RECOVERY OF A PRAIRIE PLANT COMMUNITY FOLLOWING SERICEA LESPEDEZA (*LESPEDEZA CUNEATA*) REMOVAL: TESTING FOR A SOIL LEGACY EFFECT

A Thesis by

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Master of Science

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The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Biological Sciences.

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Gregory Houseman, Committee Chair

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ABSTRACT

Sericea lespedeza (*Lespedeza cuneata*) is an invasive legume threatening plant communities in the southeastern and southcentral United States. In addition to reducing native species abundance, current evidence suggests that *L. cuneata* invasion may alter soil conditions in host communities. If correct, *L. cuneata* may create a soil legacy effect that impacts community recovery, even if control measures have effectively removed *L. cuneata*. I examined the recovery of a prairie plant community in Jefferson county, Kansas to determine if the historical presence of *L. cuneata* affected 1) the relative abundance of all species and 2) the colonization of native species in the community four years following *L. cuneata* removal. To address this, *L. cuneata* seeds were sown into 300 plots at a wide range of densities (0 to 10,000 seeds m^{-2}) under different combinations of simulated disturbance and soil fertilization. After a three-year establishment period, the percent cover and stem density of *L. cuneata* was recorded, and the community was burned and sprayed with herbicide to eliminate *L. cuneata*. Fertilization and disturbance treatments were discontinued, and thirteen native forb species were sown into all plots. The stem density of all sown species was recorded annually over a four-year recovery period, and the percent cover of all species present was recorded in the fourth year of recovery.

Analysis of community data in response to the historical presence of *L. cuneata* did not indicate the presence of a soil legacy effect. Although the relationship between community species cover and the historical cover of *L. cuneata* was significant in some cases, the variation explained by these comparisons was quite low. Similarly, the colonization of sown native species in the community was unrelated to the historical cover of *L. cuneata*. These results indicate that *L. cuneata* does not create a soil legacy effect if effectively controlled within the first three years of invasion, regardless of initial density.

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CHAPTER 1

INTRODUCTION

Plant invasions not only suppress native species, but can also alter soil conditions, which may strongly affect attempts to manage and restore pre-invasion communities (e.g. Ehrenfeld 2010). For example, plants can influence soil properties through mechanisms such as root exudation, interactions with soil microbes, and litter deposition, creating plant-soil feedbacks (PSF), which in turn promote or inhibit the success of neighboring con- and heterospecifics (Bever 1994; van der Putten et al. 2013). Although PSFs have been suggested to promote species coexistence in plant communities (Callaway et al. 2004; Ehrenfeld 2005; Lankau et al. 2011), feedbacks created by some exotic species can dramatically alter soil conditions. Invasion can affect local nutrient pools and cycling rates (Renz and Blank 2004; Haubensak et al. 2004; Corbin and D'Antonio 2004), microbial community composition and mutualisms (Kourtev et al. 2002; Stinson et al. 2006; Mummey and Rillig 2006; Pringle et al. 2009; Jordan et al. 2011 Grove et al. 2012), and even change soil erosion patterns (Crooks 2002; Hacker and Deither 2009). These alterations can foster overwhelming dominance of the invader and a concomitant reduction of native species intolerant to these conditions, thus changing the pattern of succession in these communities (Kardol et al. 2007; Conser and Connor 2009; Grman and Suding 2010; Van de Voorde et al. 2011; Jordan et al. 2012).

In some cases, simple removal of an invader can ameliorate the impact caused by invasion (Rey Benayas et al. 2009; Riddin et al. 2016). In others, alterations caused by invasion can persist even after removal, creating a legacy effect that continues to impact the host community (Bever 1994; Corbin and D'Antonio 2012; Skurski et al. 2014). Multiple invasive species have been found to reduce or disrupt the colonization of critical arbuscular mycorrizal fungi (AMF) symbionts on native species in soils that were previously occupied by an invader (Stinson et al. 2006; Grove et al. 2012; Shannon et al. 2014). Likewise, invasive species that alter soil chemical properties such as local nutrient pools (e.g. Liao et al. 2008), pH (Conser and Connor 2009) and cycling rates (Corbin and D'Antonio 2004; Dickie et al. 2014) are likely candidates to create soil legacy effects. Unfortunately, few studies test the persistence of these effects after the invader is removed, so the potential for soil legacies from these alterations is poorly understood.

Current understanding of legacy effects is hampered by a paucity of field experiments and reliance on short-term results. Most PSF studies are carried out in greenhouses (Kulmatiski et al. 2008), which are invaluable for initial study of a potential effect, but lack the realism and potential importance of other factors excluded by greenhouse studies. Factors such as disturbance and soil resource availability are unaccounted for despite their potential importance to the strength and direction of PSF interactions (Kardol et al. 2013; Suding et al. 2013) and likelihood of legacy effects. In addition, the few field-based legacy effect studies available frequently focus on previously established invader populations, and while providing important insight within environmental context, are unable to fully tease apart inherent soil spatial variability from the effects of the invader itself on soil conditions. Current evidence is also overwhelmingly based on studies carried out twelve months or less (Kardol et al. 2013), which may not translate to long-term impacts on community recovery. Controlled, long-term field studies are therefore necessary to examine the strength of legacy effects over time, and ultimately to inform effective restoration management decisions following invader removal.

I address this issue by examining the recovery of a prairie plant community following an experimentally controlled invasion. The species of interest, Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don.], is an invasive legume species native to central and eastern Asia that has become well-established in grassland communities across a large portion of the eastern and midwestern United States (Gucker 2010; Figure 1). Upon invasion, *L. cuneata* strongly reduces the abundance of native species (Brandon et al. 2004) and tends to form dense, monotypic stands (Eddy and Moore 1998; Silliman and Maccarone 2005). Herbicide application is typically utilized to substantially to reduce *L. cuneata* biomass (Cummings et al. 2007; Gucker 2010). Even after effective removal, however, the effects of *L. cuneata* invasion may continue to impact the host community. Several studies have shown the allelopathic potential of *L. cuneata* in which seed leachates, root exudates, and leaf leachates of *L. cuneata* negatively affected the germination and growth of several grass species (Kalburtji and Mosjidis 1992, 1993a, 1993b; Dudley and Fick 2003), in addition to germination of conspecifics (Houseman and Mahoney 2015). Similar to other invasive species (e.g. Mummey and Rillig 2006), Yannarell et al. (2011) also found significant differences among bacterial and fungal communities between *L. cuneata* invaded and uninvaded sites. Lastly, Coykendall and Houseman (2014) demonstrated that *L. cuneata* produces more biomass and greater root nodulation in soil with a history of its own presence compared to previously uninvaded soils. Taken together, these results indicate that *L. cuneata* invasion can alter soil conditions, and potentially create a soil legacy effect.

To test this idea, I quantified the response of a grassland plant community in northeastern Kansas following the removal of an experimentally controlled invasion by *L. cuneata*. Following effective control of *L. cuneata*, the community was monitored over a four-year period to determine if historical *L. cuneata* abundance had a significant effect on the recovering community. Specifically, I determined whether the historical presence of *L. cuneata* affected 1) the relative abundance of species present in the community, and 2) the ability of sown native species to establish in the community following its removal.

CHAPTER 2

METHODS

2.1 Site Description

The experiment was conducted at the University of Kansas Field Station (KUFS) in Lawrence, Kansas, USA (39.054728° N, -95.194525° W). The site was converted to cool-season grass pasture in the mid-20th century. Beginning in 1974, the site was allowed to naturally revert to native grassland dominated by Indian grass (*Sorghastrum nutans*) and managed by periodic burning and haying. The site experiences 94 cm of average annual precipitation, 70 percent of which falls during the growing season between April and September. Temperatures range from 6° C to 19° C annually on average (Kansas Biological Survey 2009). Topographically, the experiment site within KUFS is relatively level, between 333 and 335 meters above sea level and the soils consist of Grundy silty clay loam (1 to 3 percent slopes) formed from loess deposits that is somewhat poorly drained (Soil Survey Staff 2009; Figure 2).

2.2 Experimental Design

The experiment reported here was a follow-up to an initial experiment designed to test the effect of *L. cuneata* propagule pressure on invasion under different disturbance and soil fertility conditions (Houseman et al. 2014). Simulated disturbance, fertilization, and *L. cuneata* seed addition treatments were applied in a randomized, complete block design to 0.75 x 0.75 m^2 plots distributed across three blocks (Figure 3). The disturbance treatment included three levels: simulated haying, simulated grazing, and no disturbance. Grazing was simulated by removing the upper half of all standing biomass within plots in June, July, and August. In addition, an approximately 15 cm patch of the soil surface was disturbed annually to simulate soil disturbance by large herbivores. Haying was simulated by removing all but approximately 5 cm of standing biomass mid-summer each year. These disturbance treatments were crossed with two levels of fertilization: plots either received 16 g N · m^{-2} NPK fertilizer annually or no addition of fertilizer. Seeds were collected from local *L. cuneata* populations and sown at a rate of 0, 32, 60, 124, 252, 500, 752, 1,000, 5,000 or 10,000 seeds per m^{-2}. Prior to seed addition, the experimental site had no known occurrence of *L. cuneata*, although it was present with 1 km of the site.

The initial experiment conducted by Houseman et al. (2014) was maintained for three growing seasons. Fertilizer was applied annually, however the grazing and haying treatments were only applied during the first two years to allow full growth of *L. cuneata* and peak biomass in all plots during the third and final year of the initial experiment. The stem density and percent cover of *L. cuneata* was recorded for each plot in the third growing season (2009), after which the experimental site was burned during the fall of that year and sprayed with Escort herbicide (Dupont, Wilmington) the following spring to effectively remove *L. cuneata* from all plots (Coykendall and Houseman 2014). Fertilizer and disturbance treatments were also discontinued following *L. cuneata* control efforts. Subsequently, seeds of thirteen native forb species were sown into all plots (Table 1). Beginning one year after seed addition, the stem density of all sown species was recorded annually between August and September during the four-year recovery period. Any *L. cuneata* stems found during this period were manually removed. In the fourth growing season following *L. cuneata* removal, the percent cover of all species present was recorded in addition to the stem density of sown native species.

2.3 Statistical Analyses

I used permutational multivariate analysis of variance (PERMANOVA) to detect historical effects of disturbance and fertilization treatments applied by Houseman et al. (2014) using Primer v6 + PERMANOVA (PRIMER-E Ltd 2006). For plant establishment and recovery, a log-transformed Bray-Curtis similarity matrix was constructed for both species cover and sown species density from the final year of the recovery period (2014). A value of one was added to the stem density for all plots to avoid erratic behavior of similarity values in plots with low or no sown species density (Anderson et al. 2008). Pair-wise tests were conducted *post hoc* to determine significant differences among groups following significant PERMANOVA results. All *post hoc* multiple comparisons tests were adjusted using a Holm-Bonferroni correction to compensate for inflation of Type 1 error rate. Multivariate homogeneity of group dispersions was evaluated using the PERMDISP analysis within Primer v6 + PERMANOVA to detect significant departures from homogenous dispersion (10,000 permutations).

I used linear regression via R version 3.3.1 (R Core Development Team 2016) to evaluate the response of relative native species cover to the historical abundance of *L. cuneata*. Species were designated as native or non-native according to descriptions from the USDA Plant Database and Haddock (2016). Relative native cover was subsequently calculated as a proportion of the total cover versus the cover of non-native species for each plot. The lm function was used to test models and the gvlma package (Pena and Slate 2014) to evaluate regression assumptions. An arcsine transformation was applied to relative native cover data to meet assumptions of normality. The response of total stem density of sown natives to the historical abundance of *L. cuneata* was evaluated using a generalized linear regression model based upon a negative binomial distribution (glm.nb) using the MASS package in R (Venables and Ripley 2002) due to non-normality associated with count data.

Distance-based redundancy analysis (RDA) of species cover (2014) and annual stem density of sown natives (2010 – 2014) was conducted to evaluate the multivariate community response to the historical abundance of *L. cuneata* via the distLM function in Primer v6 +

PERMANOVA. Although RDA analysis does not make explicit normality assumptions, both the historical abundance of *L. cuneata* and community data were log transformed to avoid effects of skewed data and extreme outliers (Anderson et al. 2008). The log-transformed Bray-Curtis similarity matrix was used for all analyses as previously described for the PERMANOVA analysis. Results were based on 10,000 permutations of the data.

CHAPTER 3

RESULTS

Community data were analyzed separately in response to historical *L. cuneata* stem density and percent cover; the results using these explanatory variables were very similar in comparison. For the sake of simplicity and because percent cover is more representative of aboveground plant size, only the results of the community data in response to historical cover of *L. cuneata* are presented here.

The historical disturbance and fertilization treatments significantly affected community species cover, despite being discontinued during the recovery period (Pseudo-$F_{2, 243} = 2.84$, $P < 0.001$ and Pseudo-$F_{1, 243} = 3.95$, $P < 0.001$, respectively). Pair-wise tests indicated that plots that received simulated grazing ($t_{197} = 0.93$, $P < 0.001$) or haying ($t_{143} = 1.90$, $P < 0.001$) were significantly different from plots that received no experimental disturbance, but were not significantly different from one another ($t_{144} = 1.95$, $P > 0.5$). Consequently, species cover responses were analyzed separately for historically disturbed (grazed or hayed) and undisturbed plots in subsequent analysis. Conversely, density of sown natives was not affected by historical disturbance (Pseudo-$F_{2, 243} = 0.62$, $P > 0.7$) or fertilization (Pseudo-$F_{1, 243} = 0.54$, $P > 0.6$), therefore plots were analyzed together for these data.

Four years following *L. cuneata* control, native species relative cover was unrelated to the historical cover of *L. cuneata* (Figure 4; Table 4). Likewise, total stem density of sown natives did not respond ($z_{249} = 0.098$, $P = 0.92$) to the historical cover of *L. cuneata* (Figure 5). Multivariate analysis of community data revealed similar results. Multivariate RDA indicated that species cover was related to the historical cover of *L. cuneata* regardless of historical treatment groups (Table 5). Like the univariate comparisons however, the historical cover of *L.*

cuneata explained little variation in any of the RDA analyses ($r^2 \leq 0.024$). Additionally, RDA analysis did not indicate a significant response of sown native species to the historical cover of *L. cuneata* during any year of the recovery period (Table 6).

CHAPTER 3

DISCUSSION

4.1 General Discussion

The purpose of this experiment was to determine whether *L. cuneata* creates a persistent soil legacy that negatively affects the recovery of a native grassland community from invasion. In short, we found little evidence of a soil legacy created by *L. cuneata*. All univariate comparisons of relative native species cover in response to historical *L. cuneata* cover were non-significant (Table 4). Likewise, there was no relationship between total stem density of sown native species and the historical cover of *L. cuneata* ($P = 0.92$).

Multivariate analysis was also conducted to evaluate the community response that might not be revealed by univariate analysis of relative native cover or total colonization of sown native species. Redundancy analysis (RDA) of species cover revealed a significant effect of historical *L. cuneata* cover on the plant community in all historical treatment groups. Consistent with univariate results however, historical *L. cuneata* cover explained very little variation in all comparisons ($r^2 \leq 0.024$, Table 5) suggesting that its impact is detectable, but exceedingly low. In addition, RDA analysis of sown native stem density in each year of the recovery period did not indicate a significant relationship between the establishment of these species and the historical cover of *L. cuneata* in any of these comparisons ($P > 0.09$; Table 6). Consequently, both univariate and multivariate results indicate that that the historical cover of *L. cuneata* has negligible effects on the colonization of native species and overall species recovery in the community after *L. cuneata* had been effectively controlled.

These results were somewhat unexpected, given previous reports that *L. cuneata* alters soil conditions. Root exudates and leaf residues of *L. cuneata* have been shown to reduce the germination and growth of several prairie grass species, including *S. nutans* (Kalburtji et al. 2001; Dudley and Fick 2003), suggesting *L. cuneata* could affect neighbors via soil allelopathy. The litter of *L. cuneata*, containing high concentrations of phenolic tannins, has also been demonstrated to alter release rates of both macro and micronutrients in invaded areas (Kalburtji et al. 1999). This in turn may affect microbial communities (Callaway et al. 2004), and is consistent with patterns reported by Yannarell et al. (2011). However, under field conditions these effects do not seem to be important. Nevertheless, changes in the microbial community may play a role in facilitating the invasion of *L. cuneata* (e.g. Hu et al. 2014), as seen with other invasive species (Wolfe and Klironomos 2005; Reinhart and Callaway 2006; Pringle et al. 2009; Klironomos 2002). Experimental evidence suggests that soils with a history of *L. cuneata* enhance subsequent *L. cuneata* growth (Coykendall and Houseman 2014). If true, post-invasion communities may still facilitate *L. cuneata* growth after effective control, and be more susceptible to re-invasion than non-invaded communities. This is an intriguing concept and an important consideration for management of restored communities, but requires further study to examine this type of post-removal legacy.

Results of this study illustrate the importance of longer-term field experiments for evaluating invader-driven legacy effects versus relying on greenhouse experiments. Review of current literature by Kulmatiski et al. (2008) found that greenhouse studies of PSFs consistently report larger, more negative effect sizes compared to their field-based counterparts, which were significantly more neutral. This could be due to the fact that seedling plants are typically competing with one another in greenhouse studies, but juvenile plants may be more sensitive to

PSFs and legacy effects than their adult counterparts (Hersh et al. 2012). In addition, fluctuations in abiotic conditions influential to plant success (e.g. water and sunlight availability) are often ignored or are difficult to mimic in the greenhouse. Greenhouse studies are valuable in their ability to isolate potentially important effects, but these effects may be lost, or non-significant, in the context of the entire plant community response (Schittko et al. 2016).

In addition to differences between field and greenhouse experiments, the time-span of studies may affect the strength and detection of soil legacies. Evidence from plant-soil feedback experiments (Kulmatiski et al. 2008; Kardol et al. 2013) suggests that short-term studies report stronger and more negative effects than those that last two years or longer. Short-term responses to soil conditioning via PSF interactions therefore may not represent the more realistic, long-term plant responses to changes in soil conditions. The likelihood of environmental fluctuations or occurrence of disturbance increases with the duration of the study and can affect PSF interactions (Ehrenfeld et al. 2005; Kardol et al. 2013). Whether these considerations apply to soil legacies is unknown, as long-term field legacy studies are very rare. Results of this study, taken with previous PSF studies, certainly suggest that more controlled, long-term experiments are needed.

A final important consideration is whether results of this study may be dependent upon site context. Other field-based studies report changes in nitrogen cycling and deposition, soil pH, and soil microbial communities that can affect post-invader communities (Mummey and Rillig 2006; Liao et al. 2008; Conser and Connor 2009), but these effects are variable and site-specific (e.g. Bezemer et al. 2006). For example, Haubensak et al. (2004) found that two invasive shrubs (*Genista monspessulana* and *Cystis scoparius*) alter soil nitrogen, but the impact of these alterations ranged from large to almost negligible across coastal grassland sites. The importance of site-specific legacy effects, and restoration of these effects, have been noted elsewhere (e.g.

Ehrenfeld 2010; Hamman and Hawkes 2013). Likewise, our lack of evidence for a *L. cuneata* soil legacy effect should be interpreted carefully in the context of other ecosystems.

4.2 Implications for Practice

In the context of restoration and land management, this study provides evidence that native communities are likely to recover quickly following early detection and effective control of *L. cuneata*. The facilitation of *L. cuneata* growth in soils with previous history of invasion could indicate sensitivity of restored communities to re-invasion of *L. cuneata*, however. Communities managed for *L. cuneata* invasion should therefore be monitored carefully following effective control to detect and suppress possible re-establishment events. This study also does not address the possibility of *L. cuneata* populations creating soil legacy effects if established longer than three years. Effects of *L. cuneata* establishment may be stronger in heavily invaded communities, and should be a priority for monitoring post-removal.

An unintended result of this study also worth noting was the detection of the historical disturbance and fertilization treatments applied by Houseman et al. (2014). These treatments had not been applied for six years (disturbance) and five years (fertilization) at the time that the data were collected, but still had a highly significant effect on species cover data ($P < 0.001$). This is surprising given the time since application, but lends further evidence to the importance of considering the historical land management in field-based experiments (e.g. Jacquemyn et al. 2011) and on the outcome of restoration efforts (Grman and Suding 2010; Hamman and Hawkes 2013).

TABLES

Table 1. Common name, scientific name, and family of the thirteen native forb species sown into all plots following *L. cuneata* removal.

Common Name	Scientific Name	Family
Lead Plant	*Amorpha canescens*	Fabaceae
New England Aster	*Symphyotrichum novae-angliae*	Asteraceae
Prairie Coreopsis	*Coreopsis palmata*	Asteraceae
Purple Prairie Clover	*Dalea purpurea*	Fabaceae
Illinois Bundle-flower	*Desmanthus illinoensis*	Fabaceae
Purple Coneflower	*Echinacea purpurea*	Asteraceae
Maximilian Sunflower	*Helianthus maximiliani*	Asteraceae
False Sunflower	*Heliopsis helianthoides*	Asteraceae
Round-head Bush Clover	*Lespedeza capitata*	Fabaceae
Wild Bergamont	*Monarda fistulosa*	Lamiaceae
Smooth Beardtongue	*Penstemon digitalis*	Scrophulariaceae
Grayhead Prairie Coneflower	*Ratibida pinnata*	Asteraceae
Rigid Goldenrod	*Solidago rigida*	Asteraceae

Table 2. PERMANOVA results for species cover and stem density of sown natives in response to historical disturbance and fertilization treatments four years following *L. cuneata* removal, based upon a log-transformed Bray-Curtis similarity matrix and 10,000 permutations.

		Species Cover			Stem Density		
Source	Df	MS	Pseudo-F	P-value	MS	Pseudo-F	P-value
Block	2	11244	9.30	< 0.001	17589	21.52	< 0.001
Disturbance	2	3435	2.84	< 0.001	502	0.62	0.72
Fertilization	1	4334	3.59	< 0.001	443	0.54	0.66
Disturb x Fert	2	1199	0.99	0.47	817	0.80	0.57

Table 3. Results of pair-wise PERMANOVA tests for species cover (log transformed) between groups that received no experimental disturbance (No Disturbance), simulated haying (Hay), and simulated grazing (Graze) based on 10,000 permutations. *P*-values adjusted using a Holm-Bonferroni correction.

Comparison	Df	t-statistic	P-value
No Disturbance, Hay	143	1.90	< 0.001
No Disturbance, Graze	197	0.93	< 0.001
Hay, Graze	144	1.95	0.54

Table 4. Linear regression results of native species relative cover (arcsine transformed) in response to the historical cover of *L. cuneata* within historical treatment groups. *P*-values adjusted using a Holm-Bonferroni correction.

Group	Df	Slope	r^2	P-value
All Plots	249	1.8e-07	0.0063	0.76
Disturbed (Graze and Hay)	148	3.6e-07	0.0115	0.76
No Disturbance	99	6.3e-09	0.0002	1.00
Fertilized	133	8.5e-07	0.0300	0.22
No Fertilizer	114	3.1e-08	0.0010	1.00

Table 5. Results of distance-based redundancy analysis (RDA) of species cover in response to historical cover of *L. cuneata* within historical treatment groups. Bray-Curtis similarities were regressed on the historical cover of *L. cuneata*, both of which were log transformed (10,000 permutations). *P*-values adjusted using a Holm-Bonferroni correction.

Group	Residual Df	r^2	Pseudo-F	P-value
All Plots	249	0.016	4.03	0.005
Disturbed (Graze and Hay)	148	0.024	3.61	0.005
No Disturbance	99	0.019	1.91	0.051
Fertilized	133	0.023	3.08	0.009
No Fertilizer	114	0.019	2.25	0.036

Table 6. Results of distance-based redundancy analysis (RDA) for stem density of sown native species in response to the historical cover of *L. cuneata* one (2011), two (2012), three (2013), and four years (2014) following *L. cuneata* removal. Historical cover of *L. cuneata* and Bray-Curtis similarities were log transformed for all comparisons; results are based upon 10,000 permutations.

Year	Residual Df	r^2	Pseudo-F	P-value
2011	249	0.0090	2.26	0.092
2012	249	0.0026	0.64	0.58
2013	249	0.0038	0.96	0.44
2014	249	0.0020	0.49	0.68

FIGURES

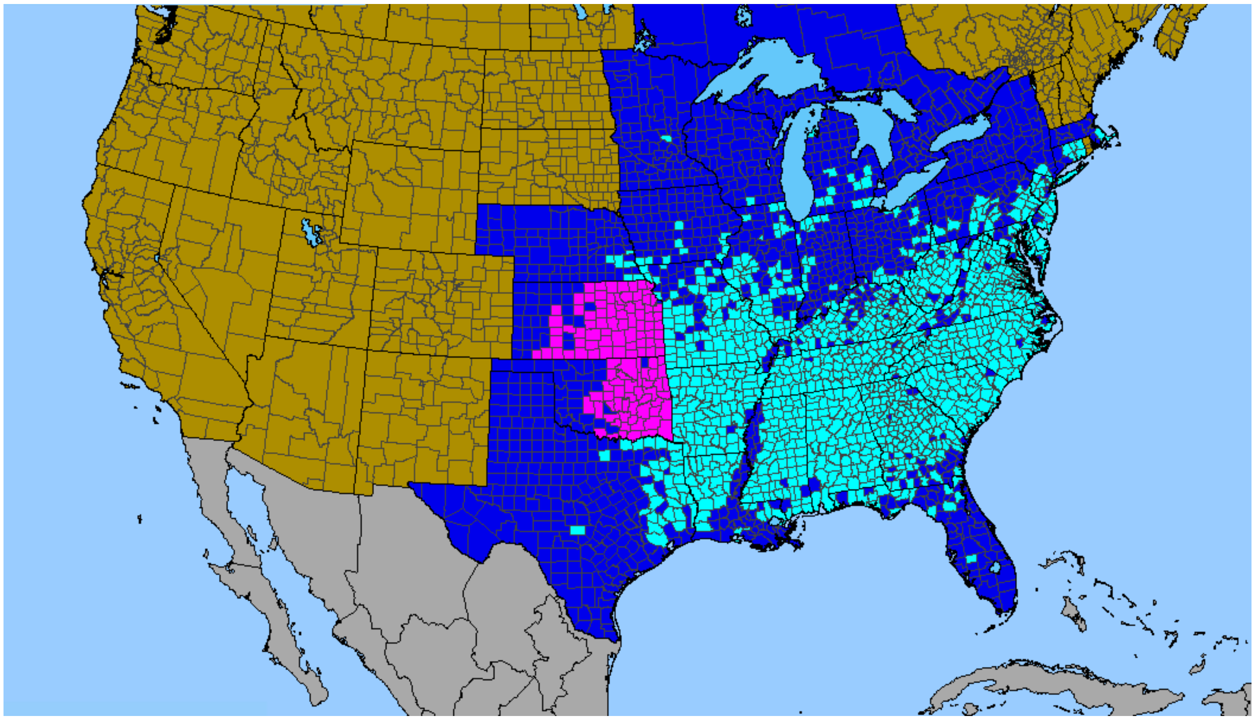

Figure 1. Distribution of Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don.] in the contiguous United States. Dark blue areas indicate a record of *L. cuneata* within the state, light blue areas indicate a county record, and purple areas indicate a county record in addition to designation of the species as a noxious weed. All other areas outside of dark blue regions have no record of *L. cuneata* presence. Map generated via the Biota of North America Program (BONAP).

Figure 2. Overview of the study site located at the University of Kansas Field Station (KUFS) in Lawrence, Kansas, USA (39.054728° N, -95.194525° W). Image depicts study site in August 2010, one year following *L. cuneata* removal.

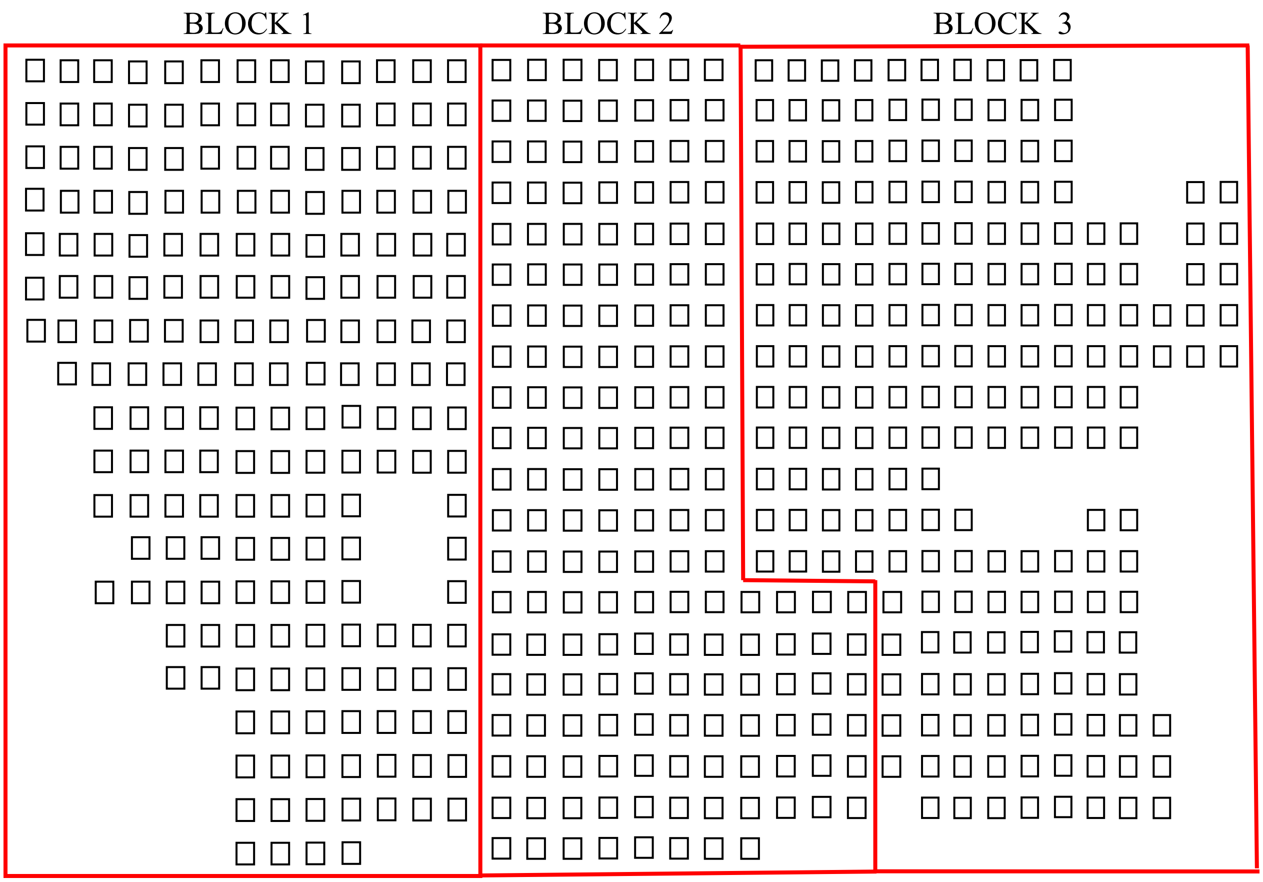

Figure 3. Spatial layout of plots as established by Houseman et al. (2014). Each square represents one 0.75 x 0.75 m^2 plot, separated by 0.5 m walkways and distributed among three blocks.

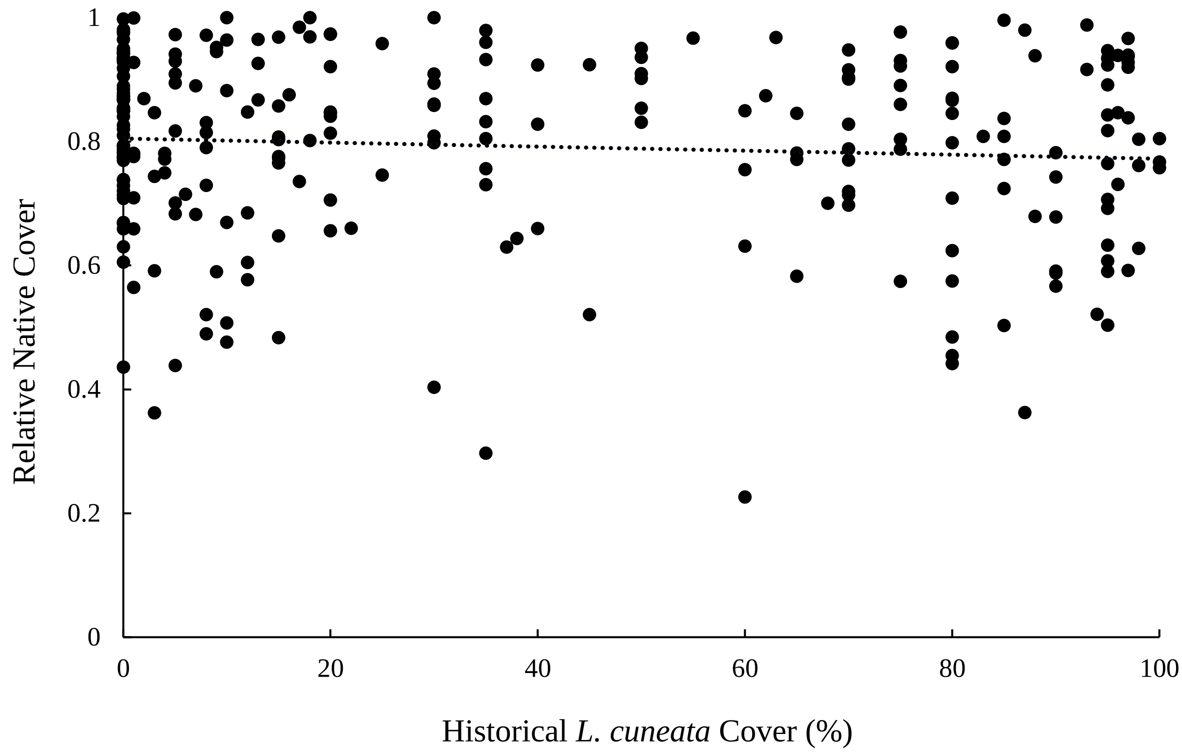

Figure 4. Relative native species cover in response to the historical cover of *L. cuneata* for all plots. Similar to comparisons within historical treatment groups, linear regression of arcsine transformed relative native species cover was non-significant (*P* = 0.76, following a Holm-Bonferroni correction).

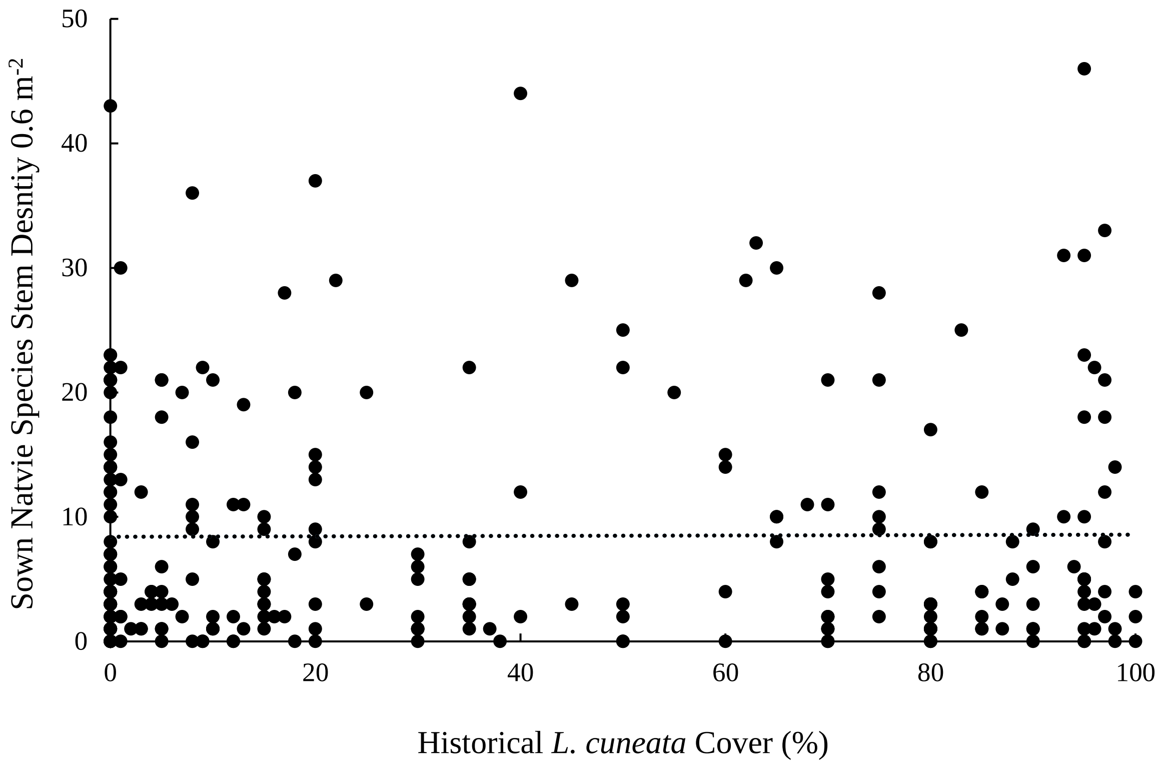

Figure 5. Total stem density of sown native species in response to the historical cover of *L. cuneata*. A negative binomial regression model of the data was non-significant ($z_{249} = 0.098$, $P = 0.92$).

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