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Spatial Patterns in a *Prosopis – Juniperus* Savannah

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ABSTRACT

We determined the distribution patterns and distance to nearest neighbor for *Prosopis glandulosa* and *Juniperus pinchotii* trees and saplings in west Texas to examine the intra- and interspecific spacing patterns of juvenile and mature trees to relate these patterns to their establishment dynamics on deep and shallow soils. Ordination was used to compare microsite vegetation associated with open grassland habitat and habitat proximal to big and small *Prosopis* and *Juniperus* plants. Analysis of similarities provided a multivariate index and probability of differences of vegetation between and among groups. Big *Juniperus* trees were randomly distributed on both soils, while the big *Prosopis* trees were random on the deep soil but aggregated on the shallow soil. Saplings of both species were strongly aggregated on both soils. Big and small *Juniperus* plants were positively associated with the dominant, established *Prosopis* trees and with litter cover but were negatively associated with bare soil and C_4 grasses. In contrast, small *Prosopis* plants were negatively associated with both *Juniperus* and *Prosopis* trees on either soil and were positively associated with bare soil and C_4 grasses. *Prosopis* trees facilitate establishment of *Juniperus* on deep or shallow soils, but *Prosopis* presence is probably not necessary for *Juniperus* establishment on either soil. The presence of big and small *Juniperus* plants close to and under the canopies of *Prosopis* trees and the inability of *Prosopis* seedlings to establish near *Prosopis* or *Juniperus* plants indicates that *Juniperus* trees would eventually dominate on the deep as well as the shallow soils.

KEYWORDS: Competition; Facilitation; Grassland invasion; Woody plant encroachment

INTRODUCTION

Excessive cover of *Juniperus pinchotii* in southwestern North America diminishes watershed function, biodiversity and wildlife habitat values of rangelands. Dense stands reduce herbaceous productivity and limit the movement, handling, and production of livestock with negative impacts on the livelihoods of people living in these areas (Scifres 1980; McPherson and Wright 1990; Dye et al. 1995; Fuhlendorf et al. 1996; Johnson et al. 1999). Historically,

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Juniperus occurred in the Rolling Plains of Texas on shallow, poorly-developed soils associated with hillslopes while the interspersed older, flatter, deeper, well-developed soils of level topography were dominated by *Prosopis glandulosa*. Over the past century, brush has increased in these ecosystems across both flat and slope landscape positions with the dominant brush species being *Juniperus* on the slopes and *Prosopis* on the flats. Since the establishment of the cattle industry in the late 1800s, *Juniperus* has increased markedly on the clay flats and bottomlands previously occupied almost exclusively by *Prosopis* (Ellis and Schuster 1968). Based on observations, we hypothesize that the presence of *Prosopis* is facilitating this movement of *Juniperus* into a different environmental state.

The first step in the encroachment of grassland by woody species is the establishment of the woody plant seedlings. Competition from neighbors has a greater effect on growth of establishing seedlings than on adult plants (Grubb 1977; Fowler 1986; McPherson and Wright 1989a). Spatial relations in semi-arid and arid savannas have been studied to enhance understanding of pattern and process of woody plant establishment and competitive interactions (Prentice and Werger 1985; Smith and Goodman 1987). The objective of this study is to examine the intra- and interspecific spacing patterns of juvenile and mature *Juniperus* and *Prosopis* trees to relate these patterns to their establishment dynamics.

There is conflicting evidence in the literature regarding the positive and negative effects of neighboring plants on *Juniperus* establishment and subsequent growth. A tree-ring analysis of *Juniperus pinchoti*i trees indicated two consecutive years of above-average precipitation was associated with their establishment in the western Rolling Plains of Texas (McPherson and Wright 1989b). The rate of *Juniperus* encroachment was facilitated by the presence of *Prosopis* on a semiarid High Plains site but not on a more mesic Rolling Plains site (McPherson et al. 1988). However, Teague et al. (2001) report that establishing *Juniperus* seedling growth was enhanced under intact canopies compared to removed canopies of *Prosopis* in a relatively mesic Rolling Plains site. Elsewhere in Texas facilitation of *Juniperus* growth has been reported with other woody species (Jackson and Van Auken 1997). Since junipers grow mainly in fall, winter, and spring when *Prosopis* trees are dormant and leafless, the lack of competition may largely be due to these two species using resources at different times of the year. Greater nutrient availability beneath *Prosopis* canopies, reduction of summer temperatures, and temporal separation of resource use benefit *Juniperus* seedlings growing in the presence of *Prosopis* (Teague et al. 2001).

Few studies directly compare competition between herbs and J*uniperus* seedlings, but the weight of evidence indicates that establishing *Juniperus* seedlings are suppressed by neighboring grasses (Smith et al. 1975; McPherson and Wright, 1987; Teague et al. 2001) as are *Prosopis* seedlings (Van Aukin and Bush 1997). Most studies associate mature trees with herbaceous plants or other shrubs or succulents. Shrubs and succulents were often positively associated with *Juniperus* (Gehring and Bragg 1992; Dye et al. 1995) and with *Prosopis* (Archer et al. 1988). Warm-season herbs are generally negatively associated with both *Juniperus* trees (Ansley et al. 2004; Teague et al. 2008; Gehring and Bragg 1992; Dye et al. 1995) and *Prosopis* trees (Teague et al. 2008, 2016; Heitschmidt and Dowhower 1991). Cool-season herbs, when the dominant herbaceous plant form, were negatively associated with increasing *Juniperus* (Miller et al. 2000; Bates et al. 2000) and with increasing *Prosopis* (Heitschmidt and Dowhower 1991). Often the cool-season herbs association is neutral and sometimes positive with increasing *Juniperus* (Teague et al. 2016; Gehring and Bragg 1992; Dye et al. 1995) and with *Prosopis* (Ansley et al. 2004; Teague et al. 2008, 2016).

There are two extreme patterns of spatial distribution of perennial plants in semiarid environments. Firstly, regular patterns that are thought to arise through competition for resources by single individuals. This regular spacing of even-sized individuals of the same species has been assumed to result from density-dependent mortality caused by intraspecific competition for an evenly distributed resource (Phillips and McMahon 1981). Competitive interference of neighbors produces patterns that change from aggregated or random in pioneer stands to more regular in older stands. The second, aggregation, stresses the role of microsite mosaics and the presence of established plants in creating aggregated patterns that have been explained in terms of establishment ecology, e.g., establishment close to seed sources, vegetative regeneration or the occurrence of protective sites (Skarpe 1991). However, aggregated patterns may also be due to disturbances (Sprugel 1976), and random spacing can be as a result of processes directly producing such a pattern or from a combination of causal factors (Prentice and Werger 1985).

The objectives of this study are to examine spatial patterns of mature and juvenile *Juniperus* and *Prosopis* trees and their interrelationships to determine establishment patterns on two communities with different soils as well as associated vegetation, litter, and bare soil cover of those trees and tree-free sites. We infer from this likely phytosociological relationships in these plant communities and how soil site influences interactions between these species.

MATERIALS AND METHODS

Site description. This study was conducted on the Y Experimental Ranch (YER), located 25 km southwest of Crowell (33° 52' N, 100° 00' W) in North Central Texas. The climate is continental with an average of 220 frost-free growing days. Mean annual precipitation at Crowell is 617 mm, varying from 260 to 990 mm, with peaks in May and September. Annual mean monthly temperature is 17 °C, ranging from 36 °C in July to -2 °C in January. Elevation is 500 m at the research site and slope is 1% to 3%.

The study sites were located within a large 1623 ha pasture 5-8 km north of the North Wichita River. This pasture consisted of trees of mixed age (seedling to 80+ years) and had history of very little brush control (ca. 5% of the area) as well as similar wildfire occurrence and grazing. The vegetation is comprised of two distinctive communities dominated by either *Juniperus* or *Prosopis*. The *Juniperus* community occurred on shallow clay-loam soils (Vernon-Weymouth clay-loam complex; fine, mixed, active, thermic, Typic Haplustepts and fine-loamy, mixed, thermic Typic Ustochrepts) that have exposed rock or gypsum areas with sparse herbaceous vegetation as well as deeper soils with considerably more herbaceous vegetation. The *Prosopis* community occurred on deeper, clay-loam soils (Tillman clay-loam; fine, mixed, superactive, thermic, Typic Paleustolls) with a greater spatial continuity of herbaceous vegetation. The bulk of this pasture consisted of slopes with shallow soils on which *Juniperus* was prolific while *Prosopis* proliferated on flats with deeper, more developed soils that made up only about 5% of the pasture. Both communities had similar herbaceous standing crop with a patchy distribution of species (Dowhower et al. 2001; Parajulee et al. 1997).

The herbaceous vegetation of both communities was dominated by C_4 grasses *Hilaria mutica*, *Buchloe dactyloides*, and *Bouteloua curtipendula*. *Prosopis* communities had a greater C_3 herbaceous composition with *Nassella leucotricha*, *Bromus japonicus*, *Hordeum pusillum*, and *Bromus uniloides*, while *Juniperus* communities had relatively greater amounts of *Tridens muticus*, *Sporobolus compositus*, and *Schizachyrium scoparium*. Forbs on both soils were dominated by *Ambrosia psilostachya* and *Gutierrezia texana* (nomenclature according to Diggs et al. 1999).

Sampling. Three sites were sampled on both deep and shallow soils of ca. 20 ha. Adjacent to the deep soil sites, shallow soil sites were selected in moderately productive portions of the shallow soil complex. Within each site, 15 points spaced 50 m apart were established along random compass directions. Sampling of border areas was avoided.

Plant distribution and density were determined using the t-square distance method (Besag and Gleaves 1973; Krebs 1989). This technique is reported to be robust for determining density for regular, random, and aggregated distributions (Krebs 1989). From the random points, distances from point to nearest tree and that tree to its nearest neighbor tree were measured using the t-square 180° exclusion angle for the second tree. Mean distances are expected to be 2 × for the distance of the random point to nearest tree and √2 × for t-square distance between trees. Multiplying these two distances yields area-per-tree and its reciprocal times-area yields trees-per-unit area.

Trees were divided into two size classes: big (trees) (>1.5 m in height and width) and small (trees and saplings) (<1.5 m in height and width, but many were likely 10+ y of age). Distance techniques were applied separately to big *Prosopis*, big *Juniperus*, small *Prosopis*, and small *Juniperus*. Also, tree to nearest competing tree species distance was measured, as was small tree to nearest same species big tree distance. Target trees were searched for to a distance of 30 m. Distance was assumed to be 40 m if not found because a value of zero would equate to very high density and a missing value would equate to an average density instead of a low density. Tree to nearest neighbor distance was treated as missing if the point to "tree" was not found. Size of all *Prosopis* and *Juniperus* trees included in distance sampling was determined by measures of maximum width, minimum width (perpendicular), and height. Canopy cover was estimated as the area of an ellipse and canopy volume as canopy cover x 0.8 x canopy height. Percent cover of trees was determined by multiplying density by cover determined from mean canopy diameters.

At each of the six sites, 30 different big *Prosopis*, 30 different small *Prosopis*, 15 different or same big *Prosopis*, plus 30 different or same mixed-size *Prosopis* totaling potentially 105 *Prosopis* were sampled. However, some of these trees are represented by more than one neighboring class or are not found within the 30-m search area. The same situation applies to *Juniperus*. Size frequency classes were established for canopy diameter classes of 0-0.5 m, 0.5-1 m, and 1 m increments up to 10 m based on trees encountered in distance sampling. These values were adjusted proportionately based on densities of small to large trees determined from t-square sampling.

The habitat around each big and small target *Prosopis* and *Juniperus* tree and nearest open area was visually estimated as described by Daubenmire (1968). The area estimated included that in a circle encompassing the outer canopies of the trees. Open areas were defined as the area at least 1.5 m beyond tree canopies having a radius of 2 to 4 m. Percent cover of herbs, bare soil, litter, and other shrubs was estimated within each assessment circle to describe the habitat within. Vegetation associated with target big and small *Prosopis* and *Juniperus* and open areas was sampled at each of these random points.

The area of each habitat assessment circle was the sum of the two tree radii plus distance between the two tree stems. The competing species tree cover was the area of that tree divided by similarly derived total area. Cover calculated in this manner can exceed 100% when, on average, trees are completely within the neighboring tree's canopy. Microsite tree cover estimated in this manner was meant to be linear relative to competitive effects of neighboring trees and is referred to as relative cover.

Statistical analysis. The Hines test (Hines and Hines 1979; Krebs 1989) was used to determine regular, random, or aggregated distribution of plants and physical parameters. Standard error was calculated according to Diggle (1983). Analysis of variance of cover data was by soil, because preliminary analysis indicated significant differences ($P < 0.05$) between soils occurred for all functional groups and for several soil × habitat interactions. Tukey's means separation test was used to separate habitat types at $P < 0.05$.

Ordination was used to compare microsite vegetation associated with big and small *Prosopis* and *Juniperus* and open areas of the three deep and three shallow soil sites (Primer package, Clarke and Warwick 2001). Ordination using Multidimensional Scaling of the Bray-Curtis similarity index of square root transformed plant cover data was employed. Analysis of similarities (ANOSIM, Clarke and Green 1988) was used to provide an index, Global dissimilarity R, and probability of plant group similarities. The best combination of environmental factors (tree cover by species for the site or tree species relative cover, bare soil, and litter cover) and the amount of variation they accounted for in multidimensional ordination space was determined using the Spearman coefficient within the BIO-ENV procedure (Clarke and Ainsworth 1993).

RESULTS

Cover, density, and size distribution. On the deep soil site, *Prosopis* trees occurred more frequently and were larger than on the shallow soils (Table 1). The *Juniperus* plants on the deep soil were predominantly in the diameter classes of 0.5–3 m. Small trees contributed only about 1% canopy cover on both sites. Big, dominant trees averaged about the same size on either soil as indicated by tree densities being proportional to canopy cover.

Table 1. Density and cover (mean ± SE) for individual sites of big and small *Prosopis* and *Juniperus* on deep and shallow soils on the Y Experimental Ranch, Texas.

	Soil site	
Tree species and Size	Deep	Shallow
	Plants ha^{-1}	
Big *Prosopis*	260 ± 79 $_{a}$	70 ± 56 $_{b}$
Small *Prosopis*	40 ± 35 $_{d}$	43 ± 31 $_{c}$
Big *Juniperus*	93 ± 28 $_{c}$	267 ± 96 $_{a}$
Small *Juniperus*	107 ± 53 $_{b}$	239 ±118 $_{a}$
	Cover %	
Big *Prosopis*	38.2 ± 11.9 $_{a}$	4.4± 2.9 $_{b}$
Small *Prosopis*	0.2 ± 0.1 $_{c}$	0.2 ± 0.1 $_{c}$
Big *Juniperus*	4.4 ± 1.2 $_{b}$	39.3 ± 14.5 $_{a}$
Small *Juniperus*	0.8 ± 0.4 $_{c}$	0.4 ± 0.2 $_{c}$

Means for each soil and column with different letters differ at $P < 0.05$

The size (canopy diameter) class distributions indicate a predominance of *Juniperus* trees on the shallow soils with greater densities of *Juniperus* trees in the 0.1-0.5 m seedling and 2-5 m tree diameter ranges (Table 2). On these shallow soils, *Prosopis* plants had lower densities and consisted mostly of plants in the 1-3 m diameter classes. Canopy cover on the shallow soil sites varied from 26-60% for *Juniperus* and 2-8% for *Prosopis*.

Table 2. Hines test statistic (h_T) for big and small *Prosopis* and *Juniperus* plants on deep and shallow clay-loam soils on the Y Experimental Ranch, Texas. Values of h_T < ($P_{0.05} = 1.163$) indicate a regular pattern, values of h_T > ($P_{0.05} = 1.390$) indicate aggregation, and values between indicate random distribution (Krebs 1989).

Soil site	Plant size class	n	h_T
Deep clay-loam	Big *Prosopis*	45	1.21
	Small *Prosopis*	45	1.52*
	Big *Juniperus*	45	1.32
	Small *Juniperus*	45	1.53*
Shallow clay-loam	Big *Prosopis*	45	1.64*
	Small *Prosopis*	45	1.66*
	Big *Juniperus*	45	1.23
	Small *Juniperus*	45	1.69*

* Indicates aggregated distribution P< 0.05.

Spatial patterns of established trees and seedlings. The big *Juniperus* trees were randomly distributed on both soils ($P < 0.05$), while the big *Prosopis* trees were random on the deep soil but aggregated ($P < 0.005$) on the shallow soil (Table 3). Regular distribution of trees was not detected, although the Hines test statistic (h_T) value for big *Prosopis* on the deep soils (h_T = 1.21) was closer to regular (h_T $P_{0.05 =}$ 1.16) than to random (h_T $P_{0.05}$ = 1.27). On the *Juniperus* dominated shallow soil habitat big *Prosopis* trees were aggregated into a few locations. The spatial pattern of smaller *Prosopis* and *Juniperus* plants was entirely different. Small plants of both species were strongly aggregated on both soils ($P < 0.005$) (Table 3).

Table 3. Plant class interactions using the Hines test statistic (h_T) for big and small *Prosopis* and *Juniperus* plants on deep and shallow clay-loam soils on the Y Experimental Ranch, Texas. Values of h_T< ($P_{0.05,\ n = 15}$ 1.163) indicate a regular pattern, values of h_T > ($P_{0.05,\ n = 15}$ = 1.390) indicate aggregation, and values between indicate random distribution (Krebs 1989).

Plant class interactions	h_T	h_T
	Deep soil	Shallow soil
Big *Prosopis* - *Juniperus*	1.82**	1.95***
Small *Prosopis* - *Juniperus*	1.35*	1.71***
Small *Prosopis* - Big *Prosopis*	1.23*	2.81**
Big *Juniperus* - *Prosopis*	1.43*	1.66**
Small *Juniperus* – *Prosopis*	1.39**	1.69**
Small *Juniperus* - Big *Juniperus*	1.54**	1.37*

* Indicates aggregated distribution P < 0.05; ** P < 0.005

With only two exceptions, the Hines values indicate aggregated interspecies distributions (Table 4). The two exceptions were both on deep soil sites: big *Prosopis* was randomly distributed relative to other big *Prosopis* trees and small *Prosopis* plants were also randomly distributed relative to big *Prosopis* trees.

Table 4. Aerial cover (%) of bare soil, litter and the vegetation groups associated with open grassland, and big and small *Prosopis* and *Juniperus* plants

	Bare soil	Litter	C_4 Short grass	C_4 Mid grass	C_4 Tall grass	C_3 Mid grass	Annual grass	Perennial forbs
Deep Soil								
Open grassland	9^{a}	26^{d}	20^{a}	36^{a}	-	4	4	0.2
Small *Prosopis*	8^{ab}	29^{d}	21^{a}	32^{ab}-	-	6	4	-
Big *Prosopis*	4^{bc}	40^{c}	16^{ab}	22^{bc}	-	14	5	-
Small *Juniperus*	4^{bc}	52^{b}	11^{b}	21^{bc}	-	10	3	-
Big *Juniperus*	2^{c}	60^{a}	9^{b}	14^{c}	-	12	3	-
Shallow Soil								
Open grassland	30^{a}	16^{d}	14^{a}	35^{a}	1.7	.0	-	1.8^{a}
Small *Prosopis*	14^{b}	34^{c}	5^{b}	45^{a}	0.1	1.0	0.9	0.2^{b}
Big *Prosopis*	9^{b}	48^{ab}	6^{b}	32^{a}	-	2.3	-	1.0^{a}
Small *Juniperus*	16^{b}	40^{bc}	7^{b}	32^{a}	2.7	.6	-	0.6^{a}
Big *Juniperus*	8^{b}	56^{a}	5^{b}	28^{b}	1.4	1.1	-	0.3^{ab}

Means for each soil and column with different letters differ at $P < 0.05$

Distances between *Prosopis* and *Juniperus* size classes. On the deep soils, small *Prosopis* had a 24% greater distance from big *Prosopis* trees than the mean distance between all *Prosopis* trees (Fig. 1), indicating a strong negative association. In contrast, both small and big *Juniperus* had a 30% and 24%, respectively, shorter distance from all *Prosopis* trees than the mean distance between all *Prosopis* trees indicating a strong positive relationship.

On the shallow soils, small *Juniperus* had an 18% greater distance from big *Juniperus* than the mean distance between all *Juniperus* plants, again indicating strong negative association between size classes (Fig. 2). In contrast, big *Prosopis* had a 28% shorter distance from all *Juniperus* plants than the mean distance between all *Juniperus* plants, indicating a strong positive association while small *Prosopis* did not differ from all *Juniperus* distance.

Figure 3 illustrates the dominants, Prosopis on deep soils and Juniperus on shallow soils, are close to the random point and to their nearest neighbor indicating high density and their greater size indicating higher cover. On the deep soils, the big *Prosopis* plants are larger than the big *Juniperus* plants but the converse is evident on the shallow soils. Big *Prosopis* on shallow soil had about half the canopy area of big *Prosopis* on deep soil. Big *Juniperus* on deep soil were about one-third the canopy area of big *Juniperus* on shallow soils. On both soils, either size *Juniperus* plants are relatively near to big *Prosopis*.

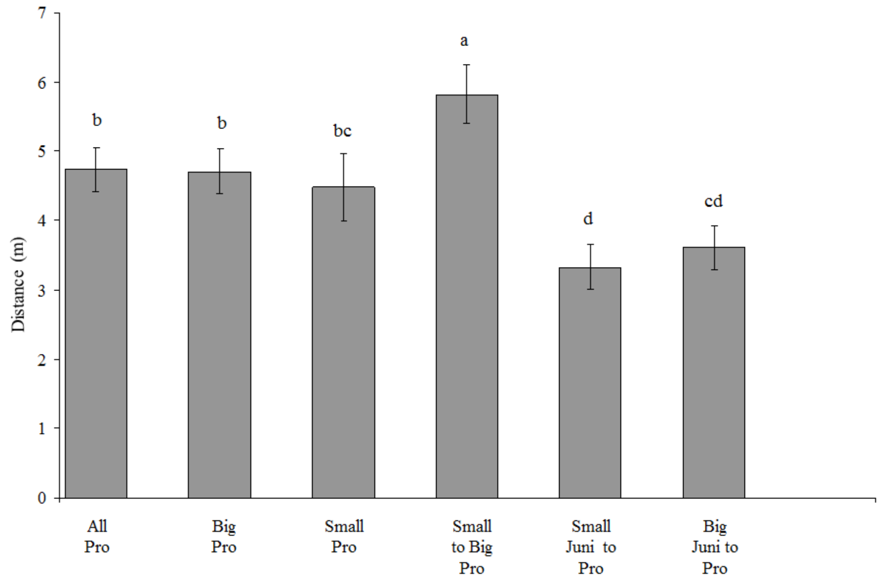


Figure 1. Distance between trees on deep soil sites on the Y Experimental Ranch, Texas. Means with a different letter differed at P ≤ 0.05. (Pro = *Prosopis,* Juni = *Juniperus*).

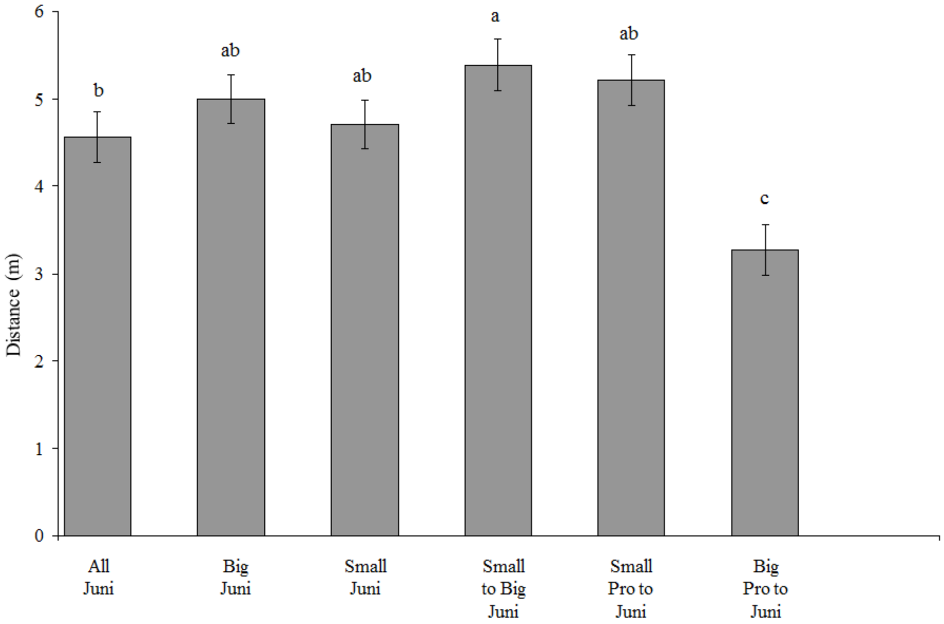


Figure 2. Distance between trees on shallow soil sites on the Y Experimental Ranch, Texas. Means with a different letter differed at P ≤ 0.05. (Pro = *Prosopis,* Juni = *Juniperus*)

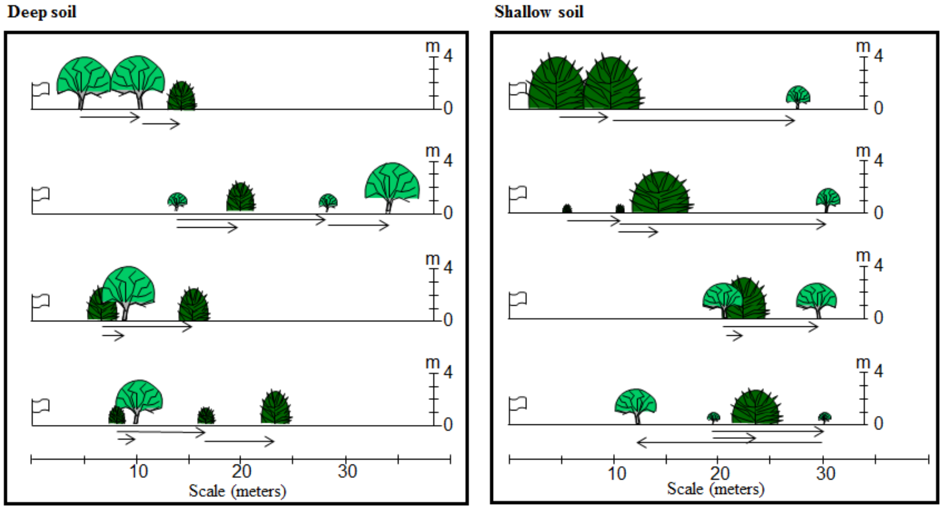


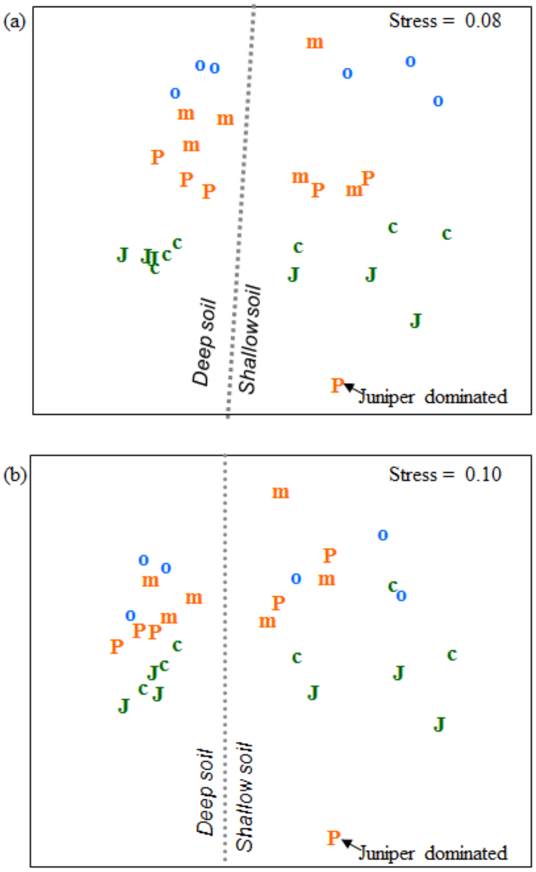
Figure 3. Scaled sizes and distances of *Prosopis* 🌳 and *Juniperus* 🌲 plants averaged for deep and shallow soils on the Y Experimental Ranch, Texas. The flags denote the random points from which sampling was conducted.

Phyto-sociological relationships of *Prosopis* and *Juniperus*. Multi-dimensional scaling of habitats associated with big and small *Prosopis* and *Juniperus and open areas* (Fig. 4a) indicated a clear division between sites on deep and shallow soils (dissimilarity R = 0.904, P = 0.001). Stress of placing these 30 sample entities (5 habitats x 2 soils x 3 reps) into 2-dimentions was reasonably low at 0.08 compared to three sample sites defining a plane with stress of 0. On deep soils, vegetation of open and small *Prosopis* habitats differed from vegetation of other target trees' habitats (ANOSIM table, Fig. 4a). Additionally, vegetation of big *Prosopis* habitats differed from big *Juniperus* habitats, while vegetation of small *Juniperus* was common to either tree species' habitat.

On the shallow soils, vegetation of open areas differed from all tree habitats and vegetation of small *Prosopis* differed from big *Juniperus* habitats. A clear division occurs between deep and shallow soils as vegetation grades from open areas to big *Juniperus* habitats. Vegetation of big *Prosopis* habitat on one shallow soil site appears to be an outlier (bottom, right, Fig. 4a) but on that site *Prosopis* was heavily dominated by juniper. Sites are more tightly clustered on the deep soils compared to the shallow soils.

Another ordination dropping the variable *Prosopis*, juniper, bare soil, and litter cover was constructed eliminating chosen factors associated with targeting trees (Fig. 4b). Dropping these variables resulted in a very similar pattern to the first ordination (Spearman's rank correlation Rho = 0.946, P = 0.001). However, differences between target tree vegetation are not as well defined. A strong difference between deep and shallow soils was evident (dissimilarity R = 0.800, P = 0.001) but fewer differences occur between target habitats within soils (ANOSIM table, Fig. 4a). On deep soils, vegetation of open areas differs from small and big *Juniperus* habitats, and vegetation of small *Prosopis* differed from big *Juniperus* habitats. On the shallow soils, vegetation of big *Juniperus* differs from open and small *Prosopis* habitats.

BIO ENV procedure for the first ordination (Fig. 4a, including tree cover, litter, and bare soil), site *Juniperus* cover, target *Juniperus* cover, site *Prosopis* cover, and bare soil cover provided the best combination of variables (correlation (r) = 0.870). For the second ordination (Fig. 3b excluding tree cover, litter, and bare soil), site *Juniperus* cover, target *Juniperus* cover, and site *Prosopis* cover provided the best combination of variables (r = 0.830); however, a single variable, site *Juniperus* cover, accounted for almost as much variation (r = 0.827). Site *Juniperus* cover also accounted for much of the variation when target trees were included in the ordination (r = 0.789). Site *Juniperus* cover is negatively correlated with site *Prosopis* cover (r = -0.883) and positively correlated to target *Juniperus* cover (r = 0.745) and bare soil (r = 0.557). Therefore, site *Juniperus* cover includes elements of these variables as well. Soil differences are indicated by site *Juniperus* cover and its opposite, site *Prosopis* cover, and bare soil. Target *Juniperus* cover indicated that big *Juniperus* trees had the greatest impact on vegetation within a soil.



Deep soil

	o	m	P	c
m	.630*			
P	1.00*	.519*		
c	1.00*	.778*	.000	
J	1.00*	1.00*	.556*	-.185

Shallow soil

	o	m	P	c
m	.667*			
P	.704*	.000		
c	.815*	-.074	.000	
J	1.00*	.556*	.259	.148

Deep soil

	o	m	P	c
m	.000			
P	.185	.074		
c	.704*	.259	.037	
J	1.00*	.936*	.333	-.148

Shallow soil

	o	m	P	c
m	.074			
P	.259	-.148		
c	.037	-.074	.000	
J	.926*	.704*	.222	.074

* Significance of Global R at p = 0.1.

Figure 4. Multidimensional scaling (MDS) ordination of (a) vegetation plus target tree cover, litter and bare soil (Dissimilarity R = 0.904, *P* = 0.001), and (b) vegetation alone (Dissimilarity R = 0.800, *P* = 0.001). Habitats are: o = open, m = small *Prosopis*, P = big *Prosopis*, c = small *Juniperus*, J = big *Juniperus*. Tables are Analysis of Similarity (ANOSIM) tables for both soils.

For vegetation groups and bare soil cover differences between soils were significant while that of litter cover was not (Table 4). Within a soil, more bare soil was associated with open area habitats while more litter cover was associated with big or small *Juniperus* and big *Prosopis* habitats. Litter cover was much less abundant at open grassland and small *Prosopis* habitats. More bare soil occurred in open habitats on shallow soils probably because shallow soils are more variable and less productive, supporting fewer plants. On deep soils, which are more productive and support more plant biomass, open areas had similar herbaceous cover to small *Prosopis* habitats (Table 4).

C_4 shortgrass and midgrass cover was much more abundant on the deep than the shallow soils and was greater in open and small *Prosopis* habitats than in big *Juniperus* habitats with amounts in big *Prosopis* and small *Juniperus* habitats being intermediate (Table 5). C_3 midgrasses were present in greater abundance on deep soils but were not differentially associated with any of the *Prosopis* and *Juniperus* plant habitats.

DISCUSSION AND CONCLUSION

In this region of the Rolling Plains of west Texas, lack of brush intervention for 80+ years has resulted in grasslands transforming into brush thickets dominated by *Prosopis* on clay-loam flats and *Juniperus* on clay-loam slopes. Juniperus (which is more visible on soil survey photos, soil survey1964) appeared to about double since 1964. The distribution of the dominant tree for deep or shallow soils, although having random distributions, had values near regular distributions that are hypothesized to be associated with high interspecific competition (Phillips and McMahan 1981). Factors that may be responsible for values of distributions falling short of regular are the limited time since a change in environmental factors (i.e., fire frequency and intensity, grazing species, duration, and intensity, or climate change in precipitation distribution and quantity) and/or lack of uniformity of the soil. Small trees and saplings of either species on either soil had aggregated distributions likely indicating a decrease in sites suitable for their establishment.

Big *Juniperus* also had a random distribution on deep soils. Considering their smaller size compared to shallow sites implies more recent encroachment onto deep soils. The short distances of big *Prosopis* to *Juniperus* on either soil indicates that *Prosopis* facilitates the establishment of *Juniperus*. Further, many of the big *Prosopis* sampled on shallow soils were observed to have large dead limbs with dramatically reduced canopy cover when dominated by *Juniperus*. Vegetative communities were very dissimilar between deep and shallow soils and communities associated with big *Juniperus* were quite dissimilar to other tree and open communities. Generally, C4 grass and bare soil cover decreased and litter cover increased in association with big *Juniperus* or *Prosopis* while C3 grass cover was variable.

In this study on the deep soils, small *Juniperus* plants were positively associated with the dominant, established *Prosopis* trees and with litter cover but were negatively associated with bare soil and C_4 grasses. It is not clear to what extent the presence of litter directly facilitated *Juniperus* seedling establishment. Litter decreases evaporation from the soil surface and ameliorates soil surface temperatures, which are likely to benefit establishing seedlings. The spatial and temporal separation of resource use between *Juniperus* and *Prosopis* plants has an effect. *Prosopis* trees have a relatively deep taproot in comparison to the shallow lateral root system of *Juniperus* plants, and junipers grow mainly in fall, winter and spring when *Prosopis* trees are dormant and leafless (Teague et al. 2001).

Juniperus seeds are known to be dispersed by birds and small and large mammals (Whittaker et al. 1979; Chavez-Ramirez and Slack 1993). There is much evidence that established *Prosopis* trees facilitate *Juniperus* establishment; by providing avian perches, *Prosopis* and other woody species facilitate dispersal under tree canopies while mammals would distribute seed throughout all habitats. The trees themselves also modify the microclimate, facilitating germination and establishment. There is reduced herbaceous competition and increased litter cover under *Prosopis* canopies (Heitschmidt and Dowhower 1991; Laxson et al. 1997). In contrast, relative growth rates of *Juniperus* seedlings are decreased in open grassland relative to under *Prosopis* canopies. Greater nutrient availability beneath *Prosopis* canopies and reduction of summer temperatures by shading also benefit *Juniperus* seedlings growing under *Prosopis* canopies. Removal of *Prosopis* canopies reduced *Juniperus* seedling growth rate, underscoring the role that *Prosopis* trees perform in facilitating *Juniperus* seedling establishment (Teague et al. 2001).

On the shallow soils, small *Juniperus* plants were generally independent of *Prosopis* presence, but both large and small *Juniperus* plants were strongly associated with big *Prosopis* plants wherever they occurred. Large portions of the shallow soils at this location are too shallow for *Prosopis* plants to establish at all. Shallow soils in this region are very variable, probably accounting for patchiness and non-random distribution of the big *Prosopis* on this soil. *Prosopis* trees are deep rooted (Heitschmidt et al. 1988) and will grow to full size only on deeper soils, which are limited to small patches on the shallow soils of this soil series. The relatively shallow-rooted *Juniperus* plants are not similarly constrained and dominate the vegetation on these shallow soils (Ellis and Schuster 1968; Correll and Johnston 1970; McPherson et al. 1991). Small *Juniperus* plants were also located relatively near big *Juniperus* on shallow soils, indicating that their establishment may also have been facilitated by big *Juniperus* on both soils. Although *Prosopis* facilitated establishment of *Juniperus* on both deep and shallow soils, it appears that *Prosopis* presence is probably not necessary for *Juniperus* establishment on either soil.

In contrast to small *Juniperus*, the presence of small *Prosopis* plants was negatively associated with both *Juniperus* and *Prosopis* trees on either soil. Small *Prosopis* plants were positively associated with bare soil and C_4 grasses. It is likely that this is primarily due to *Prosopis* seedlings establishing more successfully away from the canopies of established woody plants rather than the presence of C_4 grasses that provide a relatively hospitable environment for them to germinate and establish successfully. *Prosopis* is sensitive to shading and shows little regeneration in the shade of mature woody plant canopies (Haas et al. 1973; McPherson et al. 1988; Ruthven et al. 1993). The association between establishing *Prosopis* plants and bare soil is understandable as these sites would provide minimal competition for establishing seedlings, even though such sites would have decreased infiltration (Thurow 1991) and full exposure to the sun, which can be limiting to seedling establishment (Teague et al. 2001), whereas shallow-rooted *Juniperus* seedlings are weak competitors and are limited by grass (Smith et al. 1975; McPherson and Wright 1987; Teague et al. 2001). In contrast, competition from grass does not limit establishment of *Prosopis* because *Prosopis* seedlings quickly develop a root system below that of grasses (Brown and Archer 1991).

The largest plants in this study showed random distribution and on the deep soil sites big *Prosopis* distribution was random tending to regular. A regular distribution of a monospecific dominant is encountered in various environments (Smith and Walker 1983; Smith and Goodman 1987; Szwagrzyk and Czerwczak 1993; Grundy et al. 1994). It is widely believed that competition will convert aggregated and random populations of plants into regular ones (Fowler 1986), and it is possible that in time *Prosopis* and *Juniperus* distribution would become regular. However, before *Prosopis* trees could develop a regular distribution it is probable that *Juniperus* would eventually dominate on these deep soils and become a monospecific thicket. Two points support this: the presence of big and small *Juniperus* plants close to and under the canopies of existing *Prosopis* trees and the inability of *Prosopis* seedlings to establish near established woody plants. Although many of the established trees were relatively old at the time of this study (ca. 80-100 years), it is likely that the timespan for transition from grassland to savannah to brush thicket would be roughly the same as the age of the oldest trees. Several more generations of trees with the current regime of fire exclusion would result in *Juniperus* dominance. This would have a profound effect on the biotic community since *Juniperus* can increase to the exclusion of all other woody and herbaceous plants (Ansley et al. 1995). The use of prescribed fire with responsible grazing management has been shown to be a cost effective means of preventing *Juniperus* plants from excluding other vegetation and maintaining an open, functionally sound savannah ecosystem with high biodiversity (Wright and Bailey 1982).

REFERENCES

Ansley RJ, Pinchak WE, Teague WR, Kramp BA, Jones DL, Jacoby PW. 2004. Long-term grass yields following chemical control of honey mesquite. J Range Manage. 57:49-57.

Ansley RJ, Pinchak WE, Ueckert DN. 1995. Changes in redberry juniper distribution in Northwest Texas (1948 to 1982). Rangelands. 17:49-53.

Archer S, Scifres C, Bassham CR. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs. 58:111-127.

Bates JD, Miller RF, Svejcar TJ. 2000. Understory dynamics in cut and uncut western juniper woodlands. J. Range Manage. 53:119-126.

Besag J, Gleaves JT. 1973. On the detection of spatial pattern in plant communities. Bull Int Stat Inst. 45:153-158.

Brown JR, Archer S. 1991. Ecosystem level processes. In: Heitschmidt RK, Stuth JW (EDS). Grazing Management: An ecological perspective. pp 108-140. Timber Press, Portland, Oregon.

Chavez-Ramirez F, Slack RD. 1993. Carnivore fruit use and seed dispersal of two selected plants of the Edwards Plateau, Texas. Southwest Nat. 38:141-145.

Clarke KR, Ainsworth M. 1993. A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser. 92:205-219.

Clarke KR, Green RH. 1988. Statistical design and analysis for a 'biological effects' study. Mar Ecol Prog Ser. 46:213-226.

Clarke KR, Warwick RM. 2001. Changes in marine communities: an approach to statistical analysis and interpretation. 2nd edition. PRIMER-E: Plymouth, England

Correll DS, Johnston MC. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.

Daubenmire R. 1968. Plant Communities: A textbook of Plant Synecology. Harper and Row Publishing, New York.

Diggle PJ. 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, London.

Diggs GM, Lipscomb BL, O'Kennon RJ. 1999. Illustrated Flora of North Central Texas. Botanical Research Institute of Texas, Fort Worth, US.

Dowhower SL, Teague WR, Ansley RJ, Pinchak WE. 2001. Dry-weight-rank method assessment in heterogeneous communities. J Range Manage. 54:71-76.

Dye KL, Ueckert DN, Whisenant SG. 1995. Redberry juniper – herbaceous understory interactions. J Range Manage. 48:100-107.

Ellis D, Schuster JL. 1968. Juniper age distribution on an isolated butte in Garza County. Southwest Nat. 13:343-348.

Fowler NL. 1986. The role of competition in plant communities in arid and semiarid regions. Ann Rev Ecol Syst. 17:89-110.

Fuhlendorf SD, Smeins FE, Grant WE. 1996. Simulation of a fire-sensitive ecological threshold: A case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol Mod. 90:245-255.

Gehring JL, Bragg TB. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist. 128:209-217.

Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev. 52:107-145.

Grundy IM, Campbell BM, Frost PGH. 1994. Spatial pattern, regeneration and growth rates of *Brachystegia spiciformis* and *Julbernardia globiflora*. Vegetatio. 115:101-107.

Haas RH, Meyer RE, Scifres CJ, Brock JH. 1973. Growth and development of mesquite. Research Monographs 1, Texas Agricultural Experiment Station, College Station, US.

Heitschmidt RK, Ansley RJ, Dowhower SL, Jacoby PW, Price DL. 1988. Some observations from the excavation of honey mesquite root systems. J Range Manage. 41:227-231.

Heitschmidt RK, Dowhower SL. 1991. Herbage response following control of honey mesquite within single tree lysimeters. J Range Manage. 44:144-149.

Hines WGS, Hines RJO. 1979. The Eberhardt index and the detection of non-randomness of spatial point distributions. Biometrika. 66:73-80.

Jackson JT, van Auken OW. 1997. Seedling survival, growth and mortality of *Juniperus ashei* (Cupressacae) in the Edwards plateau region of central Texas. Texas J Sci. 49:267-278.

Johnson PA, Gerbolini D, Ethridge D, Britton C, Ueckert D. 1999. Economics of redberry juniper control in the Texas Rolling Plains. J Range Manage. 52:569-574.

Krebs CJ (1989) Ecological Methodology. Harper Collins, New York.

Laxson JD, Schacht WH, Owens MK. 1997. Above-ground biomass yields at different densities of honey mesquite. J Range Manage. 50:550-554.

McPherson GR, Rasmussen GA, Wester DB, Masters RA. 1991. Vegetation and soil zonation associated with *Juniperus pinchotii* Sudw. trees. Great Basin Nat. 51:316-324.

McPherson GR, Wright HA. 1987. Factors affecting reproductive maturity of redberry juniper (*Juniperus pinchotii*). For Ecol Manage. 21:191-196.

McPherson GR, Wright HA, Wester DB. 1988. Patterns of shrub invasion in semiarid Texas grasslands. Am Midl Nat. 120:391-397.

McPherson GR, Wright HA. 1989a. Direct effects of competition on individual juniper plants: a field study. J Appl Ecol. 26:979-988.

McPherson GR, Wright HA. 1989b. Establishment of Juniperus pinchotii in western Texas: environmental effects. J Arid Environ. 19:283-287.

McPherson GR, Wright HA. 1990. Effects of cattle grazing and Juniperus pinchotii cover on herb cover and production in western Texas. Am Midl Nat. 123:144-151.

Miller RF, Svejcar TJ, Rose JA. 2000. Impacts of western juniper on plant community composition and structure. J. Range Manage. 53:574-585.

Parajulee MN, Slosser JE, Montadon R, Dowhower SL, Pinchak WE. 1997. Rangeland grasshopper (Orthoptera: Acrididae) associated with mesquite and juniper habitats in the Texas Rolling Plains. Environ Entomol. 26:528-536.

Phillips D.L, McMahon, JA. 1981. Competition and spacing patterns in desert shrubs. J Ecol. 69:97-115.

Prentice IC, Werger MJA. 1985. Clump spacing in a desert shrub community. Vegetatio. 63:133-139.

Ruthven DC, Fulbright TE, Beasom SL, Hellgren EC. 1993. Long-term effects of root plowing on vegetation in the eastern south Texas plains. J Range Manage. 46:351-354.

Scifres CJ. 1980. Brush management principles and practices for Texas and the southwest. Texas. A&M Univ. Press, College Station, Texas, US.

Skarpe C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. J Veg Sci. 2:565-572.

Smith MA, Wright HA, Schuster JL. 1975. Reproductive characteristics of redberry juniper. J Range Manage. 28:126-128.

Smith TM, Walker BH. 1983. The role of competition in the spacing of savanna trees. Proc Grassl Soc South Afr. 18:159-164.

Smith TM, Goodman PS. 1987. Successional dynamics in an *Acacia nilotica – Euclea divinorum* savannah in southern Africa. J Ecol. 75:603-610.

Sprugel DG. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. J Ecol. 64:889-912.

Szwagrzyk J, Czerwczak M. 1993. Spatial patterns of trees in natural forest of East-Central Europe. J Veg Sci. 4:469-476.

Teague WR, Dowhower SL, Whisenant SG, Flores-Ancira E. 2001. Mesquite and grass interference with establishing juniper seedlings. J Range Manage. 54:680-684.

Teague WR, Ansley JR, Pinchak WE, Dowhower SL, Gerrard SA, Waggoner JA. 2008. Interannual herbaceous biomass response to increasing honey mesquite cover on two soils. Rangeland Ecology and Management. 61:496-508.

Teague WR, Dowhower SL, Baker SA. 2016. Herbaceous diversity and composition in mixed *Juniperus pinchotii-Prosopis glandulosa* communities in Southern mixed-grass prairie. Arid Land Research and Manage. 30:290-303.

Thurow TL. 1991. Hydrology and erosion. In: Heitschmidt RK, Stuth JW (EDS). Grazing management: An ecological perspective. pp. 141-160. Timber Press, Portland, Oregon, US.

VanAuken WO, Bush JK. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. Ecology. 78(4):1222-1229

Whittaker RH, Gilbert LE, Connell JH. 1979. Analysis of two-phase pattern in a mesquite grassland. Texas J Ecol. 67:935-952.

Wright HA, Bailey AW. 1982. Fire Ecology. United States and Canada. John Wiley and Sons, New York, US.