Brandeis et al. 2002).

We sampled soil chemical and physical properties throughout each grid from May to June 2001 during the period of peak availability of resources, soil water, and solar radiation (Borchert 1950) and nutrients. Concentration of extractable N is usually greatest in the spring (May and June) (Blair et al. 1998). While our soil nitrogen methods do not fully capture nitrogen dynamics, we believe the soil nitrogen data amply index nitrogen availability. Our intent was not to describe temporal soil nitrogen dynamics including the annual cycle of PAN. Around each *J. virginiana* seedling, four soil cores (15 cm) were collected and combined to form a composite sample, dried in a forced-air oven at 60°C, and ground to pass a 2-mm sieve.

Table 1. Mean ($\bar{x}$), standard deviation (SD), and coefficient of variation (% CV) of clay, plant-available nitrogen (PAN), and photosynthetic active radiation (PAR) in three plant communities at the 1 × 1 m spatial scale (n = 900 for each plant community).

	Clay (%)		PAN (ppm)		PAR ($\mu mol \cdot s^{-1} \cdot m^{-2}$)	
Community	$\bar{x}$ ± SD	CV	$\bar{x}$ ± SD	CV	$\bar{x}$ ± SD	CV
Tallgrass prairie	19 ± 5	13	14.5 ± 3.4	24	1600 ± 490	30
Old-field grassland	24 ± 8	33	12.0 ± 3.4	29	1630 ± 620	38
Upland oak forest	13 ± 5	22	11.3 ± 3.3	30	340 ± 520	152

Soils were analyzed for texture, nitrate nitrogen (NO_3-N), and ammonium nitrogen (NH_4-N). We measured PAN because nitrogen is often the most limiting nutrient to plant growth in this region (Blair et al. 1998). Soil nitrate and ammonium were extracted with one molar potassium chloride solution and measured by flow injection utilizing the cadmium reduction method for nitrate and the salicylate method for ammonium (Robertson et al. 1999). We used the sum of nitrate and ammonium values to estimate the total PAN (Schlesinger et al. 1996). Soil texture, specifically soil clay content (Table 1), was used as a surrogate of potential plant-available water, which differs markedly across textural ranges observed in the study area (Scott et al. 2013). We determined the soil texture with the hydrometer method (Gee and Bauder 1986), including percentage clay, an important indicator of soil water infiltration rate and water retention (Harlan 1957). Photosynthetic active radiation was measured approximately 50 cm above each seedling and above the herbaceous canopy with a LI-190SA Quantum Sensor (LI-COR, Lincoln, Nebraska, USA) on cloudless days within 75 min of solar noon May–July 2002.

Statistical analysis

We used path analysis, a general form of multiple regression (Dewey and Lu 1959, Sokal and Rohlf 1995), to simultaneously assess the direct and indirect effects of resource availability factors (predictor variables) on seedling survival and growth (criterion variables). Direct effects between the predictor variables and *J. virginiana* seedling survival and seedling growth were estimated using standardized partial regression coefficients. Coefficients may be >1 because a standard deviation change in the predictor variable may potentially affect more than one standard deviation change in the criterion variable (Sokal and Rohlf 1995). Indirect effects of the predictor variables (i.e., indirectly influencing *J. virginiana* seedling survival or seedling growth) were estimated using Pearson's correlation coefficients. We performed path analysis using SAS (ver. 8 SAS Institute, Cary, North Carolina, USA), and we selected $P < 0.05$ to determine the significance of path models and direct and indirect effects within path models.

Results

Juniperus virginiana seedling survival and seedling growth, two phases of the expansion process of the species, differed across the three plant communities in our study (Table 2) and the three factors we measured (Table 1). Seedling survival was lowest in old-field grassland and 10% greater in tallgrass prairie and upland oak forest (Table 2). Seedlings in tallgrass prairie were considerably larger, by about a factor of 5, after 30 months than seedlings in the old-field grassland or upland oak forest (Table 2). These results indicate that the tallgrass prairie in our study is more vulnerable to expansion of *J. virginiana* than the other two plant communities.

The relationship between abiotic factors and survival and growth of *J. virginiana* varied across plant communities and spatial scale, and variance in seedling survival and growth explained by path regression models differed substantially across plant community (Figs. 1 and 2). However, survival and growth were largely controlled by PAR and secondarily by plant-available soil water, indexed by soil clay content. In those models in which soil clay content, a surrogate for the potential plant-available water content, was a significant variable (eight of 12 models of seedling survival and growth), the direct relationship of

Table 2. Mean survival and mean ± SE of height, diameter, and change in size (growth, expressed as percentage change in seedling size from $t = 0$ months to $t = 30$ months) of *Juniperus virginiana* seedlings 30 months following the transplant into tallgrass prairie, old-field, and upland oak forest communities.

Community	Survival (%)	Height (mm)	Diameter (mm)	Change in size†
Tallgrass prairie	72	752 ± 7	12 ± 1	2250 ± 67
Old-field grassland	60	411 ± 6	7 ± 1	431 ± 30
Upland oak forest	71	451 ± 6	6 ± 1	320 ± 15

† Equation is as follows: ([final seedling size – initial seedling size]/initial seedling size) × 100.

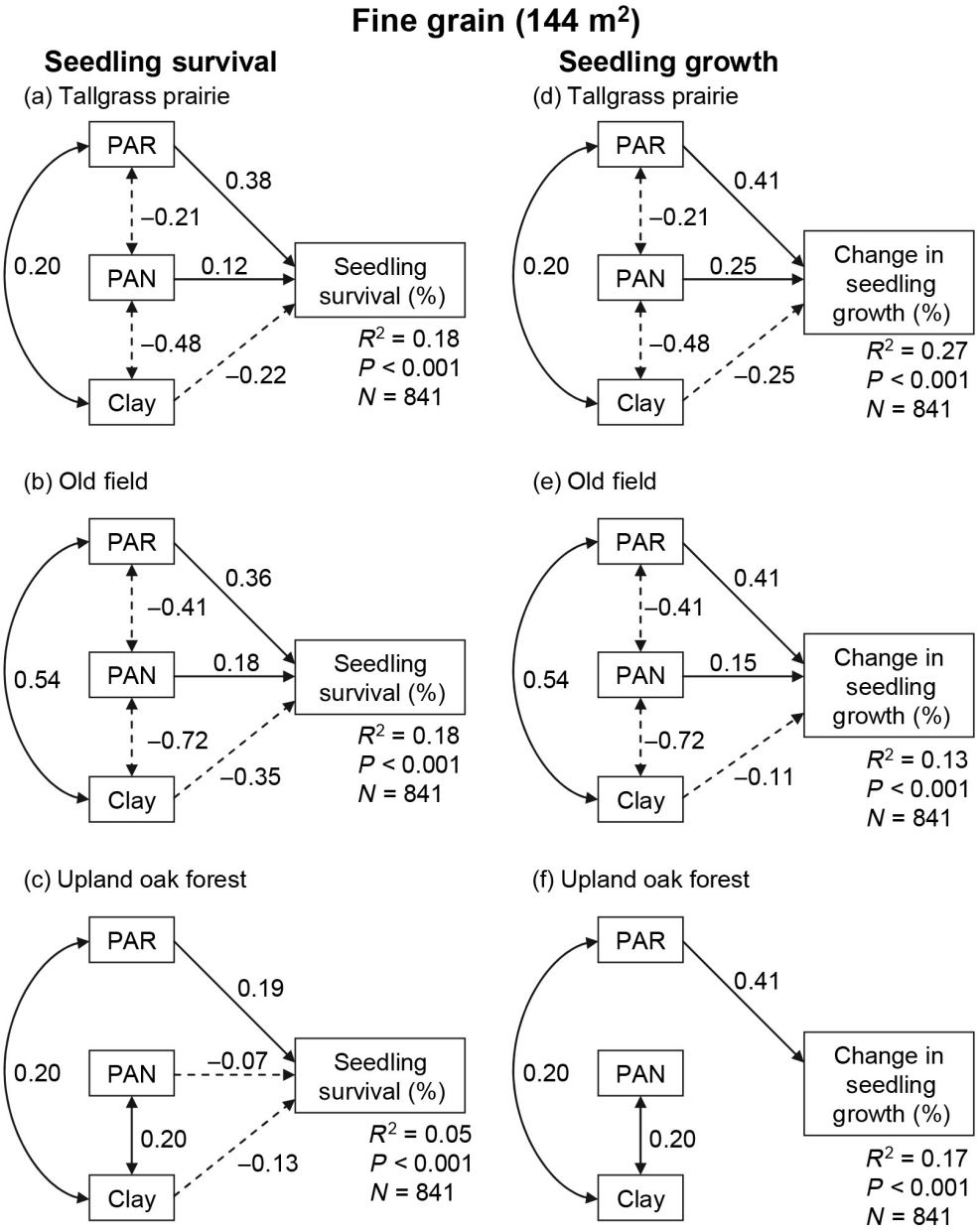


Fig. 1. (a–f) Path analysis of *Juniperus virginiana* seedling survival and seedling growth at a fine spatial scale (i.e., grain = 144 m^2) in tallgrass prairie (a, d), old-field grassland (b, e), and upland oak forest (c, f). Direct arrows to seedling survival (a–c) or seedling growth (d–f) from prediction variables photosynthetic active radiation (PAR), plant-available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate the positive relationships between variables, whereas dashed lines indicate the negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when $P \leq 0.05$.

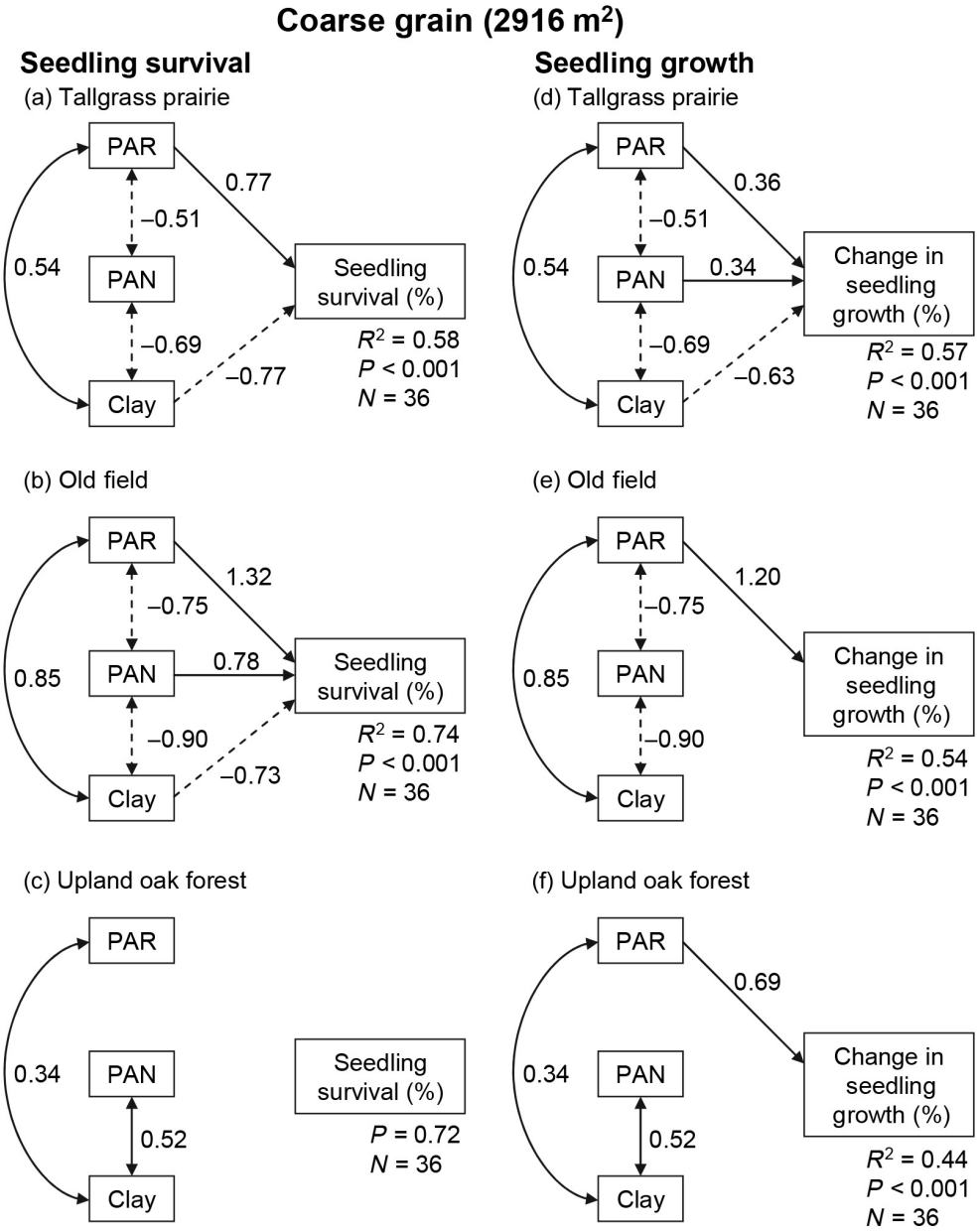


Fig. 2. (a–f) Path analysis of *Juniperus virginiana* seedling survival and seedling growth at a coarse spatial scale (i.e., grain = 2916 m^2) in tallgrass prairie (a, d), old-field grassland (b, e), and upland oak forest (c, f). Direct arrows to seedling survival (a–c) or seedling growth (d–f) from prediction variables photosynthetic active radiation (PAR), plant-available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate the positive relationships between variables, whereas dashed lines indicate the negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when $P \leq 0.05$.

soil clay content to seedling survival and growth was negative, as we expected. In contrast, the direct relationship of PAR and PAN to *J. virginiana* seedling survival and seedling growth was positive, also as we expected. PAR, a significant direct variable in 11 of 12 path models, generally had the strongest direct effect on seedling growth and seedling survival (nine of 12 path models) (Figs. 1 and 2). PAN was a significant variable in only seven of 12 models, and of these, the direct effect for PAN was low or not significant except for one model—seedling survival in the old field at the coarse scale (Fig. 2).

Path models generally performed better at the coarser spatial scale, and the most robust models were of seedling survival and growth in the tallgrass prairie and seedling survival in the old-field community, all at the coarse spatial scale (Figs. 1 and 2). Path models of seedling survival in oak forest were the least robust, explaining little variance in seedling survival at either the fine or coarse scale compared to the models in tallgrass prairie and old field.

Although PAR was the abiotic factor most strongly associated with seedling survival and growth across spatial scales and plant communities, soil clay content was correlated with PAR in all 12 models, which indicates that soil clay content is also an important indirect variable influencing seedling survival and growth by influencing PAR. We suspect that plant-available soil water, indexed by soil clay content, might mediate the influence of PAR on *J. virginiana* seedlings by influencing the growth and shading structure of surrounding plants. Therefore, soil clay content either directly influenced or indirectly influenced the seedling survival and seedling growth consistently across communities and spatial scales (Figs. 1 and 2). Moreover, the partial coefficient between soil clay content and PAR was the largest of the indirect relationships in the models combined across plant communities, and the direct negative effect of soil clay content on seedling survival at the coarse scale across plant communities (Fig. 3) was the largest partial correlation coefficient of any of the path models (Figs. 1–3). The negative direct effect of soil clay content was significant in only three of the four models for oak forest, and the coefficient for the direct effect in those was low (Figs. 1 and 2). In contrast, seedling survival in the tallgrass prairie and old field, which had higher soil clay content than in the oak forest, was strongly and negatively related to soil clay content at the coarse scale (Figs. 1 and 2).

Of the three factors, PAN was least related to seedling survival and growth, and the relationship was most often nonsignificant in the path models (Figs. 1–3). However, soil clay content was negatively correlated with PAN for both measures of *J. virginiana* success in the tallgrass prairie and old-field communities at both spatial scales and positively correlated with PAN for both measures of success in the upland oak forest community at both spatial scales (Figs. 1 and 2). PAN was directly positively related to *J. virginiana* success at the fine spatial scale in the prairie and old-field communities, but the coefficients were generally low. There was no clear relationship between PAN and *J. virginiana* success in the upland oak forest community and at the coarse spatial scale. Therefore, our results indicated that light PAR and plant-available soil water (soil clay content) largely control *J. virginiana* expansion among these plant communities.

Discussion

Our controlled experiment assessed the survival and growth of *J. virginiana* seedlings transplanted into three contrasting, intermixed vegetation types (tallgrass prairie, old field, and upland oak forest). We characterized three physical properties (soil clay content, extractable soil inorganic N, and light availability at seedling canopy level) in each set of plots and then used path analysis based on sample clustering at two different spatial scales to assess which of the three factors best explained the differences in seedling survival and seedling growth. Because the study employed large gridded plots (900 seedlings evenly spaced in 180 × 180 m plots), we were able to assess these resource factors at different spatial scales. Had we employed only a fine-scale assessment, the results would not have been as compelling because both the direct and indirect effects of the factors were stronger at the coarser of the two scales.

Our results indicate that *J. virginiana* seedling survival and seedling growth vary across vegetation types, and survival and growth are largely controlled by a combination of available light

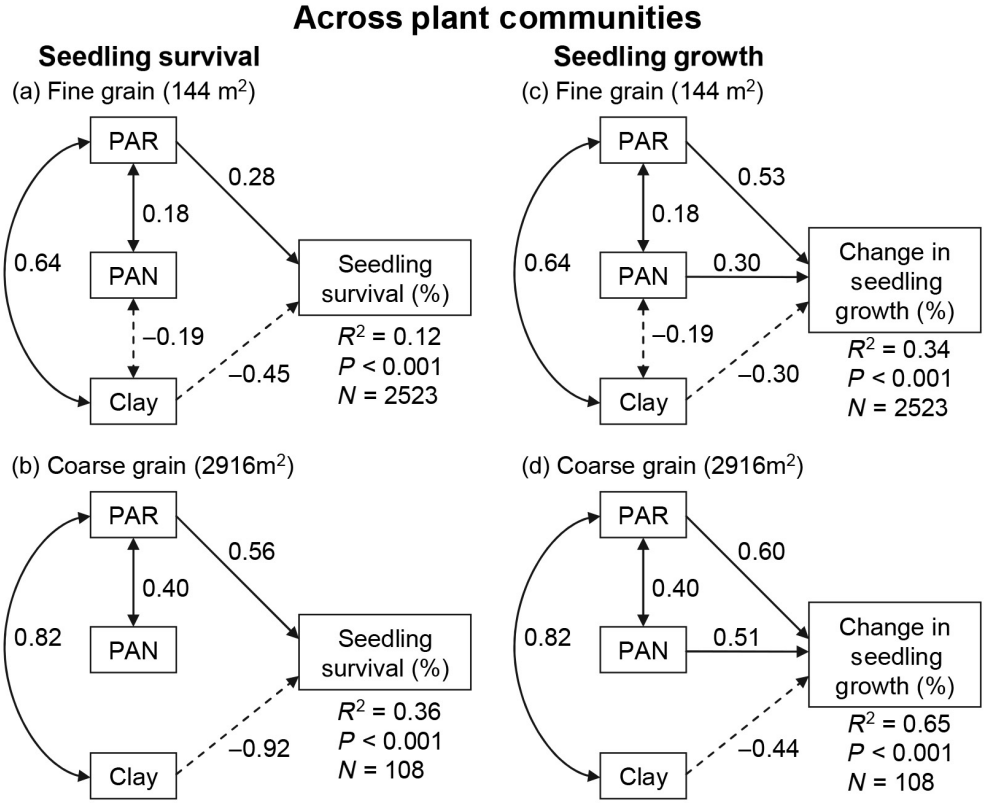


Fig. 3. (a–d) Path analysis of *Juniperus virginiana* seedling survival and seedling growth across plant communities at a fine spatial scale (i.e., grain = 144 m^2) and coarse spatial scale (i.e., grain = 2916 m^2). Direct arrows to seedling survival (a, b) or seedling growth (c, d) from prediction variables photosynthetic active radiation (PAR), plant-available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate the positive relationships between variables, whereas dashed lines indicate the negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when $P \leq 0.05$.

PAR and plant-available soil water, indexed by soil clay content. In all three vegetation types and at both fine and coarse scales, soil clay content also exerted an indirect effect by mitigating the influence of light. Therefore, even when soil clay content was not directly or strongly related to *J. virginiana* seedling survival and seedling growth, soil clay content was related to seedling survival and seedling growth through its influence on other resources, especially on PAR. This consistent relationship of soil clay content and PAR with *J. virginiana* seedling survival and seedling growth suggests that *J. virginiana* expansion into plant communities in this ecotone can be predicted largely by inherent site characteristics that can be represented collectively by soil clay content, coupled with PAR. Our results support the concept that multiple resource factors interact to create an integrated limiting condition important to plant community dynamics (Palmer 1993), or in the case of this study, the survival and growth of a single expanding species (Chapin 1980, Seastedt and Knapp 1993, Catford et al. 2009).

Our results agree with the established relationship of soil texture broadly defining plant community type (i.e., forest vs. prairie) in the oak forest–tallgrass prairie ecotone (Dyksterhuis 1948, Bell and Hulbert 1974, Hoagland et al. 1999). The tallgrass prairie and old-field sites in this study were dominated by the fine-textured Renfrow soil containing more clay content than the oak forest, which was dominated by coarser-textured Stephenville soil. Soil in the old field had greater and more variable clay content than

in the prairie, likely due to soil movement associated with cultivation. The coarser-textured Stephenville soil permits rapid water infiltration, which allows deep-rooted oak trees to establish, leading to light-limited systems. Shade-intolerant *J. virginiana* survived and grew better with higher PAR in all plant communities (Figs. 1–3). In contrast, the finer-textured Renfrow soil limits water infiltration and renders water less available to plant extraction leading to water-limited, grass-dominated ecosystems. The direct negative relationship between soil clay content and *J. virginiana* seedling survival and seedling growth was most consistent on the tallgrass prairie and old field, indicating that soil texture is an important factor on these sites. We acknowledge that other factors, such as aspect and topographic position, covary with soil texture and also can potentially influence the soil water content and consequently the survival and growth of *J. virginiana* (Schmidt and Stubbendieck 1993).

Encroachment of *J. virginiana* into open, fine-textured soils of prairie sites is seen elsewhere in North America. For example, xeric limestone prairies in the Ozarks region and the southeastern and Midwestern United States occur on shallow soils developed on limestone, dolomitic, or calcareous shale parent materials (Baskin and Baskin 2000, Rhoades et al. 2005, Lawless et al. 2006*a, b*, Baskin et al. 2007). These sites often have south or southwest aspects (McClain and Ebinger 2002, Baskin et al. 2007, Pierce and Reich 2010) and fine-textured soils (Rhoades et al. 2005, Lawless et al. 2006*b*), which reduce plant-available soil moisture. Although xeric limestone prairies occur in relatively moist regions, the plant communities on these locally dry sites are remarkably similar to tallgrass prairie communities in the Southern Great Plains. Xeric limestone prairies in humid climates are dominated by C_4 perennial grasses, especially *S. scoparium* (Baskin and Baskin 2000, Lawless et al. 2006*a, b*, Baskin et al. 2007), one of the dominant species on the tallgrass prairie and old-field sites in the present study.

Juniperus virginiana is drought tolerant and therefore well adapted to water-limited prairie in this region (Caterina et al. 2014). In fact, *J. virginiana* is more drought tolerant than the tallgrass prairie-dominant *A. gerardii* (Axmann and Knapp 1993), five species of oaks (*Quercus* spp.) and *Acer saccharum* Marsh. (Bahari et al. 1985), and *Pinus ponderosa* Lawson & C. Lawson (Bihmidine et al. 2010). Mechanisms enabling tolerance to low soil water content of *J. virginiana* include its resistance to xylem embolism and its ability to conduct water at high xylem tensions that occur during times of severe drought (Sperry and Tyree 1990).

As an evergreen conifer, *J. virginiana* photosynthesizes year around (Eggemeyer et al. 2006) and takes advantage of increased light availability when deciduous oaks are leafless and when their leaves are emerging in spring (Lassoie et al. 1983). In addition, the light saturation point for understory *J. virginiana* is half that reported for open-growing *J. virginiana*, suggesting that the plants adjust to understory conditions (Lassoie et al. 1983).

Secondary succession processes differ in nutrient-rich soils compared to nutrient-poor soils (Gleeson and Tilman 1990), and nitrogen is the most limiting nutrient in tallgrass prairie and old fields (Wedin 1995, Blair et al. 1998, Knops and Tilman 2000). Thus, degraded soil quality in old fields might result in nitrogen playing a relatively more important role in the ecotone. However, in our study, clay was consistently a more important factor than was PAN in the old field. Our single measurement of PAN did not fully capture dynamics in PAN that can possibly influence the growth and survival of *J. virginiana*, but PAN in our communities spanned a considerable range. Others also have found soil nitrogen to be relatively unimportant compared to light availability in expansion of native woody plants in intact tallgrass prairie (Heisler et al. 2004, Briggs et al. 2005).

Our study was not replicated in space, and it is not necessarily representative of the broad expanse of landscapes potentially open to expansion by *J. virginiana*. However, the results of this study suggest that the potential for using soil distribution maps and associated ecological site designations for directing *J. virginiana* management should be explored. For example, managers and policy makers could identify tallgrass prairie on medium-textured soils, in which *J. virginiana* seedling survival is high and growth can be especially rapid, to focus prescribed burning efforts to prevent further invasion or remove trees from these sites after they have established (Bidwell et al. 2013). Early management intervention is critical with rapidly growing *J. virginiana*

seedlings because seedlings grow rapidly to a height and density that fire, if re-introduced, either no longer carries through the stand or fire intensity is insufficient to kill the trees (Smith and Stubbendieck 1990, Twidwell et al. 2013).

Juniperus virginiana expansion risk in oak forests could increase if the canopy opens through natural or anthropogenic disturbance alleviating light limitation. For example, striking die-off of oaks occurred in the central United States after the droughts of the early 2000s (Bendixsen et al. 2015, Gu et al. 2015), potentially opening these forests to expansion of *J. virginiana*. Therefore, oak forests that develop canopy gaps might be monitored for seedlings so that management practices can be applied early to prevent the establishment of *J. virginiana* trees. Because different factors limit the establishment of *J. virginiana* among plant communities, effective management of *J. virginiana* will likely depend upon a multipronged approach to identify the hotspots of expansion through identifying highly susceptible ecological sites, early *J. virginiana* removal, eliminating organized planting programs (Ganguli et al. 2008*a*), and focusing control programs on trees that provide seed sources to dispersers (Holthuijzen and Sharik 1985, Horncastle et al. 2004).

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Literature Cited

Alford, A. L., E. C. Hellgren, R. Limb, and D. M. Engle. 2012. Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. Ecological Applications 22:947–958.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist 134:545–561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13–68 *in* M. Vavra, W. Laycock, and R. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.

Axmann, B. D., and A. K. Knapp. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie watershed. Southwestern Naturalist 38:325–330.

Bahari, Z. A., S. G. Pallardy, and W. C. Parker. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. Forest Science 31:557–569.

Baskin, J. M., and C. C. Baskin. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. Annals of the Missouri Botanical Garden 87:286–294.

Baskin, J. M., C. C. Baskin, and P. J. Lawless. 2007. Calcareous rock outcrop vegetation of eastern North America (exclusive of the Nashville Basin), with particular reference to use of the term "cedar glades". Botanical Review 73:303–325.

Bell, E. L., and L. C. Hulbert. 1974. Effect of soil on occurrence of cross timbers and prairie in southern Kansas. Transactions of the Kansas Academy of Science 77:203–209.

Bendixsen, D. P., S. W. Hallgren, and A. E. Frazier. 2015. Stress factors associated with forest decline in xeric oak forests of south-central United States. Forest Ecology and Management 347:40–48.

Bidwell, T. G., J. R. Weir, and D. M. Engle. 2013. Eastern redcedar control and management–best management practices to restore Oklahoma's ecosystems. NREM-2876. Oklahoma Cooperative Extension Service, Oklahoma State University, Stillwater, Oklahoma, USA.

Bihmidine, S., N. M. Bryan, K. R. Payne, M. R. Parde, J. A. Okalebo, S. Cooperstein, and T. Awada. 2010.

Photosynthetic performance of invasive *Pinus ponderosa* and *Juniperus virginiana* seedlings under gradual soil water depletion. Plant Biology 12:668–675.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. Journal of Vegetation Science 7:121–124.

Blair, J. M., T. R. Seastedt, C. W. Rice, and R. A. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pages 222–243 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. C. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Bond, W. J. 2008. What limits trees in C-4 grasslands and savannas? Annual Review of Ecology Evolution and Systematics 39:641–659.

Borchert, J. R. 1950. The climate of the central North American grassland. Annals of the Association of American Geographers 40:1–39.

Brandeis, T. J., M. Newton, and E. C. Cole. 2002. Biotic injuries on conifer seedlings planted in forest understory environments. New Forests 24:1–14.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Burke, I. C., et al. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42:121–143.

Caterina, G. L., R. E. Will, D. J. Turton, D. S. Wilson, and C. B. Zou. 2014. Water use of *Juniperus virginiana* trees encroached into mesic prairies in Oklahoma, USA. Ecohydrology 7:1124–1134.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15:22–40.

Chapin III, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233–260.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian responses to landscape change in fragmented southern Great Plains grasslands. Ecological Applications 11:47–59.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421–428.

Davis, M. A., K. J. Wrage, and P. B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86:652–661.

Davis, M. A., K. J. Wrage, P. B. Reich, M. G. Tjoelker, T. Schaeffer, and C. Muermann. 1999. Survival, growth, photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecology 145:341–350.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

DeSantis, R. D., S. W. Hallgren, T. B. Lynch, J. A. Burton, and M. W. Palmer. 2010. Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA. Journal of Vegetation Science 21:606–618.

Dewey, D. R., and K. H. Lu. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agronomy Journal 51:515–518.

Dyksterhuis, E. J. 1948. The vegetation of the western cross timbers. Ecological Monographs 18:325–376.

Eggemeyer, K. D., T. Awada, D. A. Wedin, F. E. Harvey, and X. Zhou. 2006. Ecophysiology of two native invasive woody species and two dominant warm-season grasses in the semiarid grasslands of the Nebraska Sandhills. International Journal of Plant Sciences 167:991–999.

Elton, C. S. 1958. The ecology of invasions by animals and plants. The University of Chicago, London, UK.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management 40:237–239.

Engle, D. M., B. R. Coppedge, and S. D. Fuhlendorf. 2008. From the Dust Bowl to the green glacier: human activity and environmental change in Great Plains grasslands. Pages 253–271 *in* O. Van Auken, editor. Western North American Juniperus communities. Springer, New York, New York, USA.

Ewing, A. L., J. F. Stritzke, and J. D. Kulbeth. 1984. Vegetation of the cross timbers experimental range, Payne County, Oklahoma. Research Report P-856. Oklahoma Agricultural Experiment Station, Stillwater, Oklahoma, USA.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie, and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology 17:617–628.

Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081.

Ganguli, A. C., D. M. Engle, P. M. Mayer, and S. D. Fuhlendorf. 2008*a*. When are native species inappropriate for conservation plantings? Rangelands 30:27–32.

Ganguli, A. C., D. M. Engle, P. M. Mayer, and E. C. Hellgren. 2008*b*. Plant community diversity and composition provide little resistance to *Juniperus* encroachment. Botany-Botanique 86:1416–1426.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 383–411 *in* A. Klute, editor. Methods of soil analysis. Part 1: physical and mineralogical methods. American Society of Agronomy, Madison, Wisconsin, USA.

Gehring, J. L., and T. B. Bragg. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist 128:209–217.

Gleeson, S. K., and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. Ecology 71:1144–1155.

Godfray, H. C. J., and J. H. Lawton. 2001. Scale and species numbers. Trends in Ecology & Evolution 16:400–404.

Green, P. T., P. S. Lake, and D. J. O'Dowd. 2004. Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. Biological Invasions 6:1–9.

Gu, L., S. G. Pallardy, K. P. Hosman, and Y. Sun. 2015. Drought-influenced mortality of tree species with different predawn leaf water dynamics in a decade-long study of a central US forest. Biogeosciences 12:2831–2845.

Gurevitch, J. 1986. Restriction of a C_3 grass to dry ridges in a semiarid grassland. Canadian Journal of Botany 64:1006–1011.

Harlan, J. R. 1957. Grasslands of Oklahoma. Oklahoma State University, Stillwater, Oklahoma, USA.

Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology 85:2245–2257.

Henley, J., R. D. Gelnar, and R. E. Mayhugh. 1987. Soil survey of Payne County, Oklahoma. USDA, Soil Conservation Service, Washington, D.C., USA.

Hoagland, B. W., I. H. Butler, and F. L. Johnson. 1999. The cross timbers. Pages 231–245 *in* R. C. Anderson, J. Fralish, and J. Baskin, editors. The savanna, barren, and rock outcrop communities of North America. Cambridge University Press, New York, New York, USA.

Hoch, G. A., J. M. Briggs, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Holthuijzen, A. M. A., and T. L. Sharik. 1985. The avian seed dispersal system of eastern red cedar (*Juniperus virginiana* L.). Canadian Journal of Botany 63:1508–1515.

Holthuijzen, A. M. A., T. L. Sharik, and J. D. Fraser. 1987. Dispersal of eastern red cedar (*Juniperus virginiana)* into pastures – an overview. Canadian Journal of Botany 65:1092–1095.

Hooper, D. U., and J. S. Dukes. 2010. Functional composition controls invasion success in a California serpentine grassland. Journal of Ecology 98:764–777.

Horncastle, V. J., E. C. Hellgren, P. M. Mayer, D. M. Engle, and D. M. Leslie Jr. 2004. Differential consumption of eastern red cedar (*Juniperus virginiana*) by avian and mammalian guilds: implications for tree invasion. American Midland Naturalist 152:255–267.

Horncastle, V. J., E. C. Hellgren, P. M. Mayer, A. C. Ganguli, D. M. Engle, and D. M. Leslie Jr. 2005. Implications of invasion by *Juniperus virginiana* on small mammals in the southern Great Plains. Journal of Mammalogy 86:1144–1155.

Isaaks, E. H., and R. M. Srivastava. 1989. An introduction to applied geostatistics. Oxford University Press, New York, New York, USA.

Kaelke, C. M., E. L. Kruger, and P. B. Reich. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light availability gradient. Canadian Journal of Forest Research 31:1602–1616.

Knops, J. M. H., and D. Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81:88–98.

Lassoie, J. P., P. M. Dougherty, P. B. Reich, T. M. Hinckley, C. M. Metcalf, and S. J. Dina. 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. Ecology 64:1355–1366.

Lauenroth, W. K., and D. P. Coffin. 1992. Belowground process and the recovery of semiarid grasslands from disturbance. Pages 131–150 *in* M. K. Wali, editor. Ecosystem rehabilitation. Volume 2. Ecosystem analysis and synthesis. SPB Academic Publishing, The Hague, The Netherlands.

Lauenroth, W. K., J. L. Dodd, and P. L. Simms. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36:211–222.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006*a*. Scale-dependent classification of xeric limestone prairies: Annual or perennial grasslands? Annals of the Missouri Botanical Garden 93:455–464.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006*b*. Xeric limestone prairies of eastern United States: review and synthesis. Botanical Review 72: 235–272.

Lin, J., P. A. Harcombe, M. R. Fulton, and R. W. Hall. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. Oecologia 132:428–435.

Mallon, C. A., F. Poly, X. Le Roux, I. Marring, J. D. van Elsas, and J. F. Salles. 2015. Resource pulses can alleviate the biodiversity-invasion relationship in soil microbial communities. Ecology 96:915–926.

McClain, W. E., and J. E. Ebinger. 2002. A comparison of the vegetation of three limestone glades in

Calhoun County, Illinois. Southeastern Naturalist 1:179–188.

McKinley, D. C., and J. M. Blair. 2008. Woody plant encroachment by *Juniperus virginiana* in a mesic native grassland promotes rapid carbon and nitrogen accrual. Ecosystems 11:454–468.

National Oceanic and Atmospheric Administration. 1999. Climatological data annual summary, Oklahoma. Volume 107, Number 13.

Nicotra, A. B., R. L. Chazdon, and S. V. B. Iriatre. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology 80:1908–1926.

Norris, M. D., J. M. Blair, L. C. Johnson, and R. B. McKane. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Canadian Journal of Forest Research 31:1940–1946.

Norris, M. D., J. M. Blair, and L. C. Johnson. 2007. Altered ecosystem nitrogen dynamics as a consequence of land cover change in tallgrass prairie. American Midland Naturalist 158:432–445.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–41.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

Pierce, A. M., and P. B. Reich. 2010. The effects of eastern red cedar (*Juniperus virginiana*) invasion and removal on a dry bluff prairie ecosystem. Biological Invasions 12:241–252.

Powers, N. M., and K. J. Larsen. 2014. Butterflies (Lepidoptera) on hill prairies of Allamakee County, Iowa: a comparison of the late 1980s with 2013. Great Lakes Entomologist 47:114–128.

Purves, D. W., and R. Law. 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. Journal of Ecology 90:121–129.

Rhoades, C. C., S. P. Miller, and D. L. Skinner. 2005. Forest vegetation and soil patterns across glade-forest ecotones in the Knobs Region of Northeastern Kentucky, USA. American Midland Naturalist 154:1–10.

Richardson, D. M., and P. Pyšek. 2008. Fifty years of invasion ecology: the legacy of Charles Elton. Diversity and Distributions 14:161–168.

Robertson, G. P., D. Wedin, P. M. Groffman, J. M. Blair, E. A. Holland, K. J. Nadelhoffer, and D. Harris. 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. Pages 258–271 *in* G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. Standard soil methods for long-term ecological research. Oxford University Press, New York, New York, USA.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–374.

Schmidt, T. L., and E. C. Leatherberry. 1995. Expansion of eastern redcedar in the lower Midwest. Northern Journal of Applied Forestry 12:180–183.

Schmidt, T. L., and J. Stubbendieck. 1993. Factors influencing eastern redcedar seedling survival on rangeland. Journal of Range Management 46:448–451.

Scott, B. L., T. E. Ochsner, B. G. Illston, C. A. Fiebrich, J. B. Basara, and A. J. Sutherland. 2013. New soil property database improves Oklahoma Mesonet soil moisture estimates. Journal of Atmospheric and Oceanic Technology 30:2585–2595.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. American Naturalist 141:621–633.

Seastedt, T. R., and P. P. Pyšek. 2011. Mechanisms of plant invasions of North American and European grasslands. Annual Review of Ecology, Evolution, and Systematics 42:133–153.

Smith, S. D., and J. Stubbendieck. 1990. Production of tallgrass prairie herbs below eastern redcedar. Prairie Naturalist 22:13–18.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statics in biological research. Third edition. W. H. Freeman and Company, New York, New York, USA.

Sperry, J. S., and M. T. Tyree. 1990. Water-stress-induced xylem embolism in three species of conifers. Plant Cell and Environment 13:427–436.

Starks, P. J., B. C. Venuto, W. A. Dugas, and J. Kiniry. 2014. Measurements of canopy interception and transpiration of eastern redcedar grown in open environments. Environment and Natural Resources Research 4:103–122.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125:827–852.

Tognetti, P. M., and E. J. Chanetou. 2015. Community disassembly and invasion of remnant native grasslands under fluctuating resource supply. Journal of Applied Ecology 52:119–128.

Tolk, J. A. 2003. Plant available soil water. Pages 669–672 *in* B. A. Stewart and T. A. Howell, editors. Encyclopedia of water science. CRC Press, New York, New York, USA.

Twidwell, D., W. E. Rogers, S. D. Fuhlendorf, C. L. Wonkka, D. M. Engle, J. R. Weir, U. P. Kreuter, and C. A. Taylor Jr. 2013. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. Frontiers in Ecology and the Environment 11:e64–e71.

USDA, NRCS. 2016. The PLANTS database. National Plant Data Team, Greensboro, North Carolina, USA. http://plants.usda.gov

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

Volder, A., D. D. Briske, and M. G. Tjoelker. 2013. Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Global Change Biology 19:843–857.

Wedin, D. A. 1995. Species, nitrogen, and grassland dynamics: the constraints of stuff. Pages 253–262 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman & Hall, New York, New York, USA.

Zou, C. B., D. J. Turton, R. E. Will, D. M. Engle, and S. D. Fuhlendorf. 2013. Alteration of hydrological processes and streamflow with juniper (*Juniperus virginiana*) encroachment in a mesic grassland catchment. Hydrological Processes 28:6173–6182.