

The effect of *Juniperus virginiana* on plant species composition in an Oklahoma grassland

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Abstract: We established transects under twenty *Juniperus virginiana* trees that invaded an unburned central Oklahoma grassland within the last 20 years to determine their effects on plant species composition. Species richness and stem density increased as distance from the trunk increased. Stem density was also higher towards the south side of trees. Graminoid, forb and total cover were related to distance from the trunk and transect direction. Ordination revealed weak compositional gradients related to “openness” and compass direction. Woody species tended to be most abundant underneath *J. virginiana* canopies whereas grass and forb species were most abundant in the prairie. Woody and shade-tolerant species preferentially occurred in north transects and quadrats underneath the tree. Conversely, forbs had highest abundance on edge quadrats whereas graminoids dominated south transects and prairie quadrats. Thus, invasion of grasslands by *J. virginiana* influences species composition in a spatially complex manner.

Nomenclature: USDA, NRCS (2004).

Abbreviations: DBH – Diameter at Breast Height; pCCA – partial Canonical Correspondence Analysis.

Introduction

Within the last few decades, there has been a reduction in the number and size of native grasslands in North America. Urbanization caused the conversion of native grasslands into housing developments as many people move out into what was once countryside (Samson and Knopf 1994, Licht 1997, Smith 1998). Agricultural intensification has also reduced the extent of natural grasslands (Licht 1997, Coppedge et al. 2001). However, the most widely accepted reason for the reduction in prairie area and vegetation quality is the anthropogenic removal of fire (Bragg and Hulbert 1976, Smith and Stubbendieck 1990, Licht 1997). The elimination of fire has not only caused a decrease in species richness of prairies but also their succession to forests (Axmann and Knapp 1993, Briggs et al. 2002a,b).

In the south central Great Plains of North America, the main agent of this succession is the invasion of *Juniperus virginiana*. Degradation of prairie caused by *J. virginiana*

is linked to a multitude of environmental factors such as soil moisture (Engle et al. 1987, Facelli and Pickett 1991b), incoming solar radiation (Smith and Stubbendieck 1990, Facelli and Pickett 1991a, b) and soil temperature (Weaver and Rowland 1952, Hulbert 1969). Besides changes in the microclimate, the litter of *J. virginiana* may alter prairie litter dynamics by increasing litter accumulations and retarding litter decomposition. These alterations in microclimate and litter dynamics may be detrimental to prairie species richness and diversity (Knapp and Seastedt 1986, Facelli and Pickett 1991b, Myster 1994). Facelli and Pickett (1991b) suggested that not only does litter affect environmental conditions but it also affects plant community dynamics. Litter can prevent germination or establishment by acting as a mechanical barrier that seedlings must penetrate to reach the soil surface or incoming light. For instance, Myster (1994) found statistically significant decreases in *J. virginiana* and *Cornus florida* emergence caused by increased litter on the soil surface.

A number of studies have demonstrated the effects of *J. virginiana* on grasslands. Engle et al. (1987) and Smith and Stubbendieck (1990) have shown dramatic reductions in standing biomass underneath *J. virginiana* trees. Other studies suggested that *J. virginiana* adversely affects species at specific locations (Jameson 1966, Smith and Stubbendieck 1990, Gehring and Bragg 1992). There is a shift in the dominant photosynthetic pathway as *J. virginiana* canopies close (Briggs et al. 2002a). The result is a larger proportion of C₄ species outside of the canopy as compared to more C₃ species under *J. virginiana*. Linneman (2004) demonstrated how *J. virginiana* influenced physical, chemical, and micrometeorological aspects of the environment. In the current study, we examine species richness and community composition under *Juniperus virginiana* trees in contrast to the open prairie in a central Oklahoma grassland.

Methods

Study site

We conducted this experiment at the James K. McPherson Botanical Preserve located 16 km west of Stillwater, Oklahoma (36°06'00"N, 97°12'30"W). After a brief period of row crop agriculture, the site was converted into pastureland and grazed until the 1960's. Oklahoma State University (OSU) purchased the land and managerial control was turned over to the Department of Botany. In 1995, OSU introduced a burning regime, consisting of a 3-5 year return interval, to the northwestern half of the preserve with the goals of stimulating the return of a native tallgrass prairie community and controlling *J. virginiana* invasion into the Preserve's grasslands. This study, however, is restricted to the unburned portion.

We selected four study sites where *J. virginiana* were invading grasslands. Three of the four study sites occurred along the eastern edge of the preserve, whereas one site was along the northern edge. We selected potential study trees based on four criteria: (1) distance between study trees and any adjacent *J. virginiana* of at least 1.5 times the radius of the study tree, (2) a distance of no less than 2 times the canopy radius of the study tree to the canopy edge of any adjacent trees greater than one meter in height in the north and south compass direction, (3) a minimum canopy radius of 60 cm in the north and south direction of any study tree and (4) no cover above the tree by other trees. Based on these criteria, we selected 48 potential study trees. We recorded canopy diameter in the north-south and east-west directions, tree height, stem diameter at both 10 cm and breast height (DBH) and gender of each potential study tree. We classified tree gender as male, female, or juvenile (those trees without observable

inflorescences). For trees with multiple stems at breast height, we recorded separate DBH measurements for each primary stem. No potential study tree had more than one trunk originating from the ground. We averaged canopy diameter measurements for both the north-south and east-west axes for each potential study tree and ranked them from smallest to largest. We assigned all potential trees to one of four size quartiles based on average canopy diameter; thereafter we randomly selected five trees from each quartile for further study.

Sampling design

Sampling consisted of a belt transect of contiguously placed quadrats in both the north and south compass direction for each study tree. We selected these directions because in a similar study Fuhlendorf (1992) found that microenvironmental measurements varied more between north and south than between east and west. Each quadrat measured 50 cm by 25 cm on a side with the 50 cm sides abutting adjacent quadrats. The length of the quadrats (and thereby the number of plots) was determined as 1.5 times the extent of the canopy. Based on the results from personal observations and the literature, we assigned the following categories to all quadrats: 'under' the canopy (0-60% of the canopy radius), 'edge' quadrats (60-90% of the canopy radius) and 'prairie' quadrats (greater than 90% of the canopy radius).

We identified each plant species rooted inside the quadrat and estimated its cover to the nearest percent for any cover less than 5% and to the nearest 5% for any cover over 5%. We collected unknown species for later identification. Species nomenclature and codes follow that of the USDA PLANTS database (USDA, NRCS 2004). Species present in the study along with their corresponding codes are listed in Table 2. *J. virginiana* occasionally occurs as seedlings: when we report *J. virginiana* in species composition results, we are excluding the canopy tree.

At the time of vegetation sampling, we collected other measurements from each quadrat including litter depth, height to nearest foliage, and visual estimates of the percent of litter from *J. virginiana*, percent litter cover, and percent plant cover, and percent canopy cover (Linneman 2004).

Statistical analysis

Statistical analysis consisted of multiple regressions, paired *t*-tests, and constrained ordinations. We used SPSS (Version 11.0) to conduct the regressions and *t*-tests. For the regressions (unless otherwise stated), we include distance to the trunk, a dummy variable representing north

and south, dummy variables representing gender, and a dummy variable representing each individual tree. We report standardized coefficients (b) from the multiple regressions, for selected variables. We do not report coefficients for the individual trees, as we treat them as 'nuisance' covariables.

To assist in visualizing bivariate data, we generated Lowess trend lines using SPSS (Version 11.0)

We analyzed compositional data using partial Canonical Correspondence Analysis (pCCA) because of its ability to factor out covariables. We employed manual forward selection to identify the most important and interpretable environmental variables. All ordinations were conducted using CANOCO for WINDOWS 4.5 (ter Braak and Šmilauer 2002) on both the absolute cover of each species as well as the relative proportion of cover of that species within a quadrat. Since the results of both absolute and relative analyses were similar, we present only the relative analysis here unless otherwise stated.

We interpret statistical significance cautiously due to the exploratory nature of some of the analyses, the lack of a correction for multiple comparisons, and spatial autocorrelation (Legendre and Legendre 1998, Hallgren et al. 1999). The main function of this study was to generate hypotheses tested in an experimental study involving a factorial removal of *J. virginiana* and its litter (Linneman 2004).

Results

Density and richness

The number of stems (of all vascular plant species combined) was positively related to percent distance from *J. virginiana* stems ($b = 0.652, p < 0.001$) and to south transects ($b = -0.170, p < 0.001$) for the entire data set. A paired t -test of transect direction performed separately for each canopy cover category ('under', 'edge', 'prairie') showed that stems per quadrat was significantly higher on the south side of trees for 'edge' ($p = 0.001$) and 'prairie' ($p = 0.029$) quadrats. South quadrats had approximately 25% more stems than north quadrats (Fig. 1).

A common concern of fine-scale studies of species richness is the 'rarefaction effect' (Palmer et al. 2000): an inherent correlation between richness and density that limits inference about diversity (Oksanen 1996). As our data reveal a strong rarefaction effect (Fig. 2), we factored out the 'nuisance' effect of stems per quadrat by including its logarithm as a term in a multiple regression of species richness.

Multiple regressions showed distance from the trunk (multiple regression coefficient $b = 0.141, p = 0.004$, Fig. 3) and both male ($b = 0.077, p = 0.049$) and juvenile trees ($b = 0.079, p = 0.022$) were all positively related to species richness for the entire data set. However, when each canopy cover category was analyzed separately, percent dis-

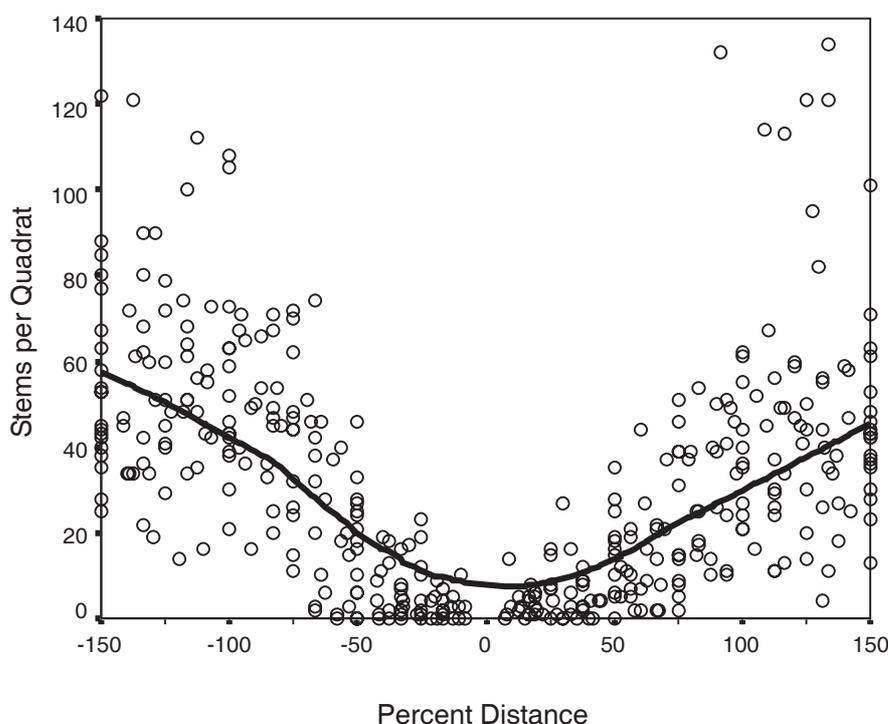


Figure 1. Stems per 0.125 m² quadrat as a function of distance from the trunk (expressed as a percent of canopy radius) based on all samples, along with a Lowess trendline. Negative percent distance indicates south transects direction and positive values indicate north transects direction.

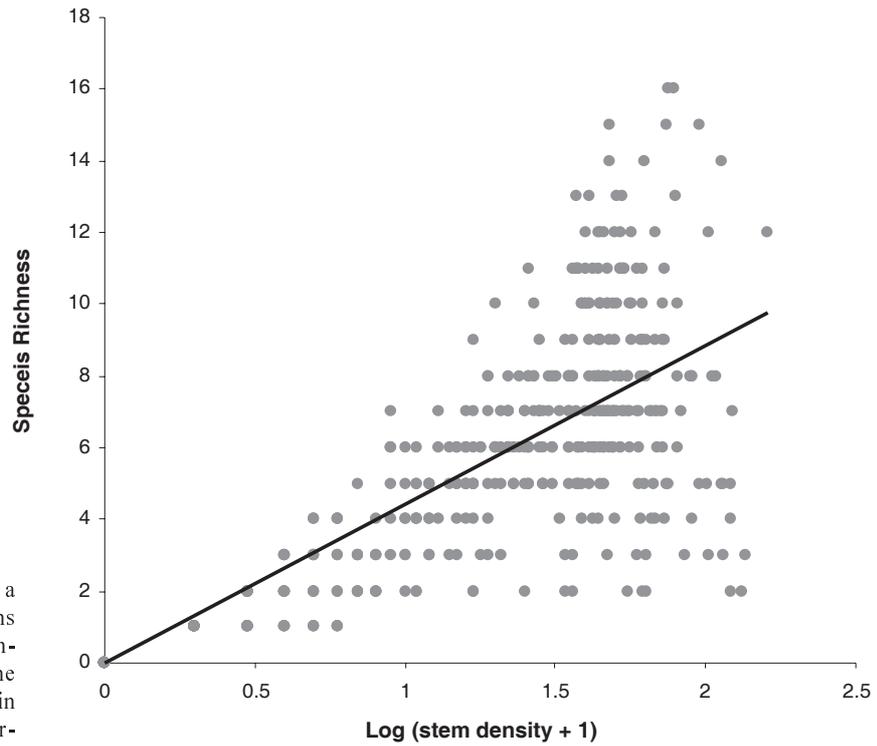


Figure 2. Species richness as a function of the number of stems of all vascular plant species combined. The linear regression line was forced to start at the origin thus yielded a coefficient of determination of 0.5226.

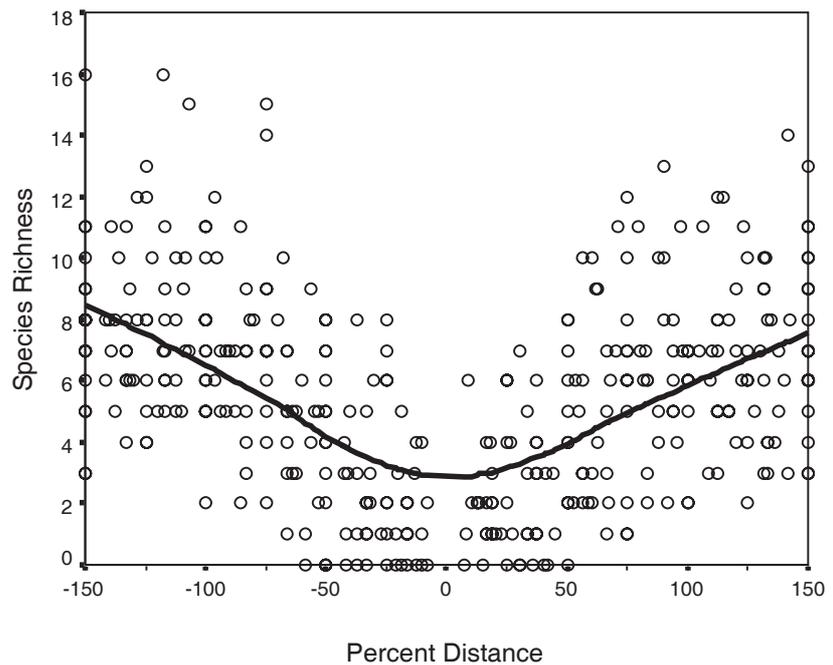


Figure 3. Species richness per 0.125 m² quadrat as a function of percent distance from the trunk (expressed as a percent of canopy radius). Negative percent distance indicates south transects direction and positive values indicate north transects direction. A Lowess trendline has been included.

tance ($b = 0.190, p = 0.005$) and juveniles trees ($b = 0.161, p = 0.023$) were significant only for 'prairie' quadrats.

Total species richness ranged from 0-16 per 0.125 m² quadrat with mean quadrat richness ranging from 2.9-7.5

(Table 1). Results from a paired t -test of mean quadrat richness for both transect directions by each canopy cover category showed that there were no statistically significant differences in richness between the north and south transects for any category.

Table 1. Mean stems per quadrat (stems per 0.125 m²) and species richness (species per 0.125 m²) for each canopy cover category.

	Number of stems (mean ± sd)	Species richness (mean ± sd)
Under	8.2±9.1	2.9±2.5
Edge	30.8±19.7	6.1±3.0
Prairie	51.0±26.7	7.5±2.9

Total vegetation cover

A paired *t*-test of total vegetation cover showed that percent of vegetation cover was significantly higher on the south side for both 'edge' and 'prairie' quadrats ($p = 0.002$ and 0.02 respectively, Fig. 4). In addition, total cover was positively affected by increasing distance based on the entire data set (multiple regression coefficient $b = 0.583$, $p < 0.001$). When the data are subdivided into groups, total cover is positively affected by distance only in the 'under' quadrats ($b = 0.277$, $p = 0.001$). Larger trees also had significantly less total cover for all quadrats ($b = -0.110$, $p = 0.017$) and specifically for 'under' ($b = -0.250$, $p = 0.006$) and 'edge' quadrats ($b = -0.329$, $p = 0.008$).

Forb cover

Results from a paired *t*-test showed that forb cover was significantly higher on the south side for both 'edge' and 'prairie' quadrats ($p = 0.01$ and 0.006 , respectively). As with total vegetation cover, distance had a significant positive effect on forb cover (multiple regression coefficient $b = 0.412$, $p < 0.001$) for the entire data set. However, when the data are analyzed by groups, distance was only significant for 'prairie' quadrats ($b = 0.011$, $p < 0.001$).

Graminoid cover

A paired *t*-test showed that graminoid cover was significantly higher on the south side for only 'edge' quadrats ($p = 0.014$). Increasing percent distance was positively related to graminoid cover for the complete data set ($b = 0.481$, $p < 0.001$). In addition, graminoid cover in 'under' and 'edge' quadrats were positively affected by distance ($b = 0.371$, $p < 0.001$ and $b = 0.227$, $p = 0.013$, respectively).

Woody cover

Although woody cover could be locally high, in general it was sporadic and contributed little to total plant cover over all quadrats. A paired *t*-test showed no significant differences between woody cover in north and south transects for any canopy cover category. In addition, per-

cent distance had no significant effect (based on multiple regression) on woody cover.

Direct gradient analysis

Partial Canonical Correspondence Analysis (pCCA; factoring out tree identity) revealed two main compositional gradients in the data. The first axis was related to *J. virginiana* canopy cover, whereas the second axis was related to transect direction (Fig. 5). Since many of the explanatory variables were redundant, we performed a simpler pCCA of five variables, based on manual forward selection. The two most dominant gradients remain related to canopy openness and compass direction (Fig. 6).

Using manual forward selection in pCCA, we sequentially tested each environmental variable within each canopy category. Significance is assessed by a permutation test of the first eigenvalue. In 'under' quadrats only litter depth was significantly ($p = 0.006$) related to species composition. 'Edge' quadrats were not significantly related to any variable whereas 'prairie' quadrats were significantly related to soil pH ($p = 0.002$), percent bare ground ($p = 0.023$) and litter depth ($p = 0.044$).

In general, plant species such as *Amphiachyris dracunculoides*, *Sabatia campestris* and *Diodia teres* occurred mostly in warmer sites towards the south (see Linneman 2004) whereas species such as *Gamochaeta purpurea*, *J. virginiana* and *Quercus stellata* occurred in cooler sites under *J. virginiana* canopy towards the north. In addition, species such as *Ambrosia psilostachya*, *Digitaria cognata* and *Sporobolus compositus* occurred on sites with higher soil pH whereas *Symphoricarpos orbiculatus*, *Paspalum setaceum* and *Acacia angustissima* occurred on sites with more acidic soils (Fig. 6).

As expected, plant species composition was predictably related to the cover categories 'under', 'edge', and 'prairie' (Fig. 7; Table 2). The woody species *Quercus stellata*, *Rhus copallinum*, *J. virginiana* and *Prunus mexicana*, the forb *Gamochaeta purpurea* and the sedge *Carex festucacea* all showed an affinity towards 'under' quadrats. Species typical of grasslands such as *Sorghastrum nutans*, *Ambrosia psilostachya* and *Sabatia campestris* were more common in 'prairie' quadrats. Although none of the most frequent species occurred preferentially in

Figure 4. Vegetation cover for three growth forms as a function of distance. Also included is total vegetation cover. The trendlines for this figure are Lowess curves. Data points were excluded from this figure to aid visibility. Woody cover is trivial, but is actually nonzero.

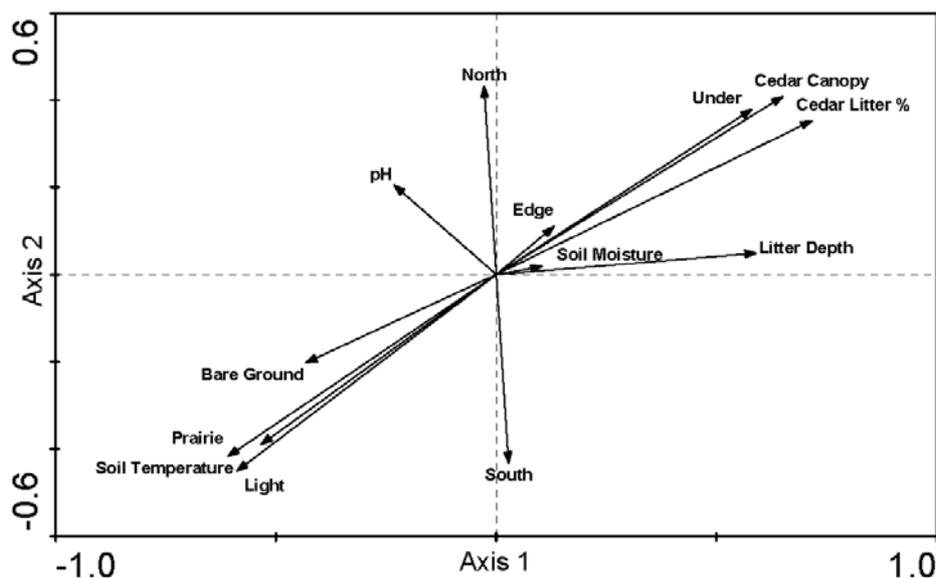
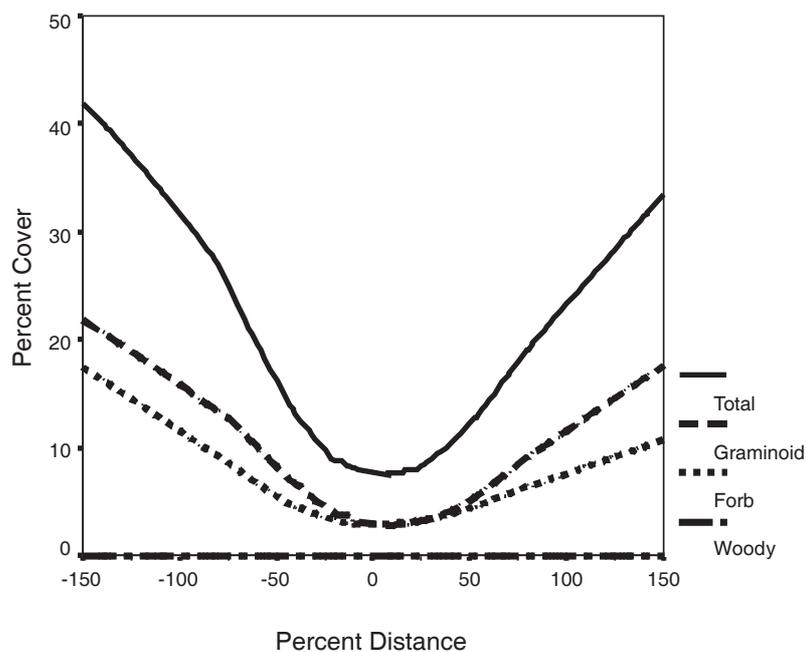


Figure 5. pCCA scatter plot of environmental variables, illustrating their correlation structure. Tree identities are covariables.

'edge' quadrats, a few infrequent species (*Bothriochloa ischaemum*, *Chenopodium album*, *Oxalis violacea* and *Vernonia baldwinii*) did favor 'edge' quadrats (Table 2).

Results from a pCCA of transect direction in 'under' quadrats (not displayed) showed that certain species marginally "preferred" ($p = 0.046$, randomization test of the first eigenvalue) particular sides of the tree. Woodland specialists such as *Symphoricarpos orbiculatus*, *J. virginiana* and *Acalypha gracilens* preferred the north side

whereas grassland species such as *Paspalum setaceum*, *Hypericum drummondii* and *Artemisia ludoviciana* preferred the south side. By itself, transect direction only accounted for 6.4% of the total explained variance in the data set. A pCCA showed a significant effect ($p = 0.001$) of distance on species composition, even after employing *J. virginiana* cover categories as covariables.

'Under', 'edge' and 'prairie' quadrats were analyzed separately with pCCA to determine what environmental

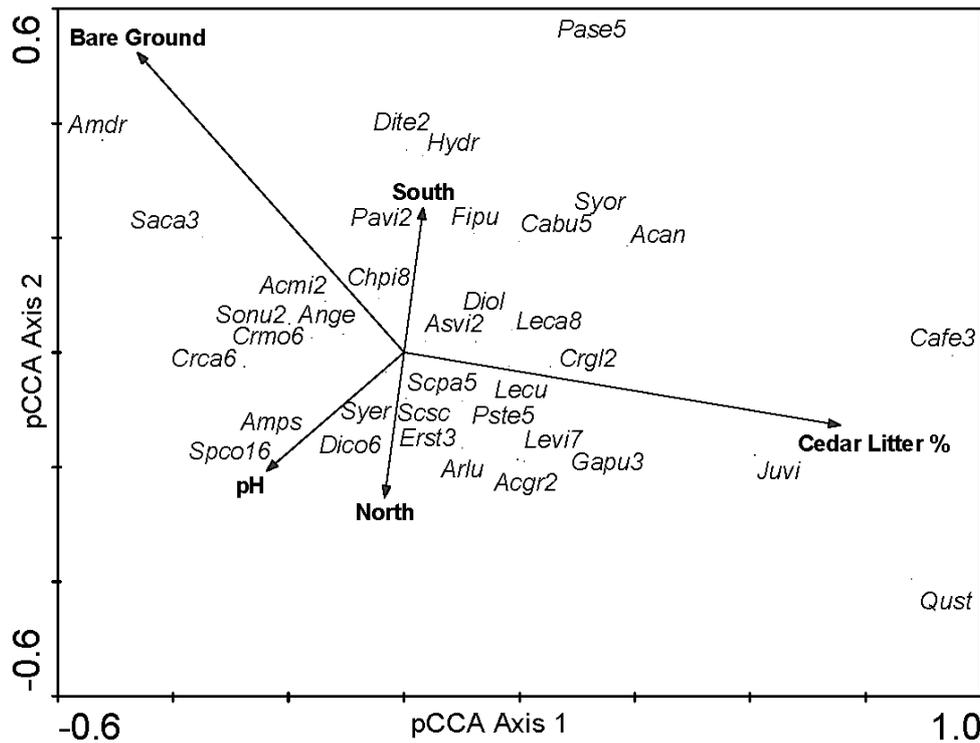


Figure 6. pCCA biplot of selected environmental variables and species scores, with tree identities used as covariables. Species codes are given in Table 2.

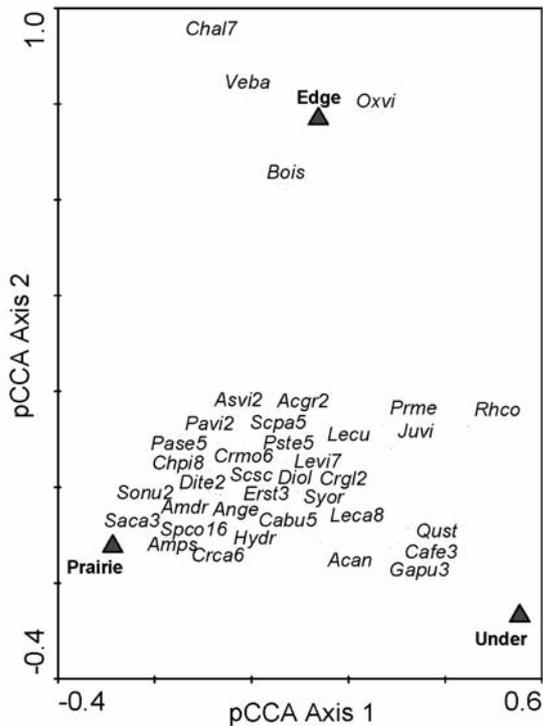


Figure 7. pCCA biplot of species and environmental centroids of canopy cover categories. Individual trees are used as covariables. Some species codes are slightly displaced to enhance visibility. See Table 2, for species codes.

variables could be responsible for any changes in species composition as distance from the trunk increased. Again, statistical inference is assessed by a randomization test of the first pCCA eigenvalue. Litter depth was the only significant factor ($p = 0.006$) related to species composition in ‘under’ quadrats. On the other hand, soil pH ($p = 0.002$), bare ground ($p = 0.023$) and litter depth ($p = 0.044$) were all significant for ‘prairie’ quadrats. No environmental variable was significantly related to composition in ‘edge’ quadrats.

Discussion

As expected, stem density, species richness, forb cover, and grass cover were higher in the open prairie than underneath the tree. However, these variables increased as a function of distance even beyond the extent of the canopy. These results are similar to those of Engle et al. (1987) who found that herbaceous standing crop increased as distance from the drip line increased from 3 m to 5 m. In our study site, solar radiation and soil temperature also increase beyond 1.5 times the radius, particularly towards the south, whereas soil moisture continues to decrease (Linneman 2004). These results suggest that a single tree’s influence extends beyond its canopy diameter.

Table 2. Species frequencies, expressed as a percentage of quadrats, by canopy cover category. This table includes all species with frequency of at least 10% of at least one canopy cover category. Less frequently occurring species are the forbs *Apocynum cannabinum*, Apcn, *Artemisia ludoviciana*, Arlu, *Chamaecrista fasciculata*, Chfa2, *Chenopodium album*, Cha17, *Gamochaeta purpurea*, Gapu3, *Geum canadensis*, Geca7, *Lamium amplexicaule*, Laam, *Lespedeza capitata*, Leca8, *Lespedeza procumbens*, Lepr, *Liatris punctata*, Lipu, *Linum imbricatum*, Liim, *Oxalis violacea*, Oxvi, *Psoraleidum tenuiflorum*, Pste5, *Solanum carolinense*, Soca3, *Symphotrichum oblongifolium*, Syob, *Vernonia baldwinii*, Veba; the graminoids *Bothriochloa ischaemum*, Bois, *Carex festucacea*, Cafe3, *Digitaria cognata*, Dico6, *Elymus canadensis*, Elca4, *Fimbristylis puberula*, Fipu, *Panicum virgatum*, Pavi2, *Parietaria pensylvanica*, Pape5, *Paspalum setaceum*, Pase5; and the woody plants *Cercis canadensis*, Ceca4, *Cornus drummondii*, Codr, *Juniperus virginiana*, Juvi, *Quercus stellata*, Qust, *Symphoricarpos orbiculatus*, Syor, *Ulmus rubra*, Ulru. Species codes and habit follow USDA, NRCS (2004).

Species Name	Code	Habit	Under the tree	Edge of canopy	Tallgrass Prairie
<i>Acacia angustissima</i>	Acan	Forb	7.14	17.11	11.17
<i>Acalypha gracilens</i>	Acgr2	Forb	8.57	19.74	18.45
<i>Achillea millefolium</i>	Acmi2	Forb	4.29	17.11	12.14
<i>Ambrosia psilostachya</i>	Amps	Forb	6.43	10.53	28.16
<i>Amphiachyris dracunculoides</i>	Amdr	Forb	2.86	10.53	18.45
<i>Andropogon gerardii</i>	Ange	Graminoid	7.86	28.95	33.50
<i>Asclepias viridis</i>	Asvi2	Forb	2.86	10.53	3.88
<i>Carex bushii</i>	Cabu5	Graminoid	6.43	10.53	19.90
<i>Chrysopsis pilosa</i>	Chpi8	Forb	8.57	21.05	23.79
<i>Croton capitatus</i>	Crca6	Forb	3.57	10.53	15.53
<i>Croton glandulosus</i>	Crgl2	Forb	16.43	23.68	27.67
<i>Croton monanthogynus</i>	Crmo6	Forb	5.00	18.42	29.61
<i>Dichanthelium oligosanthes</i>	Diol	Graminoid	32.14	43.42	42.72
<i>Diodia teres</i>	Dite2	Forb	2.86	17.11	18.45
<i>Erigeron strigosus</i>	Erst3	Forb	11.43	27.63	39.81
<i>Hypericum drummondii</i>	Hydr	Forb	4.29	5.26	19.90
<i>Lespedeza cuneata</i>	Lecu	Forb	5.71	13.16	8.74
<i>Lespedeza virginica</i>	Levi7	Forb	5.71	10.53	12.14
<i>Sabatia campestris</i>	Saca3	Forb	0.00	9.21	18.45
<i>Schizachyrium scoparium</i>	Scsc	Graminoid	33.57	64.47	69.42
<i>Scleria pauciflora</i>	Scpa5	Graminoid	10.00	25.00	30.10
<i>Sorghastrum nutans</i>	Sonu2	Graminoid	4.29	19.74	30.10
<i>Sporobolus compositus</i>	Spco16	Graminoid	10.00	50.00	58.74
<i>Symphotrichum ericoides</i>	Syer	Forb	5.00	21.05	29.13

The results of this study also imply that the tree's shadow (predominantly on the north side) influences both stem density and vegetation cover. These results are consistent with those of Gehring and Bragg (1992) who suggested that vegetation cover was lower on the north and east sides compared to south and west sides. Additionally, edge quadrats on the south side received more incoming solar radiation than their counterparts on the north side (Linneman 2004). Several researchers have suggested that lower light could substantially reduce total plant density and cover (Yager and Smeins 1999, Joy and Young 2002). Differences in solar radiation could explain the increased amount of forb and grass cover in south quadrats and the compositional trend towards open and/or upland species in south quadrats whereas woodland species were most frequent in north quadrats.

Overall, species composition showed only a weak trend as a function of distance from the trunk, until the canopy edge is reached. Seedlings of tree species were much more likely to occur underneath study trees as compared to any other location; however, no single woody species occurred in more than 8% of the quadrats. In contrast, the grasses *Schizachyrium scoparium* and *Dichanthelium oligosanthes* both frequently occurred under trees. With the exception of tree species, our results mirror those of Briggs et al. (2002a) who found that species present in the prairie were not consistently different from those found in a closed-canopy *J. virginiana* forest.

With the exception of woody plants, species growing underneath *J. virginiana* trees appear to largely be a random subset of the species from the surrounding matrix. Therefore, those species with the highest frequencies prior to *J. virginiana* establishment and growth are still likely to be the most frequent underneath canopies as each tree grows. Our results agree with those of Gehring and Bragg (1992) who suggested that frequency of tree species increases underneath *J. virginiana* trees. Both Myster (1994) and Facelli (1994) found that woody species were less inhibited by deep litter layers than herbaceous species because of their relatively larger seed mass and subsequently increased carbohydrate reserves. Therefore, if seeds from woody species became lodged within the litter layer underneath a *J. virginiana* tree they would likely have a higher probability of establishment than a grass or forb species.

In conclusion, *J. virginiana* canopies are associated with increased leaf litter, and reduced light, plant cover, stem density and species richness of the understory. These strong trends are coupled with only weak compositional trends. Since the majority of species were present in few quadrats and that the most frequent species were consis-

tently grasses associated with the prairie, the composition under *J. virginiana* trees appears to be a subset of the species present before encroachment. There is a slight preference of woody and/or shade tolerant species for conditions under *J. virginiana* trees. In addition, forbs and graminoids tend to be more frequent at greater distances. The north and south sides of trees have strong differences in the environment (Linneman 2004) which likely account for the observed compositional differences. These results, combined with those in Linneman (2004) imply that without *J. virginiana* removal, grasslands and pasturelands will continue to lose grassland species in favor of forest species. Succession of *J. virginiana*-invaded grasslands is likely to remain spatially complex, with the initial locations of tree canopies influencing fine-scale dynamics.

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References

- Axmann, B.D. and A.K. Knapp. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie. *Southwestern Naturalist* 38:325-330.
- Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.* 29:19-23.
- Briggs, J.M., G.A. Hoch and L.C. Johnson. 2002a. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5:578-586.
- Briggs, J.M., A.K. Knapp and B.L. Brock. 2002b. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. *Am. Midland Nat.* 47:287-294.
- Coppedge, B.R., D.M. Engle, S.D. Fuhlendorf, R.E. Masters and M.S. Gregory. 2001. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. *Landscape Ecol.* 16:677-690.
- Engle, D.M., J.F. Stritzke and P.L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. *J. Range Manage.* 40:237-239.
- Facelli, J.M. and S.T.A. Pickett. 1991a. Plant litter: Light interception and effects on an old-field plant community. *Ecology* 72:1024-1031.
- Facelli, J.M. and S.T.A. Pickett. 1991b. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* 57:1-32.
- Facelli, J.M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75:1727-1735.
- Fuhlendorf, S.D. 1992. Influence of age/size and grazing history on understory relationships of Ashe juniper. MSc Thesis, Texas A&M University, College Station, Texas.
- Gehring, J.L. and T.B. Bragg. 1992. Changes in prairie vegetation under eastern redcedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. *Am. Midland Nat.* 128:209-217.

- Hallgren, E., M.W. Palmer and P. Milberg. 1999. Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *J. Ecol.* 87:1-16.
- Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* 50:874-877.
- Jameson, D.A. 1966. Pinyon-Juniper litter reduces growth of blue grama. *J. Range Manage.* 19:214-217.
- Joy, D.A. and D.R. Young. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. *Plant Ecol.* 160:125-135.
- Knapp, A.K. and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36:662-667.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Licht, D.S. 1997. *Ecology and Economics of the Great Plains*. University of Nebraska Press, Lincoln, Nebraska
- Linneman, J.S. 2004. Studies of eastern redcedar ecology in central Oklahoma. MSc Thesis, Oklahoma State University, Stillwater, Oklahoma.
- Myster, R.W. 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio* 114:169-174.
- Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artifact due to plot size? *J. Ecol.* 84:293-295.
- Palmer, M.W., D.B. Clark and D.A. Clark. 2000. Is the number of tree species in small tropical forest plots nonrandom? *Community Ecol.* 1:95-101.
- Samson, F. and F. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418-421.
- Smith, D.D. 1998. Iowa prairie: Original extent and loss, preservation and recovery attempts. *Journal of the Iowa Academy of Science* 105:94-108.
- Smith, S.D. and J. Stubbendieck. 1990. Production of tallgrass prairie herbs below eastern redcedar. *Prairie Naturalist* 22:13-18.
- ter Braak, C.J.F. and P. Šmilauer. 2002. *Canoco for Windows 4.5*. Biometris-Plant Research International. Wageningen, Netherlands.
- USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Weaver, J.E. and N.W. Rowland. 1952. Effect of excessive natural mulch on the development, yield, and structure of a native grassland. *Bot. Gaz.* 114:1-19.
- Yager, L.Y. and F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. *Southwestern Naturalist* 44:6-16.

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